SOCIETY FOR ECOLOGICAL RESTORATION

Foundations of Restoration Ecology

SECOND EDITION

Edited by
MARGARET A. PALMER, JOY B. ZEDLER,
AND DONALD A. FALK

FOUNDATIONS OF RESTORATION ECOLOGY

SOCIETY FOR ECOLOGICAL RESTORATION

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Foundations of Restoration Ecology

Second Edition

Edited by
Margaret A. Palmer, Joy B. Zedler, and Donald A. Falk

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FOREWORD

The field of restoration ecology has grown and changed dramatically in the decade since the first edition of this book. The amount of academic literature on restoration ecology and the number of on-the-ground ecological restoration projects has increased exponentially. Not long ago, academic institutions might have one course on restoration ecology; today there are specific degree programs in the field. The spatial scale and complexity of ecological restoration projects have multiplied; there are now international targets to restore hundreds of millions of hectares of forests, and individual restoration projects commonly span hundreds to thousands of hectares. Of course, the challenges that restoration ecologists face are even greater, as human pressures on natural resources continue to grow. Restorationists must address complicated questions, such as defining restoration targets and selecting what constitutes a local gene pool and ecological community, determining when reference systems have been altered by a changing climate, habitat fragmentation, invasive species, or myriad other anthropogenic impacts.

What is needed to overcome these challenges and restore ecosystems, however, has not changed fundamentally. Restoration ecologists have long known that the planning and progress of restoration projects must rest on a solid understanding of ecological theory and natural history, combined with a recognition of the socio-economic and political landscape within which the project is situated. This book serves to lay those ecological foundations, while never losing sight of the goal of applying the information to improve the efficacy of ecological restoration.

Restoration scientists and practitioners have long known that crossing the theory-practice divide offers huge potential to further our understanding of how ecosystems work and is essential to restore resilient ecosystems. Bradshaw's call in 1987 to use restoration as a test to improve our knowledge of population, community, and ecosystem processes has been cited hundreds of times, and there are many examples where this opportunity has been realized. Yet the gap between theory and practice in restoration remains large. This book strives to close this gap. In each chapter, the authors provide clear descriptions of ecological theories and specific examples of how these ideas have proven to be useful (or not) in on-the-ground restoration projects. They draw on expertise and case studies from a range of ecosystem types and geographic regions to illustrate key points. Each chapter also offers guideposts for using the process of restoration ecology to inform basic research. Hence, this thought-provoking book is an important resource for students of restoration ecology at all stages of their career whose work focuses on research, education, designing and managing restoration projects, and/or policy.

This second edition is not an incremental step forward from the first edition to simply update the literature. It represents a serious reflection by the editors and individual authors about how the field of restoration ecology has changed and advanced in the past decade. Hence, the overall organization and content of the book and individual chapters is substantially different to provide a current framing of the field, including new topics and elements in every chapter. Of course, the field of restoration ecology will continue to change rapidly in the coming decade. This book provides strong foundations for the field to progress and address the enormous challenges that lie ahead.

Karen D. Holl
Department of Environmental Studies
University of California, Santa Cruz

PREFACE

For millennia, indigenous peoples have tended their lands for hunting, growing crops, and gathering wild plants for food, medicines, and dyes (Stevens 1997). Embedded in some of these cultural practices were (and are) the knowledge and skills to heal damaged lands and waters. Farmers and pastoralists continued these practices and made the major transition to agriculture, where maintaining the productivity of soil became a survival skill. One of the earliest well-documented restoration efforts began in Brazil in 1862 under the management of Manoel Archer. A major in the Brazilian National Guard, he was assigned the task of restoring the Tijuca Forest, which had been degraded when land was converted to sugar and coffee plantations. Over 100,000 seedlings were planted, and today this rainforest is an urban forest legacy.

In the United States, the practice of restoring degraded lands began to capture the attention of scientists in the 1930s, when Aldo Leopold planted pines and restored prairie vegetation to reduce soil erosion on his own land and dedicated the University of Wisconsin-Madison Arboretum for restoration of native ecosystems for teaching and research. Hundreds of restoration efforts followed suit in almost every kind of ecosystem throughout the world. As the practice grew, so too did the science, and in 1981 Dr. William Jordan at the University of Wisconsin founded the first journal in the field, *Restoration and Management Notes* (now *Ecological Restoration*). In 1987, the Society of Ecological Restoration formed, and in 1993 SER launched the first refereed journal in the field, *Restoration Ecology*. Research publications have since risen exponentially, appearing in a broad array of scientific journals.

Today, ecological restoration offers the potential to recover lands and waters from environmental damages that societies inflict on Earth's natural resources by misuse or mismanagement. Given that daunting challenge, restoration science aims to improve the practice, drawing on theory that is firmly rooted in ecology and allied fields. The tools of restoration ecology—the ability to heal damaged landscapes—may well be critical survival skills for the planet in what promises to be a very challenging century in front of us.

Our goal with the first edition of this book in 2006 was to provide an advanced text that clearly delineated relevant theory, highlighted links between theory and practice, and identified gaps in our knowledge. This new edition differs in important ways that we hope will enhance its use as a learning tool and reflect growth in the field of restoration ecology. Each chapter begins with an "In Brief" box highlighting the most important theories and concepts; most chapters include one or more highlighted case studies that serve as clear examples of theory application. The first four chapters comprise a section of the book that serves as an ecological primer on broad concepts foundational to the field, regardless of the specific topic. For example, these core concepts are equally relevant to restoration of entire ecosystems and recovery of an endangered species population in aquatic, marine, or terrestrial environments. The concepts introduced in this section are treated at more advanced levels in chapters throughout the book.

The second section of the book provides a series of chapters covering theory drawn primarily from population and community ecology. The chapters synthesize the well-established foundations pivotal to those topics most relevant to restoration—ecological genetics, ecophysiological constraints, metapopulations, invasion ecology, assembly theory, environmental heterogeneity. The essential classic literature is cited, but each chapter also brings the reader up to date on the latest research in the field and provides examples of how the theory is currently being applied in a restoration context.

The third section of the book is devoted to ecosystem-level processes and theories that are critical to restoration, including nutrient, carbon, and hydrological dynamics that can act as both constraints and goals for restoration. The inclusion of this new section reflects growing recognition that restoration requires knowledge from multiple disciplines—ecologists must work side by side with hydrologists, engineers, landscape architects and others using integrative systems frameworks.

The closing chapter of the book identifies themes among the topical chapters that reflect growth in the field or the advancement of theory. Which frontiers of knowledge will attract young scientists to merge further fundamental theory and its applications? What theoretical foundations will help the land managers of tomorrow sustain a living planet?

Margaret A. Palmer, Donald A. Falk, and Joy B. Zedler

BOOK GUIDE

PART I. Introduction to Restoration and Foundational Concepts

Restoration ecology as a science is distinct from the practice of ecological restoration but defines and guides it. The fundamental principles of systems dynamics, theories of biodiversity, and the concepts and methods of landscape ecology permeate ecological science at all levels and provide a foundational introduction to restoration ecology.

Chapter 1. Ecological Theory and Restoration Ecology

Margaret A. Palmer, Joy B. Zedler, Donald A. Falk

Restoration ecology draws on all branches of ecology and spans genes to entire landscapes. Ecological restoration seeks to recover biological assemblages and the ecological processes and structures that may allow self-sustainability and, thus, relies heavily on ecological theory. Information on the historical and contemporary range of variability of reference systems interpreted through a body of ecological theory and knowledge determines what level of recovery is possible given the current environmental context. Ecological restoration provides raw material for testing and refining theory.

Chapter 2. Ecological Dynamics and Ecological Restoration

Katharine Suding, Erica Spotswood, Dylan Chapple,
Erin Beller, and Katherine Gross

Natural systems are inherently variable and respond to disturbances in complex ways making the prediction of future system states difficult. Legacy effects, differences in initial conditions, transient dynamics, and nonlinear interactions all contribute to uncertainty in the outcome of restoration efforts. Given increasing uncertainty associated with anthropogenic change, a continuum of ecological dynamics must be considered rather than a single dynamic state or a predictable successional process. Bayesian methods and other tools are available for planning in the face of this uncertainty.

Chapter 3. Biodiversity as a Goal and Driver of Restoration

Shahid Naeem

Biodiversity is multidimensional and extends beyond species to diversity of functional traits, phylogenetic lineages, genetic composition, populations, and networks of interactions. Most species are rare and thus vulnerable to genetic impoverishment making them harder to restore than dominants. A shift to a trait-based approach, including a response-effects trait framework, has been proposed given increased interest in ecosystem function and the difficulties that can come with studying populations. Both diversity and identity effects may explain changes in function.

Chapter 4. Landscape Ecology and Restoration Processes

Jean Paul Metzger and Pedro H. S. Brancalion

The spatial configuration of patterns and processes at local to landscape scales is a major determinant of the structure and function of ecological systems. Theories from island biogeography, metapopulation and metacommunity dynamics, and probabilistic models of species accumulation contribute to understanding the distribution, abundance, and resilience of biological assemblages. Indices for quantifying landscape structure combined with theory and empirical work on spatial structure and landscape context can help guide restoration efforts.

PART II. Ecological Theory and the Restoration of Populations and Communities

Diverse theories, concepts, and empirical findings underpin the recovery of ecological assemblages. Organismal, population, and community dynamics are largely governed by physiology, genetic and habitat diversity, spatial context, and biotic interactions.

Chapter 5. Population and Ecological Genetics in Restoration Ecology

Christopher M. Richards, Donald A. Falk, and Arlee M. Montalvo

Genetic variation is the "invisible dimension" of the science and practice of restoration. That is, the consequences of genetic variation must be considered when selecting propagules to introduce to restoration sites. Because the starting pool of genetic variation has long-term legacies, a major question is whether locally adapted or a mixture of populations should be tapped for propagules. Each has risks, that is, inbreeding or outbreeding depression, respectively. Restoration sites offer virtually untapped opportunities to test theories of population genetics.

Chapter 6. Ecophysiological Considerations for Restoration

Sarah Kimball, Jennifer L. Funk, Darren R. Sandquist, and James R. Ehleringer

The process of ecological restoration may expose individuals and populations of plants and animals to unusual environmental conditions, including extremes of temperature, water, light, and nutrient concentrations. Thus, restoration success may depend in large measure on the ability of organisms to tolerate and adapt to anomalous conditions, especially in the early stages of a restoration trial. Field and laboratory experiments with ecophysiological responses in restoration settings can be keys to identifying potential challenges to establishing self-sustaining populations.

Chapter 7. Implications of Population and Metapopulation Theory for Restoration Science and Practice

Joyce Maschinski and Pedro F. Quintana-Ascencio

Maintaining self-sustaining populations is a canonical goal of restoration ecology. Population size, age structure, and other demographic properties strongly influence the persistence of populations and their ability to adapt to changing environments. In addition, for most species, populations interact to some degree as part of larger interconnected metapopulations, in which genes and individuals are exchanged over space and time. Nesting the restoration of individual populations within the larger metapopulation and metacommunity context is essential to enhancing adaptive capacity.

Chapter 8. Invasive Species and Restoration Challenges

Carla M. D'Antonio, Elizabeth August-Schmidt, and Barbara Fernandez-Going

While there are some benefits to using nonnative species in ecological restoration, problems are more often the case, since restoration causes disturbances that facilitate invasions. Ecological theory on the impacts of disturbance and postdisturbance community assembly helps shape restoration planning. Resistance and resilience respond to ecosystem structure and processes that favor desirable species. Relevant theories are alternative stable states and assembly theory including priority effects, competition, niche preemption, and related diversity/invasibility hypotheses.

Chapter 9. Assembly Theory for Restoring Ecosystem Structure and Functioning: Timing is Everything?

Vicky M. Temperton, Annett Baasch, Philipp von Gillhaussen, and Anita Kirmer

Theory on diversity suggests that systems with more species have higher levels of function than those with fewer and more similar species. Species that facilitate others are candidates for nurse plants in restoration sites. Filter theory and priority effects currently are the subject of long-term field experiments. By manipulating abiotic and biotic filters and by understanding priority effects (the importance of early introductions), restorationists can improve chances of establishing desired species in restoration sites.

Chapter 10. Heterogeneity Theory and Ecological Restoration

Daniel J. Larkin, Gregory L. Bruland, and Joy B. Zedler

Natural ecosystems are famously heterogeneous; can restored ecosystems attain this same property? Environmental variation such as microtopography, moisture and nutrient availability, and physical structure creates heterogeneity that supports diverse communities. As a consequence, heterogeneity mediates key processes of species interactions, community assembly and ecosystem function. For animal populations, heterogeneous landscapes are necessary to provide nesting, feeding, and hiding places. Environmental heterogeneity also promotes species coexistence and helps prevent homogenization of ecological communities.

Chapter 11. Food Web Theory and Ecological Restoration

M. Jake Vander Zanden, Julian D. Olden,
Claudio Gratton, and Tyler D. Tunney

Food web theory provides dynamic, interaction-driven insights for understanding why systems stabilize or sometimes fail. Complex interactions and cascading effects such as apparent competition, predator-mediated competition, and top-down/bottom-up regulation, are further complicated by cross-system subsidies or sinks. Indeed, the context dependency of species interactions that result from spatially linked food webs calls for integration of theory from multiple branches of ecology including, for example, ecosystems science, landscape ecology, trophic dynamics, and dispersal ecology.

PART III. Ecosystem Processes and Restoration Ecology

Biogeochemical and hydrological processes influence the abundance, composition, and distribution of species on earth. The flux and transformation of energy, nitrogen, phosphorus, carbon, and water control many ecological processes and often determine ecosystem function. As such, these biophysical processes and cycles are central to restoration ecology.

Chapter 12. Nutrient Dynamics as Determinants and Outcomes of Restoration

Sara G. Baer

Because nutrient dynamics influence–and change with–restoration, C:N:P ratios can provide insight into nutrient limitation in organisms and other ecosystem components. Initial site conditions set the stage for either nutrient limitation or excesses, while the fluctuating resource hypothesis helps predict a community's invasibility, and plant N-use theory and plant input-output theory predict how established plants influence nutrient cycling. Knowing how to manipulate nutrient levels (N, P, and C) and their dynamics helps restorationists achieve restoration targets.

Chapter 13. Recovery of Ecosystem Processes: Carbon and Energy Flows in Restored Wetlands, Grasslands, and Forests

Erika Marín-Spiotta and Rebecca Ostertag

Ecological communities are not merely collections of organisms: they are also critical pools of carbon and energy distributed throughout the biosphere. Forests, wetlands, and grasslands capture, store, and release atmospheric CO_2 at rates that influence both local and global climate. Ecosystem carbon dynamics are measured by the relative balance of production (carbon fixation) and respiration, scaling up to net ecosystem carbon balance. Because restoration tends to deal with disrupted or disturbed communities, carbon sequestration can become an explicit objective of restoration practice.

Chapter 14. Watershed Processes as Drivers for Aquatic Ecosystem Restoration

David Moreno-Mateos and Margaret A. Palmer

Fluxes and storage of water influence and connect virtually all ecosystems within watersheds. Thus, the restoration of individual sites depends in part on the ability to restore the magnitude, timing, and frequency of water fluxes. At the site scale, the capacity of soil to infiltrate and conduct water must be understood in order to restore desired hydrological conditions. Strong links between hydrologic and ecological theory have led to the emergence of ecohydrology as a basis for many restoration efforts, with larger-scale/watershed perspectives needed to achieve desired supplies and movements of water.

PART IV. The Spatial and Temporal Dimensions of Restoration

Ecologists have long recognized the importance of considering evolutionary history and potential as they seek to understand what they observe and what they predict. This understanding is influenced by spatial scale, and we are now seeing the emergence of more sophisticated methods for incorporating cross-scale processes into our knowledge. Ecologists are poised to play important roles in preparing society to cope with future climates and other forms of global change.

Chapter 15. Evolutionary Restoration Ecology

Craig A. Stockwell, Michael T. Kinnison,
Andrew P. Hendry, and Jill A. Hamilton

Evolution is generally thought of as a slow, ancient process, but life is evolving today as it has for millions of years. Contemporary evolution is particularly important under conditions of strong selection, including highly altered and degraded habitats characteristic of restoration practice. Species carry the genetic legacy of past adaptation, which in turn influences species performance under novel ecological and climatic conditions. Restoration experiments offer rich opportunities for adaptation research as well as a means of maintaining the legacy of evolution.

Chapter 16. Macroecology and the Theory of Island Biogeography: Abundant Utility for Applications in Restoration Ecology

Andrew J. Dennhardt, Margaret E. K. Evans, Andrea Dechner, Lindsay E. F. Hunt, and Brian A. Maurer

Even the largest restoration projects exist in a regional and global context, including species ranges, large-scale ecosystem fluxes, and abiotic templates. As a result, although no restoration project is an island, we can learn a great deal by studying cross-scale ecosystem interactions from local to global relationships. Long-term, large-scale restoration outcomes can be informed by species distributions, species-area relationships, and metapopulation dynamics. The tools of macroecology can guide restoration planning and practice beyond the local site.

Chapter 17. The Influence of Climate Variability and Change on the Science and Practice of Restoration Ecology

Donald A. Falk and Constance I. Millar

All species and ecosystems have been exposed to climatic variation in space and time throughout their evolutionary and ecological history. However, dramatic contemporary changes in Earth's climate system are forcing reconsideration of basic restoration principles, such as the use of past and current species ranges as a template for the future. As the climate envelope of some species and communities slips away, restoration ecology faces novel challenges and opportunities to help the natural world adapt to a new global climate regime.

PART V. Synthesis and Challenges

Chapter 18. Persistent and Emerging Themes in the Linkage of Theory to Restoration Practice

Margaret A. Palmer

While restoration as a practice is growing steadily, so too is the ecological science that supports it. Some ecological theories and concepts are so fundamental to understanding how to restore ecological systems that they represent *persistent* themes in ecology and its application. Other scientific theories or concepts reflected throughout this edition are relatively new. These *emergent* themes have great potential to inform restoration and also potential to be advanced or revised through adaptive restoration practices. This chapter provides a guide to these two groups of themes, examples of their applications, and a brief overview of the factors that stimulated the emergence of the newer themes.

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Books such as this one become a reality only with the support and involvement of many people. As the second edition took form, we were consistently astounded at the remarkable insights and contributions of the authors of the chapters in this book. Collectively they are a remarkable group of creative scientists, and this book truly stands on their shoulders.

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MAP, DAF, JBZ

PART I

Introduction to Restoration and Foundational Concepts

Ecological Theory and Restoration Ecology

Margaret A. Palmer, Joy B. Zedler, and Donald A. Falk

Rather than explaining ecosystem structure and function under a single "unified theory," ecologists deploy a strong and diverse body of theory to address a wide range of ecological problems (Weiner 1995; Pickett et al. 2007; Hastings and Gross 2012). Theories come in many forms—predictive statements, explanatory concepts, and mathematical and computational models (Scheiner and Willig 2011); yet all share a focus on causal explanation. In restoration, theories help to explain historical events, understand current observations, and predict future states. This last application is particularly important because ecosystems, and the task of restoring them, take place in an increasingly altered world (Steffen et al. 2015). Grounded in theory and empiricism from the ecological sciences, *restoration ecology* provides the science essential to the practice of *ecological restoration*, which in turn can be used to test those theories in real world contexts (Palmer and Ruhl 2015; Suding et al. 2015).

What Is Restoration Ecology?

Population, community, and ecosystem ecology are well-established branches of ecological science that focus on specific levels of organization, while restoration ecology is much younger and more comprehensive. As "the study of the relationships among organisms and their environment in a restoration context," restoration ecology draws on all branches of ecological science and spans genes to entire landscapes (Falk et al. 2006). The homology with the general definition of ecology is not coincidental; restoration ecology can be thought of as a special domain of ecological research, defined by context. Typically, this context includes a natural system of some kind that has been altered in composition, structure, or

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function. The central aim of restoration ecology is thus to describe and quantify those departures from a characteristic ecosystem state (including the full range of spatial and temporal variation), understand what drives and regulates them, and then project how the system can be moved back toward a less disturbed state (Hobbs and Suding 2009). Restoration ecology also integrates a number of related disciplines, including hydrology, geomorphology, oceanography, and others, particularly various social science disciplines.

Ecological theories can inform the design, implementation, and assessment of restoration projects that range in area from small sites to watersheds. Conceptual theories tend to be the broadest, such as the theory of evolution by natural selection, or models of macroecology (chaps. 3, 15, and 16). Other theories may be specific to a particular type of ecosystem or group of organisms, such as biogeochemical cycling, community assembly, or disturbance ecology (Young et al. 2001; chaps. 2, 9, 12, 13). Theories that employ mathematical or statistical models may take the form of simple equations derived from first principles or complex sets of equations drawn from extensive empirical observations. For example, a recent set of theoretical models links a wide range of organism and community traits on the basis of energetics (Schramski et al. 2015). Predictions from models can be very general: for example, that restoring large or well-connected parcels of land will enhance restoration of biodiversity (Tambosi et al. 2014; chap. 4). They can also be specific to a particular time period or ecological system; for example, restoring seagrass in Middle Tampa Bay (FL) to levels observed in the 1950s requires reducing chlorophyll below some threshold (Sherwood et al. 2016), and restoring grasslands benefits from relating plant functional diversity to nutrient cycling and soil carbon (Bach et al. 2012).

Theories provide us with templates and logic paths for predictions. Theories are used to guide the framing of research questions, the design of experiments, collection of data, and ways to organize information to understand the natural world. Theories can be used to explore the impacts of assumptions we might make about ecosystems, and deviation from theories can help inform future research. For all of these reasons theory is fundamental, not only to restoration ecology but to the practice and advancement of ecological restoration.

What is Ecological Restoration?

The Society for Ecological Restoration (SER 2004) defines *ecological restoration* as, “the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed.” Restorationists attempt to move the composition, structure, and dynamics of a damaged system to an ecological state that is within some acceptable limit relative to a less altered and (probably) more sustainable system

(Falk 1990; Allen et al. 2002). Informed by the work of Clewell and Aronson (2013), we simplify the SER (2004) framework and attributes of restored systems to define science-based ecological restoration as in Palmer and Ruhl (2015) (table 1-1).

In this simplified framework, *features* refer to the structural components of an ecosystem. For example, floodplains are a key component of river ecosystems; their connection to the water and land is an aspect of pattern. Similarly, the structure of a forest includes tree size classes and canopy properties; one aspect of its

Table 1-1.

Three essential attributes of intact ecosystems that ecological restoration projects aim to recover. Projects are informed by, and also contribute to, a diverse range of ecological theory.

Attributes of Restored Ecosystems and Ecological Theory	Explanation	Relevant Ecological Concepts and Theory
Biological assemblages are characteristic of a reference system of similar type.	*Assemblage* refers to the identity, relative abundance, and functional attributes of co-occurring taxa. *References* are relatively undisturbed systems where assemblages are within the historical range of variability.	Trait-based theories Functional ecology Diversity indices Species range limits and controls on abundance Community assembly and succession Cross-scale spatial heterogeneity
Features and processes are needed to sustain the characteristic biological assemblages and support ecological functions are present.	*Features* include local habitat and system-level structure and spatial pattern in the watershed or landscape that are within the range of variability of reference sites. *Processes* include dynamic functions characteristic of the system that are necessary to the maintenance of the assemblages and features.	Relationship of biodiversity to ecosystem functions (*BEF*) Biogeochemical cycles Hydrologic dynamics Ecosystem engineers Disturbance regimes Dispersal, migration theory
Restored system has the potential to be self-sustaining.	Self-sustaining systems require little or no human intervention or maintenance over the long term, in part due to suitable landscape and environmental contexts and exchanges of organisms, matter and energy.	Range of variability Metapopulation dynamics Ecological resilience Stability theory (alternative states, tipping points) Nonlinear dynamics and feedbacks Landscape and spatial ecology

pattern is the spatial distribution of trees on the landscape. *Processes* (also called *functions*) include a wide range of dynamic attributes, such as primary production, stream discharge, fire regimes, dispersal and migration, population dynamics, and biogeochemical cycling. Processes vary over time and space, and ideally lead to recovery of a self-sustaining dynamic system that requires less human intervention than during the process of restoration (Beechie et al. 2010).

The framework for defining ecological restoration specifies that it "aims to" recover the properties of an intact system such as species assemblages, food webs, and functional attributes similar to reference systems (chaps. 7, 8, 9, and 11). However, restoration can take decades, and even when a design is science based, unexpected alternative states or incomplete recovery may result (chap. 2). An unexpected outcome is different from knowingly targeting an end state other than full ecosystem recovery and fidelity to an appropriate reference system (Clewell 2000; Egan and Howell 2005). Attempts to reverse environmental degradation that are not ecological restoration include the use of hardscapes or nonnative species to reduce excessive soil erosion and run-off, and other types of engineered systems that cannot be self-sustaining given their design or placement in a highly modified landscape context, such as strip mines, chemically polluted brownfields, or severely eroded sites (Palmer and Ruhl 2015). Other examples of projects with limited objectives (Suding et al. 2015) include maximizing a single ecosystem service, such as stabilizing a steep slope using a monoculture of nonnative, deep-rooted trees (Mao et al. 2012), or postmining reclamation of a formerly forested region to a nonnative grassland (Yeiser et al. 2016). So long as objectives are not too narrowly focused (e.g., on a single social goal), recovering a broad range of ecosystem services is possible and the chances of this may be increased if efforts are invested in maximizing functional biodiversity and associated ecological processes (chap. 3).

A "fully restored" ecosystem is inferred to be self-sustaining and resilient; that is, it has the capacity for recovery from expected change and stress (SER 2004). In cases where landscape-scale processes no longer occur naturally, restoration can compensate for some constraints on self-sustainability by reintroducing the missing process (chaps. 4 and 16). Examples include controlled burning to restore grasslands or forests, and flood pulsing to restore riparian habitat and stream channels. Moreover, invasion by an aggressive nonnative species or an uncharacteristic disturbance may trigger the need for ongoing maintenance (Shaish et al. 2010; Dickson et al. 2014). In such cases, "restoration" *sensu stricto* may never be finished. It is uncertain whether fully restored ecosystems will be resilient to all future stressors, especially with changing climate and other stressors that occur at a greater rate or magnitude than the system has experienced over recent evolutionary time (chaps. 5, 6, 15, and 17).

The Restoration-Theory Linkage

The acid test of our understanding is not whether we can take ecosystems to bits on paper, however scientifically, but whether we can put them together in practice and make them work. —A. D. Bradshaw (1983)

Restoration ecology and ecological restoration are reciprocal concepts. Ecological theory informs the practice of restoration but the converse is also true: restoration science and practice can contribute to basic ecological theory (Bradshaw 1983; Jordan et al. 1987; Perring et al. 2015). Ecological restoration is especially useful for testing theories associated with understanding the processes that govern ecosystem trajectories (assembly rules, postdisturbance succession, alternative stable states; chaps. 2, 8, and 9). For example, work in Poland showed that restoration of drained fens may result in communities with different levels of plant functional diversity due to the differential effects of competition and habitat filters (Hedberg et al. 2014). This work demonstrated that knowing which filters act in a particular setting is essential to predicting which species or functional groups are likely to dominate (chaps. 3, 6, and 9). Efforts to restore natural fire regimes in forested communities have informed general understanding of fire ecology where disturbance dynamics have been disrupted (Falk et al. 2011; Young et al. 2015). Restoration studies have informed our understanding of the link between biodiversity and habitat heterogeneity or complexity (Bell et al. 1997; Zedler 2000; Palmer et al. 2010; chap. 10). Because restoration scientists work, by definition, in systems that have been disrupted, their observations and experiments have especially informed—and been informed by—theories of the ecology of disturbance (Temperton et al. 2004; Lake 2013; chap. 9).

As Bradshaw's (1983, 1987) famous remark anticipates, the use of restoration research to test theory and challenge dogma has grown dramatically (Young et al. 2005; Zedler et al. 2007). For example, recent work by Ford et al. (2015) showed that the expected trophic cascade effect of restoring a top predator (Kenyan wild dogs that significantly reduced a dominant ungulate herbivore) did not increase tree abundances, even though the herbivores were known to suppress tree abundance and despite a positive correlation between trees and dog abundance. The authors suggest alternative hypotheses including significant time delays in indirect effects and the possibility of a reticulate food web such that, once the dominant herbivore declines, herbivory by other species increases. In a very different type of ecosystem, work by Hamilton et al. (2014) supported ecological theory linking dietary niche breadth to the size structure of a predator population. Fishing pressures selectively removed large sheepshead fish in a California kelp bed, but when the size structure of the fished population was restored, the predator's dietary niche expanded, with implications for urchins, algae, and kelp.

Conducting large-scale experiments that test basic ecological theory while restoring a site simultaneously can advance both the practice and the science of restoration (Zedler and Callaway 2003). For example, a nitrogen-addition experiment coupled with restoration of an endangered tidal marsh plant demonstrated that nutrient levels affected the annual plant's abundance, suggesting that in some instances strategic modification of biogeochemical properties can reinforce species-level responses (Parsons and Zedler 1997). Efforts to reintroduce wildland fire as a keystone ecosystem process have enabled forest scientists to study fire effects on vegetation dynamics, biogeochemical cycling, and carbon sequestration in more detail than would be possible in uncontrolled wildfires (Schoennagel and Nelson 2010). Working on strip-mined areas in Brazil, Silva et al. (2015) showed that nutrient limitation, plant community composition, and microbially mediated biogeochemical reactions interacted to determine soil development, carbon sequestration, and restoration trajectories. Their tests included trait-based, functional ecology theory, which Laughlin (2014) recommended for experimentation in restoration sites to advance both theory and practice.

Ecological theory and contemporary modeling approaches can also be coupled to explore ways to enhance restoration projects. As an example, a recent study by Crandall and Knight (2015) used spatially explicit modeling to explore factors that may weaken the positive feedbacks that often allow exotic species to replace natives. Theory suggests that dominance by exotics is due either to major fitness advantages, or because they create positive feedbacks that benefit conspecifics more than individuals from other species. As the population size of the exotic species increases, self-reinforcing feedbacks may become stronger, making it difficult to eradicate nonnatives (Stevens and Falk 2009; Larkin et al. 2012; Yelenick and D'Antonio 2013). Crandall and Knight's (2015) work suggests that once exotics have become established and dominate a system, it is less likely that the system can be moved back to a native state unless disturbance strongly reduces the fitness of the exotic relative to the native. This theoretical work implies that intervention before an exotic becomes dominant is essential, but in later stages of invasion, experimenting with different disturbance regimes, perhaps implementing them even more frequently than was the case historically, can be productive (e.g., "manipulating disturbance"; chap. 8).

These examples illustrate our fundamental premise: ecological restoration benefits from a strong grounding in theory, while at the same time ecological theory benefits from the unique opportunities to test theory in restoration contexts. Specific examples of this reciprocity are provided throughout this book, covering major areas of ecological theory spanning multiple levels of ecological organization from genetics to whole ecosystems (table 1-2).

Table 1-2.

Broad areas of ecological theory that are foundational to the science of restoration ecology

Relevant Ecological Theory	Restoration Questions	Key Themes, Issues, and Models	Contributors
Restoration ecology and ecological restoration	What is ecological restoration? What is the relationship between the science of ecology and restoration?	Historical and contemporary range of variability; scientific restoration pathway; adaptive restoration; passive/active restoration; process-based restoration; ecological structure/function; reference system.	Palmer, Zedler, and Falk (chap. 1)
Ecological dynamics	Has the ecosystem moved into an irreversible state? Will recovery trajectories lead the system to alternative states?	Ecosystem trajectories; stability; basins of attraction; reversible/irreversible threshold models; hysteresis models; successional models; fast vs. slow processes; alternative stable states; biotic feedbacks; resilience.	Suding, Spotswood, Chapple, Beller, and Gross (chap. 2)
Biodiversity and ecosystem function	What level of biodiversity is needed to restore ecosystem function?	Genetic, taxonomic, phylogenetic, and functional diversity; commonness and rarity; extinction debt; biodiversity and ecosystem function; complementarity; portfolio effect.	Naeem (chap. 3)
Landscape ecology and spatial processes	How does landscape position influence recovery potential?	Landscape composition, configuration and mosaic; matrix; functional units; local and landscape restoration; spill-over effects; connectivity process; complementation; supplementation.	Metzger and Brancalion (chap. 4)
Population genetics	What propagule sources and numbers should be introduced? How genetically diverse should a reintroduced population be?	Genetic variation; effective population size; founder effect; genetic drift; landscape genetics; environmental envelope; species range model; environmental niche; reintroduction; augmentation; translocations.	Richards, Falk, and Montalvo (chap. 5)

Table 1-2. *continued*

Relevant Ecological Theory	Restoration Questions	Key Themes, Issues, and Models	Contributors
Ecophysiological controls on species persistence	What are the potential physiological challenges in restored environments?	Environmental stress tolerance; nutrient cycling; photosynthetic and transpiration rate; biomass allocation; light saturation and photoinhibition; water use efficiency; stomatal conductance; leaf temperature; plant water availability; plant nutrient requirements.	Kimball, Funk, Sandquist, and Ehleringer (chap. 6)
Population dynamics and metapopulations	Will restored populations persist? How many subpopulations are needed to establish resilient metapopulations?	Metapopulation dynamics; population demographic matrices; extinction probability; self-sustaining population; stochastic variation; spatial integral projection models; Bayesian networks; elasticity analysis; minimum viable metapopulation; source-sink dynamics.	Maschinski and Quintana-Ascencio (chap. 7)
Invasive species dynamics and community invasibility	How should sites be managed to exclude undesirable species?	Alternative stable states; assembly theory; priority effects; diversity/invasibility; competition; invasibility/resistance or resilience; fluctuating resource hypothesis; niche preemption; legacy effects; functional/trait diversity.	D'Antonio, August-Schmidt, and Fernandez-Going (chap. 8)
Community assembly	Will species interactions and order of introduction influence restoration trajectory?	Facilitation; nurse plants; filter theory; priority effects; biotic/abiotic filters; priority effects; biodiversity-ecosystem functioning; species/functional diversity; complementarity; community assembly; founder effects.	Temperton, Baasch, von Gillhaussen, and Kirmer (chap. 9)

Table 1-2. *continued*

Relevant Ecological Theory	Restoration Questions	Key Themes, Issues, and Models	Contributors
Heterogeneity	How can restoration maintain landscape variability and enhance biodiversity?	Microtopographic variation; nonequilibrial states; patch mosaic; fractal; coexistence; regional diversity; landscape context; species distributions; disturbance mediation; habitat selection; ecosystem function; community assembly.	Larkin, Bruland, and Zedler (chap. 10)
Food webs and trophic structure	Can knowledge of trophic interactions guide restoration interventions?	Trophic guild; food web connectance; food web assembly; interaction web; diversity/stability; energetic web; top down/bottom up; predator-mediated and apparent competition; biomanipulation; extinction risk.	Vander Zanden, Olden, Gratton, and Tunney (chap. 11)
Nutrient dynamics	Are nutrient dynamics determinants of restoration outcome?	Stoichiometry; C:N:P ratio; P sorption, P desorption; ammonification, nitrification, denitrification; N-use theory; plant input-output theory; fluctuating resource hypothesis; resource ratio hypothesis; nutrient spiraling, nutrient excess/deficiency; soil C saturation theory; C sequestration.	Baer (chap. 12)
Carbon, energy, and ecosystem processes	Can restoration influence carbon fluxes and storage and contribute to global carbon sequestration?	Carbon dynamics; ecosystem carbon sequestration; net ecosystem carbon balance; net primary productivity; postdisturbance recovery; wetland, grassland, and forest ecosystem processes; fire effects on carbon cycle.	Marín-Spiotta and Ostertag (chap. 13)

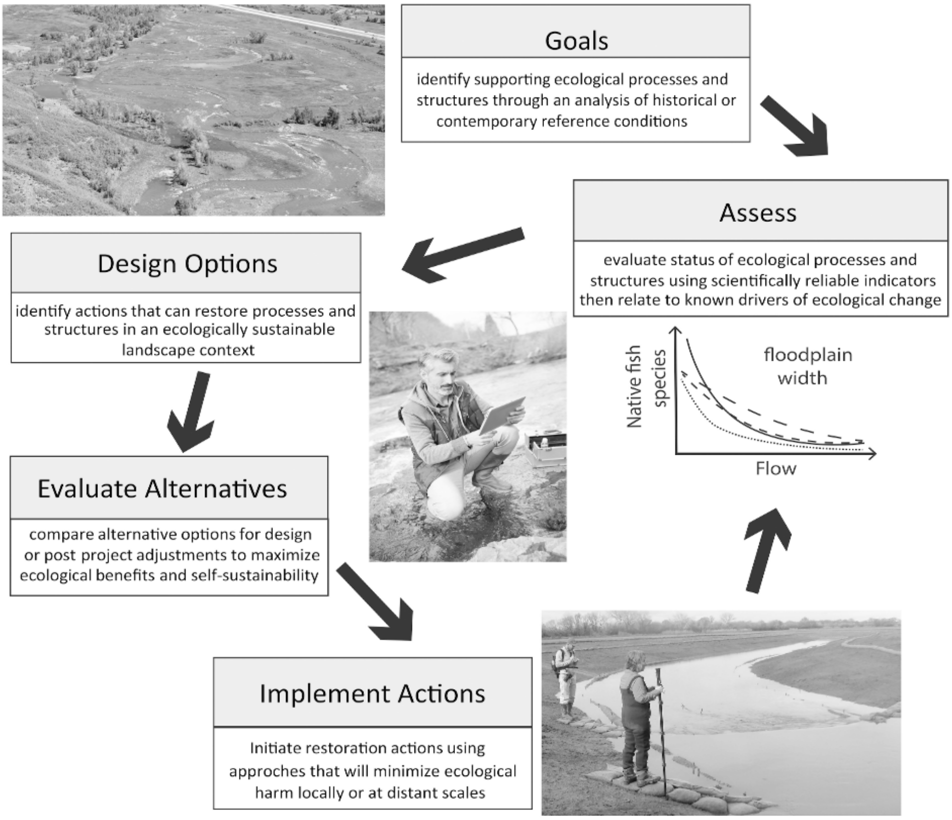
Table 1-2. *continued*

Relevant Ecological Theory	Restoration Questions	Key Themes, Issues, and Models	Contributors
Watershed processes	Are large scale interventions necessary to restore local water availability?	Interception and infiltration; soil hydraulic conductivity; water storage; splash, sheet, rill, and gully erosion; water yield; hydrologic regime; network configuration; surface vs. subterranean watersheds.	Moreno-Mateos and Palmer (chap. 14)
Evolutionary ecology	How will organisms adapt to restored environments?	Contemporary evolution; fitness optima; strong selection; antagonistic pleiotropy; life history evolution; quantitative trait evolution; adaptive phenotypic plasticity; reciprocal transplants; population genetic divergence; landscape genetics; migrational load; restoration genomics.	Stockwell, Kinnison, Hendry, and Hamilton (chap. 15)
Macroecology and island biogeography	How does a restored site or population interact with its larger ecological and bioclimatic context?	Cross-spatial processes; species distribution models; macroevolutionary adaptation; fundamental and realized niche; bioclimatic envelope models; species-area relationships; metapopulation models; habitat connectivity; dispersal probability; neutral theory.	Dennhardt, Evans, Dechner, Hunt, and Maurer (chap. 16)
Climate variability and change	How do species and communities adapt to climate variability? Does projected future climate change require revising restoration principles?	Climate variation; paleoclimate; species adaptation to variable environments; climate regimes; Quaternary, Holocene, Anthropocene climate; species range shifts; community reassembly; phenology; tree mortality; megadisturbance; reference conditions; ecosystem reorganization; assisted migration.	Falk and Millar (chap. 17)

Foundations of Restoration Practice

Some view ecological restoration as an art or a skill honed by practice, experience, and tutelage. As we have suggested, ecological theory is a foundation for restoration practice; however, restorationists can also learn from empirical "vernacular" experimentation and traditional ecological knowledge (TEK) (Martinez 2014). Both modes of learning develop over time, based on varying trials (intentionally or otherwise) and selecting approaches that best achieve desired outcomes, informing others of advances and adapting practices to new knowledge. Both approaches also identify "what works" over multiple trials, which can sometimes extend over many years. Together, science-based, experiential, and TEK approaches can guide restoration goals, treatments options, and experimental designs (Rieger et al. 2014). Implementation of the project should be accomplished in an adaptive management framework in which scientific monitoring informs each step of the process, including the need for additional actions to move the restoration project forward (fig. 1-1).

As a general principle, the first step in restoring an ecosystem is to remove or at least reduce causes of degradation so the system can begin to recover on its own via natural processes (Batchelor et al. 2015). Following this, the preferred or lowest-cost approach to the restoration of degraded ecosystems is often to allow them to recover on their own. This approach, sometimes referred to as *passive restoration*, is based on the premise that natural systems have their own recovery pathways, mechanisms, and timetables, which may not be mirrored in human-driven designs or implementation. In a sense, this approach is a null test of the potential for spontaneous recovery without human intervention. For instance, many forests recover essential attributes following low-severity wildfire, because biota are preadapted to such events (Keeley et al. 2011). Healthy stream systems adjust their channel morphology in response to flooding and seasonal variation in streamflow as it interacts with sediment inputs and redistribution; river forms remain dynamically stable if this process is not interfered with by human actions such as building of dams or levees to constrain channels (Wohl et al. 2015). Perhaps the classic example of passive restoration is fisheries management, when populations can recover spontaneously (Hilborn and Ovando 2014) once overfishing or harmful harvest practices are eliminated. Similarly, eradication of nonnative mammalian predators on islands (>800 projects to date) allowed passive recovery of seabird colonies with stable metapopulations on New Zealand islands near source populations (Buxton et al. 2014). Likewise, removal of livestock grazing led to passive recovery of native riparian vegetation in rangelands of the US Central Basin (Hough-Snee et al. 2013), and fencing areas to limit human access resulted in the recovery of Mediterranean coastal dunes (Acosta et al. 2013).



Goals

identify supporting ecological processes and structures through an analysis of historical or contemporary reference conditions

Assess

evaluate status of ecological processes and structures using scientifically reliable indicators then relate to known drivers of ecological change

Design Options

identify actions that can restore processes and structures in an ecologically sustainable landscape context

Evaluate Alternatives

compare alternative options for design or post project adjustments to maximize ecological benefits and self-sustainability

Implement Actions

Initiate restoration actions using approches that will minimize ecological harm locally or at distant scales

Figure 1-1. Steps in ecological restoration are informed by theory and methods of restoration ecology science. Photo on lower right courtesy of Joshua Viers.

More often, however, restoration requires multiple efforts, because species, sites, or their landscapes, have been pushed beyond the ability to recover passively. In these cases, the preferred approach is *process-based restoration*, which is well grounded in ecological theory. Here, actions aim to restore underlying processes that create and maintain ecological systems, such as dispersal, biogeochemical cycling, hydrologic dynamics, watershed infiltration capacity, and fire, rather than micromanaging every aspect of community composition and structure (Zedler 1996; Beechie et al. 2010). The water-flow regime is a master variable that influences almost all aspects of stream and river ecosystems; thus, restoring flows affects almost every other aspect of stream restoration from a biophysical and organismal point of view (chap. 14). Similarly, fire regimes are integral to the restoration of many forests, woodlands, and grasslands; restoring this keystone process can allow the systems to reequilibrate in other respects such as forest structure and composition (Bond and Keeley 2005; Falk 2006). Process-based restoration is far more likely to result in a more sustainable system than efforts focusing only on compositional or structural elements, such as the shape and size of a stream channel or planting the desired species in soils that cannot supply sufficient nitrogen. Without restoring the critical processes that maintain these ecosystems, ongoing maintenance will likely be required, for example, to clean the water, maintain species metapopulations, or maintain forest structure (Palmer et al. 2014; Roccaforte et al. 2015; chaps. 4 and 7).

A comprehensive restoration approach that focuses on restoration of both processes and structures is, of course, ideal and supported strongly by ecological theory and empirical observation. One of the first large-scale grassland restorations began at the University of Wisconsin–Madison Arboretum, where land dedicated by Aldo Leopold in 1934 achieved diverse prairie via combinations of plantings and prescribed burning (Meine 1988) (fig. 1-2). Unfortunately over time, urbanization increased runoff and eutrophication, and regulations reduced opportunities for burning. Woody and weedy plants expanded and displaced native plants. Recent research has quantified links between structure and processes in experimental wetlands in the Arboretum, showing that prolonged hydroperiod alone fostered cattail invasions that decreased plant diversity and increased discharges of dissolved phosphorus, contrary to project design. Adjacent wetlands with higher infiltration rates had less cattail cover, more diverse vegetation, and lower rates of nutrient discharge (Doherty et al. 2014).

Figure 1-2. Curtis Prairie (University of Wisconsin–Madison) was cultivated and then used to pasture horses before being planted to establish tallgrass prairie, from 1935 to the 1950s (left photo). In a 1966 census, P. and J. Zedler recorded 212 native plant species and 33 exotics (e.g., center photo); in 2002, T. Snyder found 230 natives and 35 exotics. The largest shift during those thirty-six years was the expansion of shrubs, notably the native gray dogwood, *Cornus racemosa*, which increased from 15% to 53% frequency of occurrence in square-meter plots. The 2011 control burn (right photo) left many live woody stems and rhizomes. In 2015, mowing was added to burning to control woody plant invasion. Management to achieve tallgrass prairie continues, despite eighty years of restoration effort. Photo collage courtesy of Sarah Friedrich.

Ecological Theory and the Reference Concept

The concept of a reference system is a bedrock principle in restoration, and such systems often serve as a template to guide restoration and to identify when recovery is complete (Egan and Howell 2005). However, in practice the most important role for reference systems may be to provide ecological information about the system of interest (Higgs et al. 2014). A scientific analysis of historical or contemporary environmental conditions within which such a system exists (existed) involves the use of ecological theories (e.g., on species interactions, biogeochemical fluxes, disturbance regimes, or dispersal) and applicable experiments to determine whether the composition, biophysical processes, or structural aspects of a potential restoration site are outside the reference range (fig. 1-3). The historical or contemporary range of variability in species assemblages, biophysical processes, and ecosystem features derives from the factors that control system states, the rate of change in response to environmental change, and the ongoing direction of change (Gildar et al. 2004; Wiens et al. 2012).

In fact, ecological restoration has never been limited to the literal use of historical conditions as a target for restoration (i.e., "returning to the past") (Clewell 2000). Some projects may attempt to recover species native to a region, but the modern science of restoration emphasizes that the ability to do this is highly context dependent (Zedler et al. 2012). If the range of conditions necessary to support historical species is not readily recoverable, then more aggressive interventions or alternative targets may need to be explored (e.g., functional targets; chap. 3). Even in these cases, however, the role of reference systems remains: to provide a guide to the dynamics of the degraded system, in essence suggesting where that system would be currently had it not been disrupted (Falk 1990). In the end, maintaining or restoring resilience or adaptive capacity may be as, or more, important than literal historical authenticity (chaps. 2, 15, and 17).

Identifying the appropriate spatial and temporal scale in evaluating ranges of variability is not a trivial task (White and Walker 1997). How long a history and how large an area provide a relevant baseline for a particular restoration site? Some have suggested that the most appropriate spatial scale for identifying the historical range of variability should be where the intensity of ecological interactions, system components, or states of environmental variables changes substantially, for example, major discontinuities or steep gradients (Post et al. 2007). Rapid temporal shifts in the environment might help explain a major state change, for example, when an earlier state was sustained by processes and ecological components that no longer exist, or that may not persist into the future (Jackson and Hobbs 2009). This approach can be combined with projections of climate-induced changes in

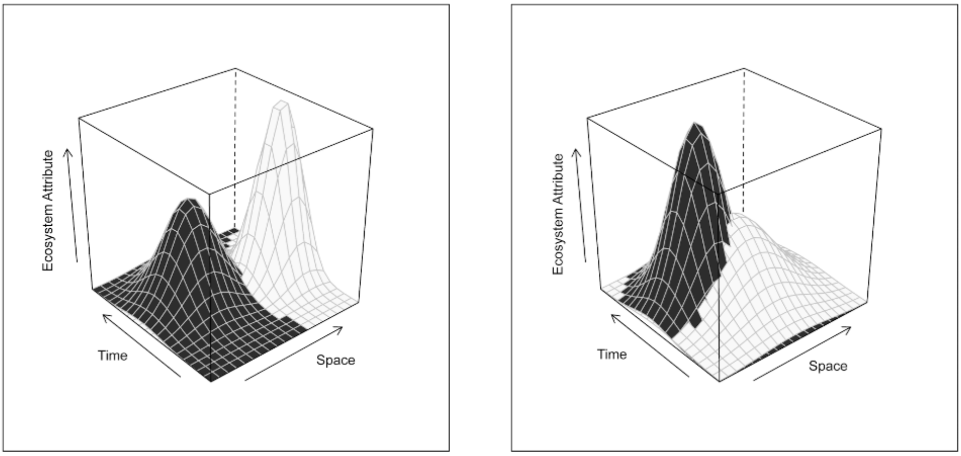


Figure 1-3. Ecological systems and their structural and functional attributes are dynamic in time and space. Understanding such variability is critical to determining if a system needs restoring and to what extent. Once the system is restored it is unlikely initially to occupy the same ecological space as predisturbance. The figures show the distribution of some ecological attribute, such as native species richness, for a reference ecosystem (black) and for a second ecosystem of interest (gray). In the prerestoration state (left panel), variability in species richness for the ecosystem (gray) is outside the range of variability for reference systems, indicating that the ecosystem needs restoring. In the postrestoration state (right panel), the two distributions overlap, indicating that the system has been restored (but note that both systems have changed). These images highlight how critical it is to recognize that reference systems are themselves not static, and also that restored systems need not be identical to a particular reference system in every respect.

dominant system processes or major environmental variables, such as temperature, to identify when historical bounds are likely to be exceeded (Mora et al. 2013). Such analyses may determine the extent to which historical ranges should influence the restoration approach and its goals (Maschinski and Haskins 2012; chap. 17).

Other ecologists argue that the field has advanced sufficiently that selection of a single spatial or temporal scale of reference makes little sense; rather, we are equipped with theory to integrate across scales, including ecological to evolutionary timeframes and organism to ecosystem targets (Chave 2013). Given the growing availability of environmental data along with new analytical tools and advanced computer capabilities, macrosystems ecologists (Heffernan et al. 2014) now use dynamic linear modeling methods to explore how broad scale and local phenomena interact, and they can predict how patterns and processes at local scales are likely to respond to environmental changes at multiple scales (Levy et al. 2014). Methodological advances such as the use of stable isotopes for food-web analyses have revealed linkages across spatially distinct ecosystems that can inform restoration designs (chap. 11), and advances from combining species distribution modeling with methods from landscape genetics have resulted in a better understanding of what restoration outcomes are possible under future conditions (chap. 5). These examples suggest that we view restoration not simply in the context of what is or is not possible given the pace of global change; rather, we ask how consideration of ecological and evolutionary processes such as metapopulation dynamics, trophic interactions, dispersal, range shifts, and microevolution can be integrated to address conservation and restoration issues even in the face of uncertainty (chaps. 4, 7, 15, 16, and 17).

The difference between variability (an ecosystem property) and uncertainty (a sampling and prediction property) is a key issue, not only in the analysis of reference conditions but more broadly in all restoration research. In some ecosystems (for example, conifer forests in western North America), certain historical reference conditions can be determined with a high degree of accuracy, such as species composition and the mean fire return interval (Friederici 2003). But many other historical properties are not known or even knowable, especially fine-scale ecological composition, structure, and processes (table 1 in Falk 2006), such as stream geomorphology or water chemistry, local-scale species distributions, dispersal and migration pathways, predation patterns, reproductive output, or disease outbreaks. The problem becomes a kind of “ecological Heisenberg effect” in the sense that the earliest documented observations were made while systems were being significantly altered, such as in North America following European settlement.

Using contemporary ecosystems (spatial references: same time, another place) would seem to avoid some of these problems of historical references (White and Walker 1997). Least impacted contemporary ecosystems may represent ongoing interactions of biotic and abiotic elements, all functioning in complex ways not directed by humans. Moreover, their properties can be observed in detail and can be measured whenever researchers need data. However, contemporary references are confounded by their own significant problems. First, the supposed “reference” may already be altered in unknown ways, due to pervasive drivers that affect the region and the target system, such as climate, altered species distributions, or land use. Second, the site may not be a good analogue for the target system, in which case the information derived may not be appropriate for the restoration setting. Third, both systems may be nonequilibrial, meaning that, even if they are comparable, they may reflect alternative successional or metastable states. This issue could be important in ecosystems characterized by high temporal variability and a wide range of potential postdisturbance successional sequences and alternative states (Fletcher et al. 2014).

The Imperative to Test and Advance Theory

The challenges associated with using contemporary ecosystems to define reference conditions become even greater when considered in the context of the pace of anthropogenically induced environmental change. It is thus critical to consider the role ecological restoration can play within the broader context of strategies to cope with such change (Aronson and Alexander 2013). Ecological restoration is an essential component of a sustainability agenda but it is not sufficient to ensure the future health and well-being of natural systems and the people they support. Global human impact continues to expand, vital resources, such as freshwater and arable soils, undammed rivers, and wild forests are increasingly threatened and depleted (Freedman 2014). Conservation is always preferable to resource degradation followed by restoration, but, even with this, it may not be possible to hold the line given rates of resource consumption on our crowded planet (Corlett 2015). In some cases, engineered solutions may be needed even though they do not bring the diverse benefits that conservation provides and that restoration has the *potential* to provide. To realize this potential, scientists are challenged to ask under what circumstances can we grow a science of restoration ecology that is soundly rooted in ecological theory? One way to address this challenge is to ask which research questions or settings require an extension of our theories and models or even the development of theories *de novo*. Extending existing theory and developing new theory to guide restoration is difficult, because restoration typically takes place across a multidimensional spectrum of specific sites within various kinds of landscapes, and where goals range from highly specific (e.g., enhance the population of one rare animal species at a specific site) to general (e.g., encourage development of a diverse and complex ecological community over a large landscape).

The need to align ecological restoration closely with a sound theoretical base is imperative for at least three reasons. First, growing demand has made restoration a booming business that requires the support of a knowledge base and research innovations. Billions of dollars are spent annually to restore polluted and sediment-clogged streams (BenDor et al. 2015,) and to reforest lands in areas that have been degraded or fragmented (Rodrigues et al. 2011), yet many restoration efforts are still trial and error improvisations. Second, ecosystem restoration can regain essential ecosystem services such as soil fertility, carbon sequestration, and water purification (chaps. 10, 12, 13, and 14). The stakes are too high *not* to restore ecosystem integrity wherever possible, especially because services are often what motivate the public and policy makers to invest in restoring natural systems (Aronson et al. 2007; Schaefer et al. 2015). In certain regions of the world, such as the global tropics, human well-being cannot be separated from the sustainability of ecosystems (Lamb et al. 2005). A third reason to enhance the linkage between ecological theory and restoration is to grow the field of ecology. Regardless of what motivates ecologists, their research will likely benefit by being tested in a restoration context, as described earlier and throughout this book. Clearly, practice can be used to both test and grow ecological theory and basic understanding (Young et al. 2005). Whether realized or not, virtually all restoration projects rely on ecological theory, from the initial stages of envisioning a project through completion.

Closing Remarks

Some theories and concepts are so fundamental to understanding the dynamics of ecological systems and how to manage them that they will always be relevant to restoration. Many of these relate to the critical role that diversity, in all its forms, plays in the structure and continuity of populations, communities, and ecosystem processes. Others relate to historical legacies and contemporary context combined with biotic and abiotic filters that can result in persistent alternative states or unanticipated trajectories following the implementation of restoration actions. As we describe in detail in the last chapter of this book, these fundamental concepts and theories are the basis for *persistent themes* that can be found in both editions of this book; seven such themes are discussed (table 18.1). However, advances in ecological science have been substantial since the last edition and thus new, *emergent themes*, are apparent in this edition, which are also outlined in the last book chapter (table 18.2). A number of these have been fostered by quantitative advances in modeling, development of new analytical or sampling methods, or creative application of existing statistical methods. Other themes have emerged as a result of growing societal interest in the provision of ecosystem services and the recognition that the current pace of environmental change challenges some conventional assumptions about what it means to restore a system. Readers may wish to read chapter 18 both before and after the other book chapters in order to develop their own list of fundamental, timeless concepts and ask if the growth in ecological science reflected in emerging themes can help meet the growing global imperatives.

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Chapter 2

Ecological Dynamics and Ecological Restoration

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Theory and Application

- In deciding on a restoration approach, it is important to consider whether recovery will follow a predictable and desired successional trajectory; get "stuck" at an intermediate stage; or shift to an alternative, undesirable, state.
- The interactions between internal processes (e.g., species interactions) and external drivers (e.g., climate change) after a reorganizing event, such as a disturbance (e.g., a fire) or restoration intervention, are the key to understand ecosystem dynamics.
- A resilience framework can inform ways to ensure recovery rather than drastic shifts in state following unpredictable environmental stressors. This framework emphasizes the importance of a landscape-scale approach to maintain function.

In ecological restoration we are faced with the challenge of making decisions about ecosystem management with imperfect information about system dynamics and trajectories. For example, a restoration ecologist evaluating a denuded floodplain might be asked to determine if the area can support a cottonwood forest. Can cottonwood seedlings naturally recruit and persist here, or do they need to be seeded? How will the upstream presence of tamarisk populations (or other invasive species) affect the establishment of the cottonwood forest? How do we prevent the conversion to a tamarisk-invaded state? Is it possible to establish a cottonwood forest on this site that would be resilient to invasion? Taking a perspective that considers how theory and practice can be integrated, we consider how questions such as these can guide our approach to the restoration of native systems.

Ecological research has long focused on the trajectory and speed of ecosystem recovery following disturbance. Unfortunately for managers, however, it is often

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difficult to predict how we might expect a given ecosystem to recover following degradation or disturbance in a way that can be applied to restoration interventions. Developing recommendations for restoration is further challenged by a lack of knowledge of how systems will respond to novel disturbances and stressors associated with human activities. The dynamics of ecological systems, particularly of a degraded system undergoing restoration, is a function of many factors, some deterministic and some stochastic, working at multiple temporal and spatial scales.

In this chapter we focus on what research has taught us about how systems change over time and respond to disturbance and explore implications for restoration. We include in our review an overview of relevant ecological theory. We address several questions:

1. When can we predict the trajectory by which a system will recover from a disturbance? Will it follow a predictable successional series, suddenly cross a threshold, or get "stuck" in an alternative state?
2. What processes influence ecosystem dynamics and recovery? Can these processes be used to indicate the likelihood for a system to exhibit threshold dynamics or to gradually return to a native state?
3. How can our knowledge of ecosystem dynamics be used to manage for ecological resilience in restoration?

To answer these questions, we need to understand the ecological dynamics that are important in predicting both changes in species composition that typify a restoration and how these relate to changes in system function at multiple scales. As emphasized in chapter 1, studies of restoration can be used to test and refine ecological theory related to community dynamics, and, links between restoration and ecological dynamics advance both the practice of restoration and theories of ecological dynamics. In our review, we survey the progress and the further potential of this connection with a focus on system dynamics.

Models of Ecological Dynamics

The choice of intervention in restoration should depend on the type of ecological dynamics that govern recovery at the population, community, and ecosystem level. Ecology has a rich history of conceptual development of models that predict these dynamics, three of which are particularly relevant to restoration (table 2-1). These include *successional models* that assume single-equilibrium dynamics along predictable pathways, *threshold reversible models* that predict discontinuous but

Table 2-1.

Important ecological theories or concepts relevant to understanding ecological dynamics in restoration

Theories or Concepts	Description	Implications for Restoration
Disturbance theory (Pickett and White 1985; Pickett et al. 1989)	A *disturbance* is a discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment.	Disturbances can be the event that creates the degradation and also a tool during restoration to modify dynamics and guide recovery. Because disturbances play a crucial role in maintenance of ecological processes, the actual goal of restoring disturbance regimes is often crucial in restoration projects (Moritz et al. 2013; Wohl et al. 2015).
Succession theory (Clements 1916; Odum 1969; Pickett et al. 1987)	*Succession* assumes that recovery from a discrete disturbance event involves continuous processes such as gradual accumulation of biomass and nutrients, which is often driven by the establishment of longer-lived later successional species as the system moves through predictable successional stages. Systems are assumed to return to their predisturbance state or follow a known trajectory after a disturbance via predictable change in composition to a single equilibrium point.	Restoration interventions may be unnecessary if succession proceeds along a predictable trajectory (Pickett et al. 2009). Interventions can act to speed the rate of succession by introducing elements of later successional stages (McClain et al. 2011).
Community assembly theory (Weiher and Keddy 1999; Booth and Swanton 2002; HilleRisLambers et al. 2012)	*Community assembly* refers to the processes by which species from a potential regional species pool colonize and interact to form the actual species assemblage at a site. The theory particularly focuses on the importance of three *filters* in determining local community composition: dispersal, physical environment, and biotic interactions.	Restoration interventions can be viewed as guiding community assembly by focusing on assembly filters that constrain recovery (Cramer et al. 2008; Matthews et al. 2009). For instance, seed addition or species reintroduction can be viewed as circumventing the constraints of a dispersal filter (Myers and Harms 2009).

Table 2-1. *continued*

Theories or Concepts	Description	Implications for Restoration
Threshold dynamics (Whisenant 1999; Hobbs and Harris 2001)	*Thresholds* are nonlinear changes, where a gradual change in one characteristic leads to a sudden or discontinuous change in another.	Knowledge of threshold responses is helpful in restoration projects because goals can be set to cross a critical transition (Selkoe et al. 2015).
Alternative stable state theory (Holling 1973; Beisner et al. 2003)	Ecosystem or communities that differ from one another by discrete characteristics (states or basins of attraction) exist simultaneously under the same set of conditions. Sufficiently large perturbations can shift states from one to another. *Resilience* refers to characteristics that act to retain the state within a basin of attraction. *Hysteresis* refers to the trajectory of collapse differing from the trajectory of recovery. *Regime shifts* refer to similar dynamics.	Alternative stable state theory describes a challenging scenario in restoration when communities and ecosystems are easily pushed into an undesirable configuration that proves difficult to recover. It also introduces the idea of building and maintaining resilience of desired states as to reduce the chance of shifts following a perturbation (Standish et al. 2014). A shift from clear to turbid states in lakes is a classic example (Bachmann et al. 1999).
Negative and positive feedbacks (Scheffer 2009)	*Feedbacks* occur when the effects on one characteristic lead to effects on another, which then affect the first characteristic. *Positive feedbacks* are self-reinforcing, producing fast and amplifying change. *Negative feedbacks* are dampening, resulting in stability. Positive feedbacks are a mechanism by which states shift in alternative stable state theory, negative feedbacks are a mechanism of stability via basins of attraction or equilibrium.	Several types of feedbacks may influence dynamics in restoration projects, including feedbacks with disturbance regimes, ecosystem processes, and climate (D'Antonio and Vitousek 1992; Yelenik and D'Antonio 2013; Hobbie 2015). Interactions between species can also result in feedbacks (Dublin et al. 1990; Kardol and Wardle 2010).

Table 2-1. *continued*

Theories or Concepts	Description	Implications for Restoration
Equilibrium/ nonequilibrium dynamics (Connell and Sousa 1983; DeAngelis and Waterhouse 1987)	*Equilibrium dynamics* refer to deterministic changes over time toward equilibrium point, where a system is stable, no longer changing over time. A disturbance shifts a system away from equilibrium and recovery occurs back toward the equilibrium. *Nonequilibrium* describes a system not at equilibrium (but could be moving toward equilibrium), while *nonequilibrium dynamics* refers to cases where processes such as variable climate or frequent disturbance keeps the system from ever reaching equilibrium, if it exists at all. Equilibrium dynamics are assumed by successional (one equilibrium) and alternative state (multiple equilibria) theory, while assembly theory encompasses elements of equilibrium and nonequilibrium concepts.	Restoration interventions often assume deterministic processes and recovery toward an endpoint, concepts that are related to equilibrium theory. Stochastic factors such as propagule arrival, climate, and disturbance, are ideas that encompass nonequilibrium concepts (Marquez and Kolasa 2013). Restoration of semiarid rangelands, for instance, has emphasized that the highly variable climate leads to nonequilibrium dynamics where interventions related to grazing intensity or species interactions have small effects related to climate (Walker and Wilson 2002; von Wehrden et al. 2012).
Transient dynamics (Hastings 2010; Fukami and Nakajima 2011)	Transient dynamics present a challenge to decision making as information over short-term monitoring is often needed to make decisions about long-term dynamics. If short-term dynamics differ from long-term dynamics, then longer term monitoring will be essential to inform management (Lindenmayer et al. 2011).	Transient dynamics present a challenge to decision making as information over short-term monitoring is often needed to make decisions about long-term dynamics. If short-term dynamics differ from long-term dynamics, then longer term monitoring will be essential to inform management (Lindenmayer et al. 2011).

reversible change, and *threshold hysteresis models* that predict alternative stable states and regime shifts. Together, these models describe a continuum of ecological dynamics, and we also emphasize in our review how environmental variation, historical factors and spatial context may affect whether an ecosystem will exhibit a particular dynamic.

Successional Models of Continuous Change

In a successional model of ecosystem change, recovery from a disturbance occurs along a predictable pathway toward a well-defined endpoint (fig. 2-1a). Recovery is assumed to be a predictable consequence of interactions among species with different life histories and feedbacks that affect ecosystem functions (Whittaker 1953; Odum 1969; Connell et al. 1987). In this scenario, community and ecosystem development proceed with little or no intervention to a target state (Khater et al. 2003; Novak and Prach 2003; McClain et al. 2011). Restoration projects that reduce human impacts to promote recovery (e.g., fencing to restrict foot traffic) rely on a natural capacity for restoration.

Restoration plans are often designed to accelerate natural succession so that it reaches the desired endpoint faster. For instance, prescribed burning of degraded grasslands can promote restoration of native plant assemblages (Roy et al. 2014), particularly if the fire management regime is applied according to historical patterns (Baer et al. 2002; Copeland et al. 2002). Direct seeding of late-successional species can accelerate successional processes in degraded pastures to tropical forests (Cole et al. 2011); tree planting can also speed soil recovery in tropical regions (Roa-Fuentes et al. 2015). Implementing desired hydroperiods in wetlands may also promote reestablishment of native wetland vegetation even in the absence of active planting (Moreno-Mateos et al. 2015).

Discontinuous but Reversible Threshold Models

Models that include the concept of thresholds in community dynamics have been important in the translation of ecological theory to restoration practices for decades, particularly in arid rangelands and lakes (e.g., Westoby et al. 1989; Friedel 1991; Carpenter et al. 1999). Precipitated by several reviews suggesting the general applicability of these ideas to habitat restoration and management (Beisner et al. 2003; Mayer and Rietkerk 2004; Suding et al. 2004), these ideas have led to an application of these models to a broader range of systems (Chartier and Rostagno 2006; Carpenter et al. 2008; Schooler et al. 2011; Favier et al. 2012).

Thresholds are defined as a point or condition at which a relatively small change in the environment causes a rapid change in an ecosystem process or condition. In

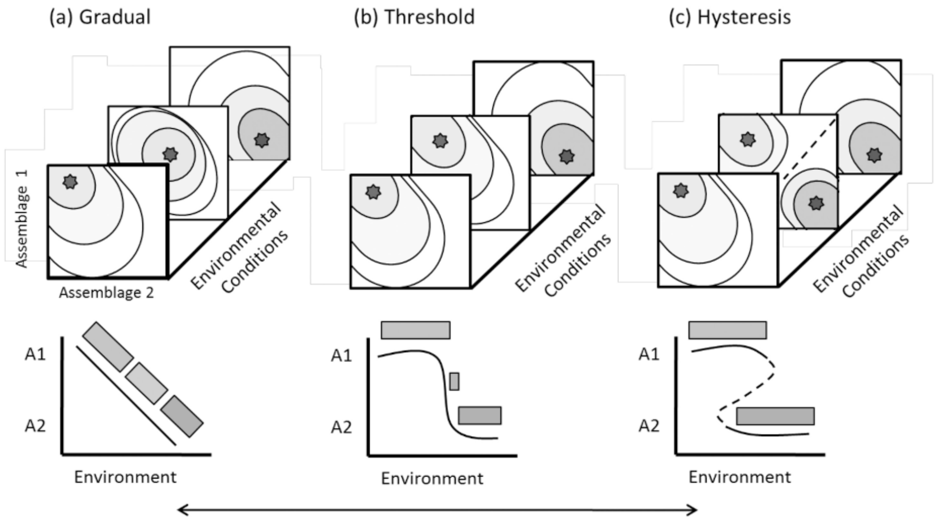

Figure 2-1. Alternative models of ecosystem dynamics. Gradual change (a), and two threshold models: nonhysteresis (b) and hysteresis (c) models. Each square defines possible relative abundances of two assemblages (or functional groups or rate of an ecosystem processes). Isoclines represent dynamics from the basin (in standard units of perturbation strength [resilience]; the stars represent attractors). The dotted line in (c) indicates boundaries of basins of attraction where a disturbance can cause alternative trajectory of recoveries. Each of these isocline graphs is arrayed along an environmental axis that represents exogenous drivers. Changes in the isoclines across the environmental gradient represent changes in composition and stability landscape. Below the isoclines, two-dimensional relationships between the biotic community composition (vertical axis) and environment (horizontal axis) are shown. Gradual change, (a) occurs when there is a linear succession of species or groups along an environmental gradient. Nonhysteresis threshold change (b) occurs where species composition rapidly changes at a given point on the environmental gradient. Changes in the environmental gradient (or other external drivers) can push a system from one state to the other. Hysteresis thresholds (c) can occur if there are multiple basins of attraction (states) within the same habitat so that the threshold where assemblage 1 will decline (collapse) differs from where assemblage 1 will increase (recovery). Human activities can change the frequency and nature of threshold events by influencing resilience, which can affect the arrangement of isoclines as well as shift the system from one to another type of dynamics (i.e., from a to b to c, as indicated by the colored rectangles).

some cases, it is possible to identify a particular environmental condition which will lead to a collapse. For example, Gao et al (2011) found that grasslands with below 20% vegetation experienced sharp increases in soil erosion and declines in soil fertility, suggesting the need for active interventions to maintain plant cover above this point. Another example for animals is the observation that urban bat communities exhibit a threshold response to evening illumination, presumably due to difficulties in capturing prey at higher light levels (Hale et al. 2015). In the case where these thresholds are reversible, reversing or removing the environmental driver that caused the degradation should result in a successional trajectory of recovery to the original (or desired) system, regardless of the magnitude of the perturbation (Suding and Hobbs 2009) (fig. 2-1b).

Thresholds can also be used to increase the success of restoration management efforts. For example, Twidwell et al. (2013) identified a critical level of surface fire intensity necessary to eliminate undesired juniper woodlands. Likewise, Catelotti et al. (2015) identified a critical frequency for river flooding needed for the recovery of Australian riparian trees.

Discontinuous and Irreversible (with Hysteresis) Models

Threshold dynamics also occur where the pathways of recovery and collapse differ. This situation, referred to as *hysteresis* (fig. 2-1c), can result in hard-to-reverse threshold dynamics, called *alternative stable states* or *regime shifts* (Scheffer 2009; van de Leemput et al. 2015). In systems with hysteresis, two or more stable states (basins of attraction) exist for one environmental condition (fig. 2-1c). Because multiple states occur at a single environmental condition, the recovery pathway to a restored system can be very different from the one that led to the degraded state (Suding and Hobbs 2009). Hysteresis can also occur without large threshold changes (Petraitis and Hoffman 2010; Hughes et al. 2013). In these cases disturbance can move the system into a new basin of attraction and toward a new recovery trajectory.

The existence of feedback loops is fundamental in hysteresis dynamics, as it is the change in the nature of the feedbacks that cause the pathways of collapse and recovery to differ. While there are a rich array of examples illustrating feedbacks (Nowacki and Abrams 2008; Barnosky et al. 2012; van der Putten et al. 2013), a focus on feedbacks may be one way to identify systems that have a likelihood of exhibiting hysteresis. Hysteresis and alternative states have been demonstrated in a wide range of ecosystems (Isbell et al. 2013; Liu et al. 2014; Ling et al. 2015) yet, operationally, the identification of hysteresis is challenging and so, the subject of much debate (Dakos et al. 2015). In a restoration context, scenarios consistent with hysteresis may be where ecological processes that structured the system prior to degradation have been altered to such an extent that recovery is not possible. For instance, recovery of macroinvertebrates in a severely degraded river with high silt loads may not be possible unless dam removal restores a natural flow regime (Hansen and Hayes 2012). Similarly, recovery of degraded coral reefs may not be possible where there are warming and bleaching events (Bozec and Mumby 2015).

A Continuum of Ecological Dynamics

Identifying whether the dynamics of a system are driven by gradual change or by complex threshold and hysteresis models would seem the appropriate starting point for predicting how degraded systems may change through restoration. However, ecological systems can exhibit transient dynamics, where one mechanism can govern dynamics in the short term and another dominate in the long term (Hastings 2010; Fukami and Nakajima 2011; chap. 9). For example, modeling long-term lake level dynamics, trends could easily be misidentified if multidecadal cycles are not considered (Molinos et al. 2015). Long-term experiments may reveal the existence of transient effects (Brown et al. 2001), yet identifying and incorporating these effects into decision making and management is challenging (Cuddington et al. 2013).

Human activities can also change recovery dynamics in ways that are not neatly described by succession or threshold models. For instance, human activity can introduce new threshold triggers by shifting discrete pulse events (e.g., treefalls) into persistent press disturbances (clearcutting) or suppression of historically important disturbance events like fire (Hobbs et al. 2006). Events that result in catastrophic mortality might be extremely rare under natural conditions (e.g. hurricanes, wildfires) but increase in frequency or extent due to severe overexploitation or land use change (Daskalov et al. 2007; Gordon et al. 2008). Changes in disturbance interval or the proportion of the landscape affected can cause the system to shift to a different trajectory (Turner 2010).

Climate change also can push a system outside an equilibrium zone and shift a system where recovery was explained by successional models to threshold models and irreversible change (Chapin et al. 2004; Hobbs 2007; Carr et al. 2012). For instance, the combined effects of climate change can reduce a systems capacity for recovery to stress events (such as overfishing or bleaching events); this interaction can lead to irreversible transitions and net habitat loss in some cases (Anthony et al 2015; Vasilakopoulos and Marshall 2015). Increased nitrogen pollution is thought to lead to threshold declines in diversity not apparent at lower nitrogen levels (Bai et al. 2010). While it is difficult to predict the combined effects of multiple stressors, a general prediction is that multiple stressors may often act synergistically to shift dynamics toward hysteresis and regime shifts (Tockner et al. 2010). These changes are often associated with decreased ecological resilience in a system (which we address below).

Indicators of Dynamics: How Can We Infer Dynamics and Ways to Intervene?

Understanding the mechanisms that govern the response of an ecological system to change requires knowledge of the type of dynamics that govern the system, but this information is difficult to obtain because these processes occur on different scales of space, time, and ecological organization (Pickett et al. 1987; Rinaldi and Scheffer 2000; Beisner et al. 2003) (table 2-2). Identifying constraints that can slow or alter the natural recovery of a system may be one way of predicting restoration trajectories (Zedler and Callaway 1999; Holl and Aide 2011; Suding 2011; Cosentino et al. 2014). They also can indicate interventions that may be most effective (fig. 2-2).

Successional models assume that dispersal, species replacement, and ecosystem development will occur over time without intervention, with recovery proceeding in a predictable way (Christensen 2014). The extent to which these assumptions are met often depends on the magnitude of degradation or spatial isolation (Bakker and Berendse 1999; Holl and Aide 2011; Hasselquist et al. 2015). For instance, spatial isolation of a site may preclude propagule arrival of key species (Hasselquist et al. 2015; Reid et al. 2015). Problematic species or landscape conditions may also alter the expected series of species replacement (Lorenz and Feld 2013; Schantz et al. 2015). These factors can cause restoration outcomes to differ widely between sites, even in similar habitats (Matthews and Spyreas 2010; Brudvig et al. 2013; Christensen 2014). These types of constraints may be one cause for discontinuous thresholds and divergence in ecosystem recovery, operating in a very different manner than feedbacks among system components.

Restoration interventions can then be aimed to address those constraints, with the goal of establishing a self-sustaining, resilient ecological system. Because many restoration projects focus on reestablishing a new community by introducing species to a restoration site, it may be illustrative to consider how a focus on species assemblages and their dynamics can indicate ways to intervene. We expect that similar frameworks should apply to restoration goals that focus on population or ecosystem-level processes.

Species Arrival and Recruitment Limitation

Species composition in restoration projects can be strongly affected by processes that determine whether (and when) propagules of a species arrive at a site and if a population can be established. Assembly theory views these processes as a series of ecological filters that constrain what species persist at a site (Myers and Harms 2009; HilleRisLambers et al. 2012; chap. 9). In the restoration of plant communi-

Table 2-2.

The understanding of ecosystem dynamics builds on ecological theory at many scales of organization, each focusing on interactions and processes that either buffer or accelerate change; extended discussions can be found in Chapin et al. (2012), Mittelbach (2012) and Vandermeer and Goldberg (2013).

Scale	Examples of Theory
Population dynamics	Persistence and extinction, population characteristics Demographic and environmental stochasticity Convergence, divergence Feedbacks, negative and positive
Community dynamics	Successional theory Alternative stable state theory Assembly theory, arrival, recruitment, priority effects Trophic interactions Metacommunity dynamics
Systems theory	Regime shifts Slow and fast variables Disturbance triggers Resistance and resilience

ties, there are often insufficient seed sources for many of the desired species (Clark et al. 2013; Reid et al. 2015). The absence of key species can create a threshold effect (Jackson et al. 2001; McConkey et al. 2012; Vasilakopoulos and Marshall 2015) as early arriving species can facilitate or inhibit subsequent arrivals (Connell and Slatyer 1977).

Lack of source populations can reduce the number of propagules arriving or establishing in a restoration site. Increasing the number of seeds sown has been shown to increase species richness and abundance in grasslands (Gross et al. 2005; Aicher et al. 2011; Houseman and Gross 2011). High rates of seed arrival may be necessary to produce the desired species composition at a site (Long et al. 2014), however this will only increase vegetation diversity in areas with the appropriate conditions (Grman and Brudvig 2014; Seabloom 2011) or management (Suding and Gross 2006). Lack of source populations or barriers to dispersal has also been found to influence restoration outcomes in many types of ecosystems including, for example, streams (Kitto et al. 2015) and tropical forests (Schweizer et al. 2015).

As discussed in chapter 4, landscape-level attributes can play a crucial role in the sequence and nature of species arrivals in restoration projects. Proximity to source populations can increase both native diversity (Ray and Collinge 2014) and the rate of succession toward a more mature community (Helsen et al. 2013).

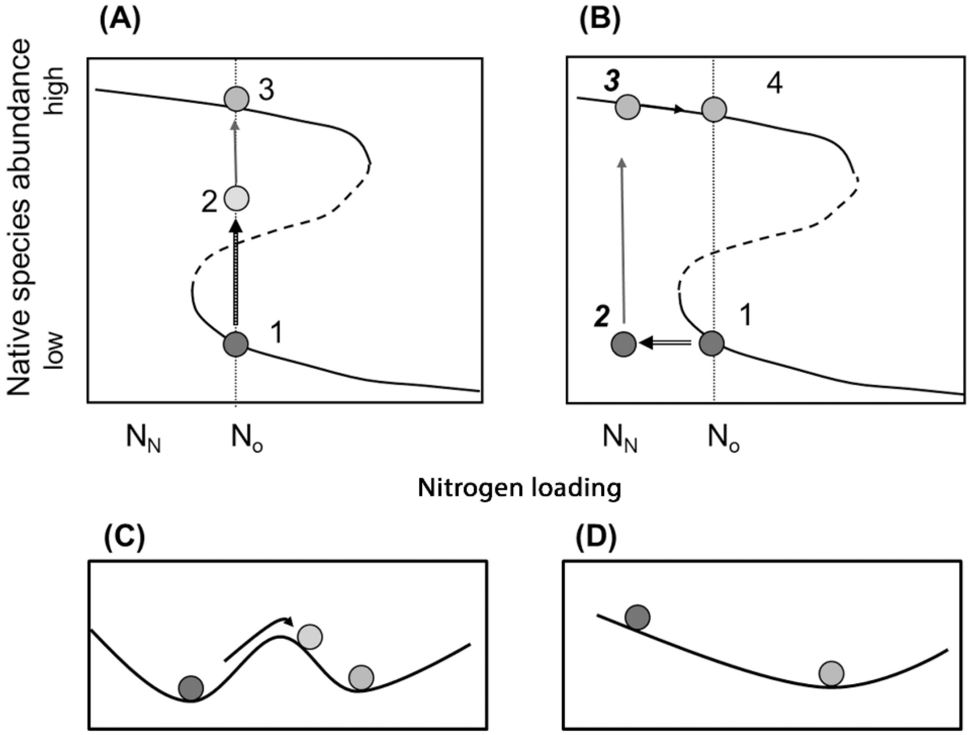

Figure 2-2. In a system with multiple equilibriums, restoration could be achieved via “fast” or “slow” mechanisms. In this hypothetical example (following figure 2-1c), there are two states, one dominated by exotic species (purple) and one dominated by native species (blue) at a given level of nitrogen input to the system (N_0). (a) Restoration via fast-process mechanisms in a system with multiple equilibriums, one dominated by exotics to one dominated by native species. A restoration action or perturbation could break feedbacks that lead to exotic species abundance (bolded arrow, from 1 to 2), forcing the system into another basin of attraction, and to a state dominated by native species (3). (b) Restoration via slow-process mechanisms. If nitrogen inputs are decreased from N_0 to N_N (double-lined arrow to the left, from 1 to 2), perhaps by decreasing nitrogen deposition, native species are predicted to respond as predicted by the trajectory (1–2–3–4). Resilience changes across the exogenous axis, as shown at N_0 (c) and N_N (d).

A large species pool can increase the chance of priority effects (Cleland et al. 2015), which could cause the development of different recovery trajectories. Conversely, a large species pool may include invasive species that can interfere with a restoration (With 2004; Matthews et al. 2009). Past land use and the surrounding landscape can also account for divergence in restored communities beyond that predicted by environmental conditions (Holl and Aide 2011; Brudvig et al. 2013; Grman et al. 2013; Smith et al. 2015).

Physical Tolerances and Abiotic Constraints

Once a species arrives at a site, either by unaided dispersal or restoration efforts, environmental conditions (soils, disturbances, climate) can affect establishment and persistence via habitat filtering. Often restoration is challenged by soils and hydrology that have been severely altered by human impacts to such an extent that they may no longer be able to support native communities. For instance, restoration where mining has removed topsoil must address abiotic conditions vastly different than the pre-degradation baseline (Klimkowska et al. 2010). These strong changes to site conditions often need to be addressed prior to the addition of propagules or other management to enhance biotic interactions (e.g., adding herbivores). In some cases, habitat degradation may be so severe that restoration of a preexisting community is not possible and so remediation may be an option. When a system does not follow the expected restoration trajectory, it may be due to larger abiotic site constraints than expected at the onset of the project.

The disturbance regime at a site can be an important abiotic filter. Restoration has a long history of reestablishing historic disturbance regimes (e.g., prescribed burning) or substituting one type of disturbance for another to mimic historical effects (e.g., grazing for fire). Interactions between the current disturbance regime and biotic components of the system can form feedbacks that constrain a restoration effort. For instance, reintroducing fire to a grassland after woody species have invaded may not be sufficient to convert the shrubby woodland back to a grassland, even though this fire regime would maintain a grassland once the invaders are removed (Brudvig and Asbjornsen 2007; Twidwell et al. 2013). Also, the same disturbance type may have different effects depending on site conditions.

Climate is an important, oft neglected, abiotic constraint on restoration. Directional changes, or increased variability, in temperature or precipitation may make reestablishment of a historical native system challenging (chap. 17). For instance, Carr et al (2012) found that extant eelgrass meadows are likely to tolerate sea level rise, but that an increase in the frequency of warm days in the summer will cause more frequent die-offs. The increased frequency of die-offs will both affect the success of restoration but also change the expected dynamics of the system, moving it toward a system that supports alternative states with hysteresis. Climate shifts have similarly been shown to cause threshold dynamics between grassland and savanna (Favier et al. 2012). It is only with detailed knowledge about how climate affects abiotic tolerance that models can forecast how dynamics change over time.

Species Interactions and Biotic Constraints

In many systems, restoration planning needs to consider how different biotic components of the system interact with one another (Gomez-Aparicio 2009; Metlen et al. 2013). A number of studies have shown that competition with and predation by other species can constrain or promote the recovery of a target species. For example, control of invasive species may be necessary to increase the establishment of native species, but the success of management interventions (fire, mowing, etc.) to control invasive species in restoration varies (Kettenring and Adams 2011). Although some work has shown that increasing the functional diversity of restoration plantings can increase resistance of restored communities to invasions; in other cases there can be little or no effect (Ammondt and Litton 2012; Cleland et al. 2013).

As described in chapter 11, changes in trophic-level interactions, requiring the removal or additions of predators, pathogens, or prey, may be necessary for a successful restoration (Chase 2003; Daskalov et al. 2007; Tanentzap et al. 2011). For example, browsing by deer slows recovery of woody species in riparian systems because they feed selectively on regenerating saplings (Hidding et al. 2013). In overgrazed rangelands, cattle can reduce herbaceous plant cover and produce positive feedbacks that contribute to the collapse of the rangeland system to desert (Van Auken 2000; Kefi et al. 2007). It may also be necessary to modify trophic pathways such as grazing and predation to promote the establishment and distribution of desired species. For example, the expansion of aspen populations in Yellowstone National Park is thought to occur in part due to a redistribution of elk that results from increasing gray wolf populations within the park (Painter et al. 2015). Manipulating food webs to restore species can, however, be quite problematic as exemplified by the impact Asian carp have had on native fisheries in lakes and rivers (Carlson and Vondrachek 2014). In the 1970s and 1980s, several species of carp were introduced in the United States to restore water quality by controlling nuisance algae but they quickly grew in population size, became widely distributed and led to the decline of many native species.

Biotic interactions may be particularly important to understanding how hysteresis dynamics can influence restoration trajectories, as priority effects can create cases where initial conditions are strong determinants of population growth and community composition. Hysteresis may be particularly likely where intransitive networks (e.g., $A > B$, and $B > C$ but $C > A$) occur among interacting species, stage classes, or functional groups (Chase 2003). For example, a short-term reduction in size-selective predation may allow prey to grow to a size where they are no longer vulnerable to predation. These larger individuals can create hysteresis dynamics, and may even prey upon the species that are predators to smaller size classes (Paine and Trimble 2004). *Intraguild predation* (Persson et al. 2007; Filbee-Dexter and Scheibling 2014) can occur where the competitively inferior species can prey upon juveniles of the competitive dominant. Similarly, competitive asymmetries (D'Antonio et al. 2001; Cameron et al. 2007; Lankau et al. 2011; Hidding et al. 2013) can occur where rankings of recruitment ability differ from adult competitive rankings, resulting in hysteresis dynamics if a disturbance reduces the competitive dominant. Interaction networks that have the potential to change from top-down (controlled by predation) to bottom-up (controlled by resource competition) control can also cause similar feedback switches (Schmitz et al. 2006; Hewitt and Thrush 2010). In all these cases, a perturbation that changes the nature of species interactions will prevent or constrain a restoration for a long time.

Biotic Feedbacks

Biotic feedbacks, where changes in the environment or disturbance regime increase the abundance or fitness of the modifying organism, which would lead to further modification of the environment, can either constrain or promote a restoration (Suding et al. 2004; Scheffer et al. 2005; Nystrom et al. 2012). Stabilizing feedbacks reduce a species advantage when abundant and can lead to coexistence and mixing of different types of organisms. In contrast, positive or self-reinforcing feedback is a signature of hysteresis and the development of alternative states. Thus, knowing the capacity for a system to maintain self-reinforcing or stabilizing feedbacks could be a very fruitful way to identify those likely to exhibit hysteresis threshold dynamics or not.

Species can modify many aspects of their environment that can create feedbacks. For instance, the nature and density of vegetation establishment in riparian zones can alter flow patterns in river systems, leading to geomorphic changes over time (Wohl et al. 2015). Similarly, the loss of vegetation or replacement by nonnative plants can change river hydrology and increase sediment inputs into a river channel, effects that then can reduce native plant recruitment (Gonzalez et al. 2015). Research is also associating the capacity for feedback effects with invasive species that are able to invade and dominate a system due to their ecosystem effects (Ehrenfeld 2003; Bennett et al. 2011). An open question remains as to how many of these self-reinforcing feedbacks are persistent and strong enough for the formation of alternative states (Diez et al. 2010; Yelenik and D'Antonio 2013). For instance, Yelenik and D'Antonio (2013) showed that strong self-reinforcing feedbacks related to the invasion of an exotic grass in Hawaiian woodlands weakened over many decades, with soil nitrogen levels falling to pre-invasion levels.

Ecological Resilience and Restoration

First introduced by C.S. Holling (1973) as a measure of a system's ability to absorb disturbance, the concept of *resilience* has since evolved to encompass the ability of a system to persist and adapt over time and under changing conditions (Gunderson 2000; Carpenter et al. 2001). Resilience is particularly critical in systems governed by hysteresis and threshold dynamics, as it determines the ability of a system to return to its structure and function and not transition to an alternative state (Standish et al. 2014; Dakos et al. 2015). Resilience can be both a desirable aspect of ecosystems, or it may hinder efforts to restore (Suding 2011). While the science that determines system resilience is still evolving, case studies are providing clues to the system attributes that can contribute to resilience, as well as how managers can incorporate these attributes into restoration activities (Beller et al. 2015).

In recent years, increasing focus has been given to the role of ecological resilience in ecosystem management and restoration. In particular, landscape factors such as connectivity, response diversity, and functional redundancy appear to be particularly important when managing for resilience (Peterson et al. 1998; Elmqvist et al. 2003; Peters et al. 2004; Folke et al. 2004; Standish et al. 2014). As ecosystems face unpredictable and unprecedented environmental stressors in the coming decades, resilience has emerged as a powerful framework for guiding management.

Anthropogenic impacts such as habitat loss and fragmentation, losses and shifts in functional groups, and the suppression or alteration of biological and physical processes can all contribute to the decreases in resilience. Increasing evidence indicates that humans influence ecosystem resilience by altering the system's capacity to cope with disturbance (Standish et al. 2014). These activities may erode a system to a state where it is no longer able to be restored, or where the efforts to do so are too expensive or time consuming to be justified (fig. 2-3).

For example, managers are often faced with situations where functional groups have either been lost (e.g., overexploitation of top predators by overfishing) or gained (e.g., introduction of exotic N-fixing plants). As functional group abundance shifts, the feedbacks associated with maintaining different community types may also shift, compromising the ability of the system to absorb disturbance without sacrificing function (DeAngelis 2012). In desert stream systems, the density of wetland vegetation increased the likelihood that a wetland would maintain its form and function following major flood events. However, if vegetation cover fell below a critical threshold, the system shifted to an unvegetated state following flood events (Heffernan 2008). These types of feedbacks are crucial for recovery in systems characterized by threshold dynamics.

An important first step in managing for ecological resilience is to assess characteristics of the ecosystem that limit recovery. This approach focuses on ecological processes, native biodiversity, and the adaptive capacity over time and at large scales, rather than solely on species composition or geophysical targets (Zavaleta and Chapin 2010). Resilience can be assessed by evaluating the capacity of system attributes to recover in response to changes such as increased frequency of extreme events, changes in freshwater flows, changes in habitat connectivity, sea level rise, habitat loss due to urbanization, or invasive species. The specific ecological processes and environmental stressors are context-specific, and those of greatest relevance are therefore determined on a case-by-case basis. Ecosystem-specific efforts to identify the relationship between processes and threats will be critical for developing effective restoration approaches (Chazdon 2008; Rogers et al. 2015) and should consider not just the current ecosystem, but also past conditions and future projections (Jackson and Hobbs 2009). Ecological theory and its empirical tests provide a roadmap and point of reference for assessing how best to manage for system resilience (Holling 2001).

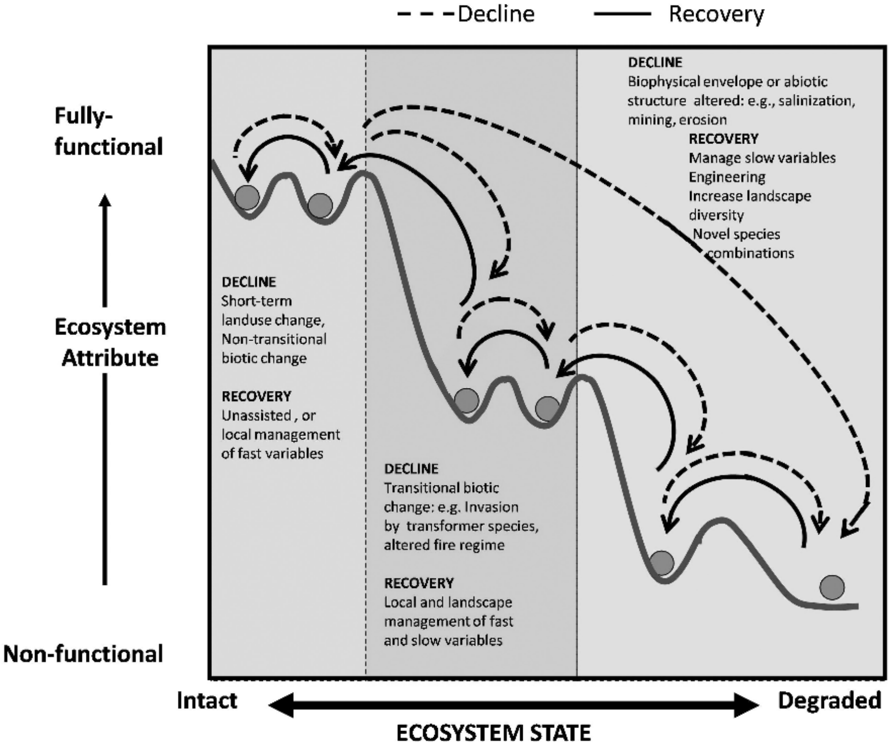

Figure 2-3. Conceptual diagram illustrating the general pathways of decline and recovery of ecosystems in relation to how desirable they are (state) and level of function (which can be specified in relation to particular system attributes or management goals). In areas with minimal degradation (blue), decline is minimal and management aims to maintain resilience. In areas with more extensive impacts (green), decline is profound and management aims to overcome resilience. In the middle are intermediate states where management may either aim to overcome resilience to push the system back to a less degraded state, or may aim to maintain resilience to prevent further decline. From Standish et al. (2014), based on diagrams originally formulated by Whisenant (1999) and Hobbs and Harris (2001).

The question then becomes How can we apply our knowledge of ecosystem dynamics to manage for ecological resilience? Are there opportunities to bolster resilience through restoration activities? In extending restoration to resilience, a primary challenge is that while the concept of resilience has widespread appeal, the mechanisms contributing to it are not yet well understood, and methods for measuring it are also still largely uncertain (Folke 2006). Methods of dealing with uncertainty are important tools for planning future actions (Polasky et al. 2011), and Bayesian models hold promise for modeling both ecological (Stewart-Koster et al. 2010) and socioecological (Jellinek et al. 2014; Hermoso et al. 2012) aspects of restoration. Guiding recovery in degraded systems will ultimately require a greater integration of statistical techniques that aim to assess the costs and benefits of actions in uncertain systems using active management scenarios. Ideally, these models will be used alongside frameworks that synthesize core system attributes that contribute to the resilience of ecological processes at a landscape scale for application in restoration and management (Beller et al. 2015).

Adaptively managed projects, where research is integrated into the decision-making framework, are a promising avenue for operationalizing resilience. This integration requires clear management objectives, a solid understanding of ecosystem processes of the focal system, and consideration of social and environmental drivers (Anthony et al. 2015). Ideally, adaptively managed projects that have a goal related to resilience should consider a combined strategy of active risk reduction and building resilience via management intervention. Risk reduction would entail trying to reduce the occurrence of key pulse-type stressors such as a pollution event, catastrophic fire, or overharvesting. Management interventions can be employed to additionally build resilience to reduce the vulnerability as the system changes due to press-type stressors (e.g., climate warming). For instance, this intervention could entail management focus on functional diversity or landscape corridors for dispersal.

Closing Remarks

Managers rarely have the luxury of time to conduct research needed to determine if a system targeted for restoration will recover via a successional trajectory, exhibit thresholds, or hysteresis dynamics. As a result, management decisions have to be made based on limited knowledge, and past experience. While it may be less expensive to assume that a system will be restored through “natural processes” or with minimal intervention, it also may be risky because no action may miss crucial opportunities to redirect or accelerate the successional processes to a desired community. On the other hand, there is danger in assuming that a system undergoing restoration that appears to have “stalled” has reached a threshold. Management activities targeted to overcome thresholds can be expensive and can lead to unexpected and sometimes negative consequences (Holl and Aide 2011). Changes in the environmental baseline via climate change adds an additional layer of complexity to decision making, as these changes can affect the type of recovery dynamics and the trajectory a system may follow.

One expectation is that managers, even though they might have a good understanding of past dynamics, may be highly uncertain of future dynamics. New or previously unidentified constraints may prove critical to future dynamics. A best management practice may be to set restoration goals that take into account current knowledge about the system as well as decision-making trigger points—criteria related to the management goals that would trigger a reassessment of approach and strategy as the restoration progresses. Incorporating trigger points into the management plan for a restoration would specify conditions that would allow managers to more effectively deal with the uncertainty inherent to restoration.

The challenge to land managers is to develop restoration plans that will move a system toward a desired state but this may become increasingly difficult given increasing climate variability (Harris et al. 2006; Stralberg et al. 2011). To use an analogy from *Through the Looking Glass* (Carroll 1871), restoration plans may require intervention to keep a system in the same place: "Now, here, you see, it takes all the running you can do, to keep in the same place. If you want to get somewhere else, you must run at least twice as fast as that!" In addition, it may not be useful, or appropriate, to use historic ranges of climatic variation in restoration planning since these conditions are now changing (Balaguer et al. 2014). Clearly articulating the goals of a restoration project, and being able to identify when these are met (or nearly so) will become increasingly important. Likely the best strategy will be to combine several tools to better identify and anticipate dynamics: a focus on understanding the dynamics and recovery of key processes that promote establishment of native species and other desired outcomes; the use of reference sites to guide management decisions and practices; and the use of models to forecast effects into the future.

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Chapter 3

Biodiversity as a Goal and Driver of Restoration

Shahid Naeem

Theory and Application

- Biodiversity is multidimensional, ergo its measure should be multidimensional; otherwise restoration targets may not be reached.
- Most species are rare and common species can be surprisingly vulnerable, so restoration must battle against a natural tendency for species to become rare.
- Restoring complementary species means maximizing ecosystem efficiency and stability, while restoring dominant species may mean more ecosystem functioning and services, but it's not likely to be stable.
- Trait-based ecological theories are valuable alternatives to population-based theories in restoration because traits are easier to quantify than population parameters, but prepare to immerse one's self in multivariate statistical and computational methods.

The diversity of life on Earth, which is the engine of ecosystem functions and the ecosystem services they provide, is the product of a long list of evolutionary and ecological processes that are mostly hidden to the casual observer. A useful and popular analogy for explaining what biodiversity is asks us to imagine looking down at a pond and seeing a variety of bubbles breaking the surface; some bubbles are small, some big, some aggregated with others, and some isolated. We then have to determine what went on under the surface to generate the pattern in bubble distribution and abundance. The bubbles that originated in the sediment probably underwent a considerable amount of change before coming to the surface—some bubbles fused with others, some underwent fission, some got trapped and never reached the surface, some drifted outside our field of view, and some originated elsewhere and drifted into our field of view.

When we look at a biological community and want to determine what pro-

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cesses are responsible for its patterns in distribution and abundance, we are looking at a collection of plant, animal, and microbial species that, like bubbles, are the endpoint of many underlying processes. This long list of processes includes origination, diversification, extinction, emigration, immigration and abiotic processes such geological events like glaciation and continental drift, biogeochemical changes in nutrient cycling, naturally occurring climate change, and more, all of which had their effects over enormous spatial ($10–10^3$ km^2) and temporal scales ($10^2–10^6$ y). Shorter-term and smaller-scale processes on the list include disturbance (e.g., drought, flood, and fire), naturally occurring biological invasion, emigration and biotic interactions (e.g., predation, facilitation, competition) that further modify biological diversity. This list of processes may seem daunting, but they are the means by which we can make sense of, and ultimately manage the extraordinary diversity of life that characterizes well-functioning ecosystems.

These processes primarily involve changes in biodiversity and ecosystem function. Every organism, from a single bacterium to blue whale, influences ecosystem functions through their metabolic processes, thus any change in the distribution and abundance of individuals, populations, or species have concomitant changes in ecosystem functions—some negligible, some huge, but change in biodiversity and ecosystem functions is inevitable. Thus, the simple theoretical construct that biodiversity and ecosystem functions are linked provides a powerful way to organize or frame our thinking about the long list of processes, natural and anthropic, that shape the modern world we live in. Figure 3-1 illustrates this framework, dividing the modern or Anthropocene landscape into habitats whose functions and services reflect different states in a relatively dynamic process of constant transition. The view of biodiversity as species of plants, animals, and microorganisms found in a habitat, makes figure 3-1 puzzling, which then makes theories about biodiversity and ecosystem functioning seem unrelated to issues such as mass extinction and species conservation. We will examine this issue in the next section.

This chapter considers several theoretical constructs that are useful in ecological restoration where the objective or target includes restoring either biodiversity or ecosystem function, or both. There are many theoretical constructs that provide valuable insights into biodiversity as it relates to restoration, but five constructs currently play important roles in contemporary restoration ecology (table 3-1). These constructs were selected because they illustrate that there is pattern in the distribution and abundance of species as well as patterns in the way biodiversity and ecosystem function are related. Understanding these patterns, what generates them, and how to translate them into restoration practice can be incredibly empowering to restoration practitioners just as they are to ecological researchers and conservationists. This is particularly important given that for many types of ecosystems the most common measure of restoration success being applied today is biodiversity (Wortley et al. 2013; Palmer et al. 2014).

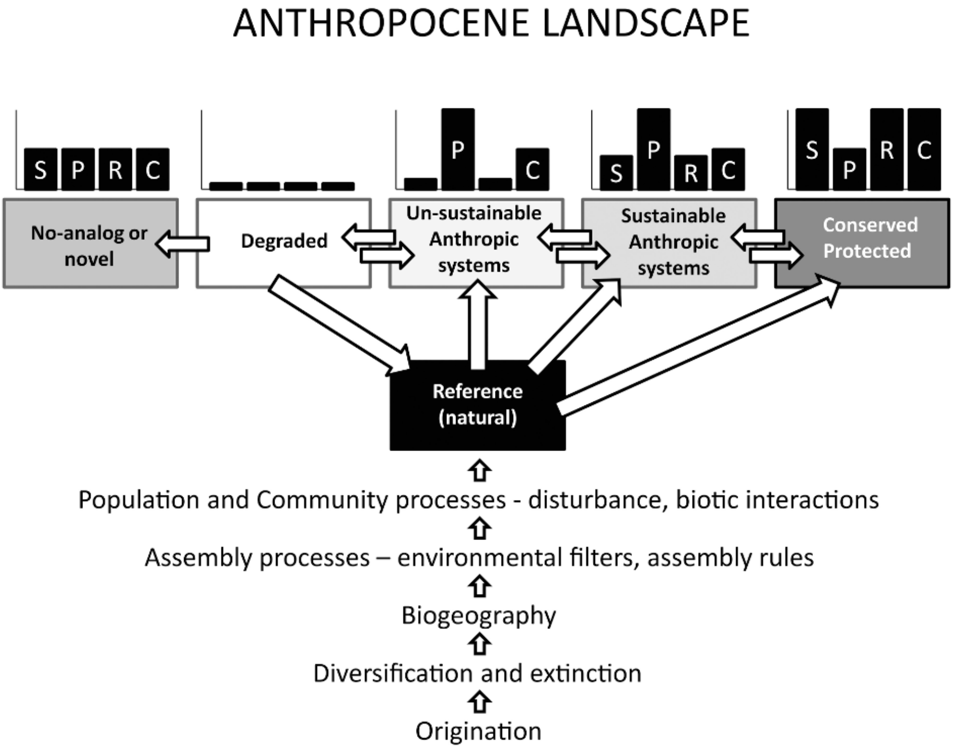

Figure 3-1. Biodiversity, ecosystem functioning, and ecosystem services in the Anthropocene. This figure synthesizes and updates several related BEF frameworks (e.g., Duraiappah and Naeem 2005; Naeem et al. 2009; Cardinale et al. 2012; Mace et al. 2012; Naeem et al. 2012; Laughlin 2014). The Anthropocene landscape can be divided into five land use / land cover types, or ecosystem types, which range from degraded to natural or reference ecosystems where human interventions or disturbances are minimal. Arrows indicate outcomes of human interventions or disturbances. Anthropic systems are managed systems that are unsustainable (e.g., high input agriculture that require constant inputs or unsustainably harvested fisheries), or sustainable (e.g., sustainable agroforestry). No-analog or novel systems consist of species combinations and often environmental conditions that have no historical analogs. “Re-wilded” (using modern species to replace extinct species) and highly engineered systems (such as bioreactors), would fall into this category. Arrows indicate actions undertaken to influence biodiversity and ecosystem functioning. Gray scale indicates level of diversity and ecosystem functioning, both magnitude and stability, with black as the highest value and white the lowest. The bar graph at the top of each landscape type represents the four primary classes of ecosystem services, where S = sustaining or supporting; P = provisioning; R = regulating; and C = cultural (Duraiappah and Naeem 2005). For clarity, the bar graph has been left out for the reference landscape type but would be similar to that shown above conserved habitats. Note that anthropic systems shift relative service deliveries to provisioning at the expense of other services. In this volume, restoration is represented by the arrow that indicates human activities that shift biological assemblages and biophysical properties of degraded systems to self-sustaining assemblages and properties characteristic of their reference systems.

TABLE 3-1.

The relevance of biodiversity and ecosystem function (BEF) theories to restoration. Factors that influence biodiversity as well as the influence that biodiversity has on other ecological processes have been extensively studied and many theories proposed that lead to predictions such as the examples listed below. The remainder of the book provides a rich array of additional examples.

Theoretical Prediction from Theories on Biodiversity	Relevance to Restoration	Restoration Study Example
BIODIVERSITY DRIVERS, including spatial heterogeneity and disturbance.	Local biodiversity is determined by abiotic and biotic factors.	See examples of specific drivers below.
Abiotic drivers: Spatial heterogeneity reduces local extinction via source-sink dynamics.	Increasing physical habitat heterogeneity may facilitate the recovery of biodiversity.	Hovick et al. (2014): grassland bird diversity was positively associated with spatial heterogeneity generated by fire and grazing.
Abiotic drivers: Intermediate disturbance facilitates biodiversity.	Facilitates coexistence by preventing exclusion by dominants.	Nyafwono et al. (2014): butterfly diversity peaked at intermediate forest disturbance, Uganda tropical forest.
Biotic drivers: Recruitment limitation constrains recolonization.	Maximize access to regional species pool, but not exotics.	De hert et al. (2013): seeds limited target orchid in Belgian dune slacks.
Biotic drivers: Invasion resistance is affected by changes in diversity.	Increased diversity can improve resistance to biological invasions.	Oakley and Knox (2013): diverse grassland plots had fewer invaders.
COMMONNESS AND RARITY: The relative abundance of species is often log-normal or log-normal-like.	Often (>80%) species are rare; restorationists may need to battle tendencies toward dominance.	Halpern et al. (2014): rank-abundance of grassland spp. differed × restoration practices.
The Extinction Debt: Colonizer-competition trade-offs in spatially heterogeneous habitats can lead to extinction of even dominant species.	Dominant species are often poorer dispersers than subordinates; in a fragmented habitat, they may be extinction-prone (species can persist, but will go extinct eventually).	Highland and Jones (2014); Haag and Williams (2014): montane meadow moths and freshwater mussels face eventual extinction in the face of excessive fragmentation and isolation.

Table 3-1. *continued*

Theoretical Prediction from Theories on Biodiversity	Relevance to Restoration	Restoration Study Example
TRAIT-BASED ECOLOGY: life history characteristics, morphology, behavior, metabolic rates govern how species respond to environmental change.	Traits of species can be more useful in restoration than taxonomic or population characteristics.	See examples below.
Niche theory: species relative distributions and abundances are governed by local adaptation to, interaction with, function in, impact on, and response to the environment.	Niche-based models may be useful.	Visser et al. (2013): niche-based climate models helped develop conservation, restoration, and management plans for Louisiana's wetlands × climate change.
The response-effect framework attributes species' influences or effects on ecosystem functions (although telling them apart is hard).	Key traits govern how a species responds to or affects environmental factors. Even a small number of traits requires computational resources.	Laughlin (2014) uses this and other trait-based frameworks in restoration and discusses software tools.
BIODIVERSITY AND ECOSYSTEM FUNCTION (BEF)	Biological diversity is important to restoration targets.	See examples below.
Complementarity vs. selection vs. identity effects: which species complement each other; which have selective or dominant impacts, and what are their unique contributions?	When possible, restore using species that have strong impacts on and/or unique impacts on ecosystem functions.	Devoto et al. (2012): simulated pollinator networks and predicted significant effects of manipulating pollinator complementarity on plant diversity restoration.
Statistical averaging = Portfolio Effects, and CV Stability: the CV of an aggregation of functions of spp. will always decline if the no. of species increases.	Restoration can benefit high levels of diversity which helps insure returns on ecosystem services. Any dimension of diversity can be applied.	Schindler et al. (2010) and Carlson et al. (2011): salmon population diversity stabilizes salmon runs.

Biodiversity as a Multidimensional Construct

Biodiversity is a slippery term and there is no one, universally accepted definition, though the Convention on Biological Diversity's (CBD's) definition, in its uncontracted form (i.e., *biological diversity*), is often used. Therefore, biological diversity is:

> the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems (Secretariat of the Convention on Biological Diversity 2001).

As there are 194 parties to the CBD, from an operational point of view, this definition at least offers widespread international subscription even if it is not traceable to any theoretical or empirical exercise and is scientifically somewhat enigmatic. Importantly, the CBD's definition is inherently multidimensional—that is, the CBD does not see biodiversity as just one thing, such as species richness. Biodiversity is clearly understood to be a term meant to capture biological diversity in all its dimensions including genetic, population, functional, taxonomic, phylogenetic, and interaction or network diversity as well as how they vary within and among populations, assemblages, communities, and ecosystems, over space and time (table 3-2).

Though biodiversity is clearly a multidimensional construct, restoration science, like much of ecology, often fails to treat biodiversity as such. Brudvig (2011), in a review of 190 restoration studies, found that 88% of the studies focused on taxonomic diversity and only 11% on functional and 0.5% on genetic diversity. Only 6% considered spatial factors like patchiness and other landscape-level factors, and only 0.5% considered assembly order and other historical factors.

The primary reason the multidimensionality of biodiversity matters is that the magnitude and stability of populations, functions, and services can all change if any dimension changes. Biodiversity represents the location of a species assemblage in multidimensional space (fig. 3-2). A degraded habitat, for example, from the standpoint of biodiversity, is one that has declined not just in taxonomic diversity (e.g., number of species), but in functional, phylogenetic and many other dimensions of biodiversity. When community composition changes, the shift is unlikely to be constrained to one dimension, which means that changes in ecosystem functions and services will not be unidimensional either. This multidimensional construct may seem abstract, but it can be readily translated into application. Each dimension quantifies relatively distinct properties of a biota and has different methods for its quantification (table 3-2). Hipp et al. (2015), although focused on phylogenetic diversity, urge researchers and practitioners in restoration

Table 3-2.

Dimensions of biodiversity and restoration implications. Note that indices commonly used to quantify each dimension are treated in Magurran et al. (2011).

Dimension	Unit	Description	Low Diversity	High Diversity	Reference	Implications for Restoration
Taxonomic	Species	Hierarchical clustering of organisms into unique groups such as species, genera, families, and orders.	Fewer species with most being rare.	More species with relatively even distributions.	Magurran 2013	Often the most available and popular dimension of biodiversity, most restoration projects and policies focus on this dimension of biodiversity (e.g., species richness or common diversity indices such as Shannon or Simpson) (see Magurran 2013 for a comparison of taxonomic diversity to other forms of diversity).
Functional	Trait	The distribution of trait values among organisms within an assemblage where *trait* is any property of a species that impacts ecosystem function or responds to environmental change.	All species have similar modal trait values across all traits.	Greater dispersion among species' trait modes with low overlap across all traits.	Schleuter et al. 2010	Although much harder to quantify, the diversity of traits in a species assemblage is more informative about ecosystem functions and properties than taxonomic diversity. This feature makes functional diversity potentially more useful for meeting restoration targets (see Laughlin 2014 for examples).

Table 3-2. *continued*

Dimension	Unit	Description	Low Diversity	High Diversity	Reference	Implications for Restoration
Phylogenetic	Branch or edge	The history of evolutionary descent among species. *Branch* or *edge* refers to a phylogenetic tree that plots time between species and their recent ancestral species.	Species closely related with short evolutionary history among them.	Species distant from each other with considerable evolutionary history among them.	Winter et al. 2013; Hipp et al. 2015	Phylogeny, though often constructed using molecular or genomic data rather than trait data, ultimately reflect ecological differences among species that led to their evolutionary divergence. What the actual ecological differences are, however, may be unknown and may not be readily deduced from genomic data. Nevertheless, it is fair to argue that phylogenetically similar species will have similar genomes, and if genomes do, in fact, map species traits, one can infer that phylogenetically similar species may have similar responses to and effects on the environment. Thus, in the absence of trait data that is necessary to estimate functional diversity, a phylogenetic diversity may serve as a proxy (see Cadotte et al. 2008; Flynn et al. 2011 for further detail).
Genetic	Gene	Degree of similarity in genetic makeup of individuals. Currently most often based on DNA sequence similarity of genes or other genome-derived information.	High degree of genetic homogeneity among individuals.	High degree of genetic heterogeneity among individuals.	Leffler et al. 2012; Kettenring et al. 2014; Hipp et al. 2015	Although often not readily visible like many traits, or directly related to an individual's responses to or impacts on environment, ecological variability and robustness within a population is often related to genetic variability. For example, a small number of genetically variable species may have stronger influences on ecosystem functions than a large number of genetically homogeneous species (see example by Latta et al. 2011). For restoration, this means knowing or at least ensuring genetically healthy populations (which can be quantified by molecular methods) may be as important, or more, than taxonomic richness.

Table 3-2. *continued*

Dimension	Unit	Description	Low Diversity	High Diversity	Reference	Implications for Restoration
Population	Population	Among individuals, genotypic and phenotypic diversity varies. Generally measured as among-individual trait and genetic variability within and among populations.	High degree of genotypic and phenotypic homogeneity among individuals within and among populations.	High degree of genetic and phenotypic variability among individuals within and among populations.	Forsman and Wennersten 2015	In the same way that genetic and functional diversity among species can improve system functional robustness, optimizing population diversity can lead to more durable restoration outcomes. For example, Engelhardt et al. (2014) examined genotypic and phenotypic variability in the aquatic macrophyte, *Vallisneria americana*. They found that restoration benefits from maximizing genetic diversity within populations, matching phenotypes of source populations to the local habitat being restored, and selecting phenotypic plasticity that best suits short- and long-term environmental variability.
Network	Link or edge between nodes.	Web of biotic interactions among species, often portrayed as a network in which species are *nodes* and biotic interactions are *links* or *edges*.	Few nodes in a linear chain.	Many nodes that are maximally connected.	Tylianakis et al. 2010	Increasing diversity within a single trophic group while holding other trophic groups constant, such as increasing plant diversity while fencing out herbivores, may have predictable outcomes (e.g., improved productivity and resilience), but if other trophic levels are not held constant, outcomes will be a function of intertrophic interactions, not just species richness (see Cardinale et al. 2011). Thus, ecosystem function is affected by network architecture, not just numbers of trophic groups or species per trophic group (see Pocock et al. and Devoto et al. 2012 for examples).

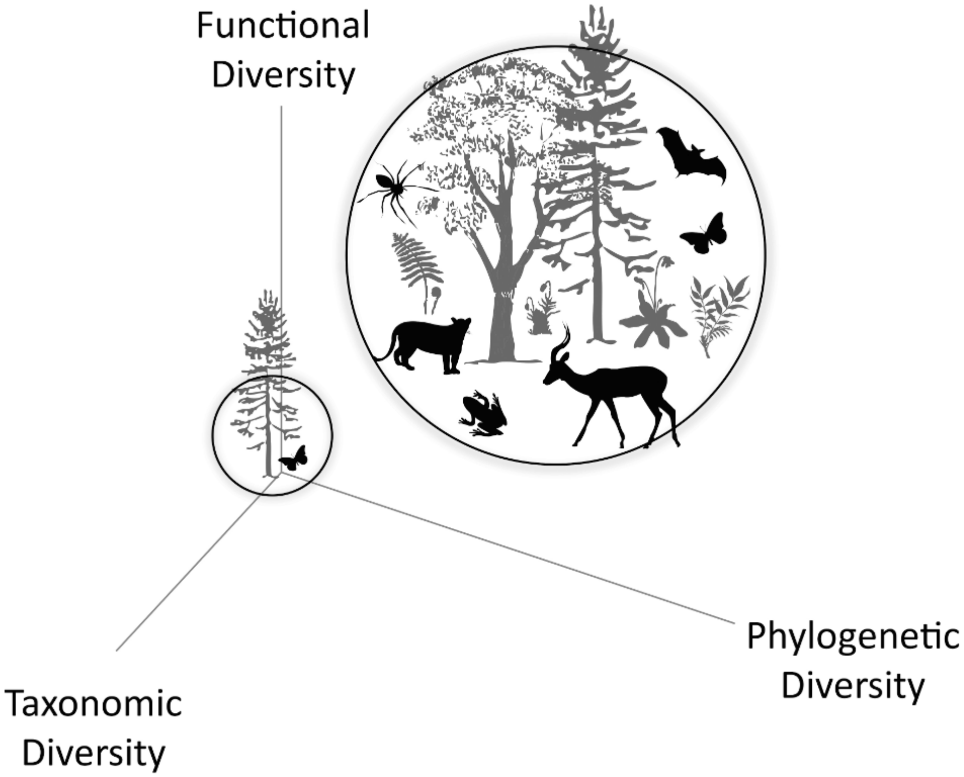

Figure 3-2. The multidimensionality of biodiversity.

Each species in an assemblage is located in a multidimensional space in which each axis describes a different way in which species relate to one another. Shown here are just three dimensions for an assemblage of species that might be typical for a forest. At the origin is an abandoned pine plantation. Out to the corner most distant from the origin is a restoration target. The target represents increases in multiple dimension of biodiversity. This heuristic portrayal of multiple dimensions of biodiversity treats the dimensions as orthogonal, but correlations among measures of taxonomic, functional, and phylogenetic diversity suggest that the number of truly orthogonal biodiversity dimensions is fewer than the number of different ways we measure diversity.

to consider other dimensions of biodiversity, how different dimensions are related to one another, and build and provide tools that make working with more than just taxonomic diversity feasible.

One might seek to develop a method that combines multiple dimensions into one measure (e.g., Leinster and Cobbold 2011), but there is greater utility in using multivariate statistical methods. For example, in experimental studies of the influence of biodiversity in ecosystem functioning, multivariate methods revealed that phylogenetic diversity was a better predictor of ecosystem functioning than taxonomic or functional diversity (Cadotte et al. 2008), though it depends on what traits are used when quantifying functional diversity (Flynn et al. 2011). Particularly promising is Flynn et al.'s (2011) use of structural equation modeling (SEM), a statistical framework for testing complex models of causality (Shipley 2001; Arhonditsis et al. 2006; Grace et al. 2012). One value of an SEM approach is that it provides a graphical view of the complex hypothesis under investigation; particularly useful for considering how multiple dimensions of biodiversity relate to ecosystem functions, properties, or services. Figure 3-3 provides an SEM framework, which expands Flynn et al.'s (2011) study to include most of the common dimensions of biodiversity and illustrates how the abstract construct of multiple dimensions of biodiversity can be used in statistically driven research. Alternatively, many of the metrics of biodiversity correlate with one another so the operational dimensionality may be reduced to a smaller set of complex dimensions (Stevens and Gavilanez 2015), though the downside to such an approach is that complex dimensions are less tractable in practice.

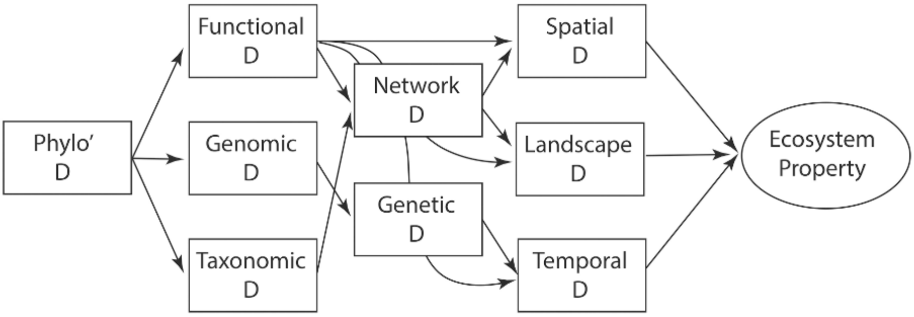

Figure 3-3. Multiple dimensions of biodiversity from a structural equation modeling (SEM) perspective.

This figure presents an SEM approach for relating nine dimensions of biodiversity to an ecosystem property, which could be a function (e.g., production), service (e.g., erosion prevention), or dynamic property (e.g., resistance to invasion or the coefficient of variation of an ecosystem function). Currently, as in Flynn et al. (2011), most studies conduct analyses with only two or three dimensions, thus SEM models are more simple than what is illustrated here. One would expand or shrink the SEM model according to the number of biodiversity dimensions available. Arrows represent hypothetical causal pathways that are similar to paths in path analyses. In this model, for example, phylogenetic diversity is treated as a factor that influences functional, genomic, and taxonomic diversity. Functional diversity is considered to further influence network (e.g., trophic traits determine), spatial (e.g., range or extent), and landscape (habitat and ecosystem preference traits) diversity. Genomic diversity, in contrast, is considered to primarily influence genetic diversity. Researchers are likely to build different models depending on species, systems, and available data. Abbreviations: D=diversity, Phylo'=phylogenetic.

Ecological Controls of Biodiversity

Biodiversity often appears to be an unregulated, loose conglomerate of species in a tangled web of interactions with little that controls the distribution and abundance of species. As described earlier, in the preceding chapters and at the outset of this chapter, biodiversity is controlled by many processes (see also fig. 3-1). We use the word *controlled* to denote the nonrandom nature of biodiversity. One could use *regulate*, *determine*, or *govern*, and often these terms are used instead of *control*, but whichever term one uses, the point being made is that biodiversity is nonrandom, meaning that it is predictable, and the underlying mechanisms are the long list of processes described earlier. The challenge for the restoration ecologist is to identify which factors are most important and how those factors may respond to management actions.

The following chapters cover many of the theoretical constructs concerning ecological controls of biodiversity important to restoration ecology including for example ecophysiological constraints (chap. 6), species and trophic interactions (chaps. 9, 11), nutrient availability (chaps. 12, 13), and environmental heterogeneity (chap. 10). But with respect to biodiversity, and in particular its relationship to ecosystem function, two additional constructs are worth considering briefly.

Commonness and Rarity—A Fundamental Pattern

One of the best known, yet still enigmatic features of nature, is the tendency for most species to be rare; something restorationists might have to battle against if the restoration area of the project is small in comparison to the original extent of the ecosystem. The longer one explores, the more diversity one finds, though with diminishing returns. This may not, at first glance, seem profound, until we add (with a little bit of exaggeration) that the declining rate of discovery per unit effort is highly predictable for all taxa in all habitats. While the observation is widely attributed to Alexander von Humboldt, the famous eighteenth century explorer, it was Frank W. Preston's (1962) mathematical treatment of the phenomenon that galvanized ecological attention to the issue. Preston argued that if nature were random, then one would not expect the variance and mean of the lognormal distribution fitted to his data to show a constant, predictable (canonical) relationship. It turned out nature did follow a canonical lognormal distribution which meant that commonness and rarity were not random, though why this was so, Preston could only speculate and he invoked competition for limiting resources. Since then, many theoretical luminaries in ecology have taken a turn at trying to explain this inexplicable predictability of commonness and rarity (e.g., MacArthur

1960; MacArthur and Wilson 1967; May 1975; Sugihara 1980; Hubbell 2001; Rosenzweig 2003).

The upshot of the prevalence of a commonness-rarity relationship in which a few species are common and the rest are rare is that restorationists should measure relative abundance and periodically use curve fitting methods (e.g., Wilson 1991; Tjørve 2003; Rosindell et al. 2011) to monitor how restored communities are changing. There are two reasons for doing this. First, systems will invariably shift away from highly even distributions of species which means having to work harder to meet diversity goals since only a few species will be dominant and most will become rare and vulnerable, unless the goals focus on just a few dominant species. Second, ecosystem functioning is sensitive to which species dominate, so if there are ecosystem function targets, one will have to monitor commonness and rarity to be certain that dominant species stay dominant. If rare species are targets of restoration (e.g., Ehrenfeld 2000; Thorpe and Stanley 2011) or important for target ecosystem functions (e.g., Lyons et al. 2005; Mouillot et al. 2013) then the challenges are greater. Though it depends on how one defines rarity (Jain et al. 2014), often obtaining sufficient stock for projects, battling the natural tendency for evenness to shift toward dominance, the absence of rare species in seedbanks (e.g., Bakker and Berendse 1999), and the higher vulnerability of rare species populations to genetic impoverishment (Weeks et al. 2011) make restoring rare species more difficult than restoring dominants. Given that one of the few rules of nature that has withstood the test of time is that the majority of species are rare, knowing the commonness–rarity curve for a community is far more valuable than species lists for establishing realistic objectives.

The Extinction Debt

The metacommunity construct mostly provides means for coexistence among species that will lead to greater biodiversity across patches than one would predict under the assumption of environmental heterogeneity, though it does much more (Leibold et al. 2004). Mouquet and Loreau (2003) expanded metacommunity theory to describe not just patterns in distribution and abundance, but also impacts on ecosystem functions and patterns of distributions along environmental gradients.

The *extinction debt* is a theoretical construct attributed to Tilman et al. (1994) and is so named because it predicts that common species will go extinct sometime in the future due to habitat loss or other human actions now, even though they appear abundant today. The theory assumes there is a competition-colonization trade-off for habitat or that good competitors are poor colonizers although other mechanisms have been hypothesized (Hylander and Ehrlén 2013). That common species are doomed just like rare species is disturbing, but it also has many implications for conservation biology (Young 2000; Kuussaari et al. 2009). It also suggests that conservation should be coupled with habitat restoration to fend off future extinctions and may even be more important in some cases (Possingham et al. 2015). That is, conserve, but then restore the landscape such that it ensures that future extinctions do not occur.

From a restoration perspective, the extinction debt argues that biodiversity targets are likely to be missed in the long term if addressing the extinction debt is not part of the restoration plan (Dobson et al. 1997; Huxel and Hastings 1999; Rappaport et al. 2015). For example, one could prevent the extinction debt by improving immigration sufficiently to prevent common species from meeting their doom, sometimes referred to as creating species credits (Hanski 2000; Jackson and Sax 2010).

Trait-Based Ecology

The daunting list of ecological and anthropic processes a restorationist must contend with can be viewed from two perspectives: population or traits. McGill et al. (2006) argue that community ecology's emphasis on populations has made its job almost untenable because populations and population processes are exceedingly difficult to study. Switching to traits, they argue, would rescue the field. Focusing on traits rather than on traditional population constructs, many of which are phenomenological, such as intrinsic rates of population increase, carrying capacities, and pairwise species interaction coefficients, would transform community ecology from one that is fuzzy and intractable to one that is sharper in its theory and more precise in its empiricism. For example, rather than focusing on intrinsic population growth rates, one could use performance *currencies* like ecophysiological traits (e.g., metabolic rates) or regenerative traits (e.g., number of seeds or clutch size).

Defining what a trait is, however, is about as slippery as defining biodiversity. McGill et al.'s (2006) definition is better detailed then most; a trait is a "well-defined, measurable property of organisms, usually measured at the individual level and used comparatively across species." They distinguish functional traits as traits that *strongly influence organismal performance*. Traits can be defined along many axes including, for example, dispersal mode, functional feeding group, water use, and so forth. A focus on traits is now very widespread in ecological research and increasingly so in restoration ecology (e.g., see chaps. 6, 8, 9, 12, 13). Researchers have argued that a trait-based approach is particularly useful when the exact make-up of former species assemblages is poorly known but there is a desire to restore site functionality (Ostertag et al. 2015) and, more generally, assessing functional trait diversity should be widely used to assess restoration outcomes (Garcia et al. 2015).

Return of the Niche

The rise of interest in traits stems, in part, from a resurgence of interest in the old and venerable concept of the niche. The concept is difficult to treat in a limited space, but briefly, the niche concerns the ways in which an organism relates to its environment. There are different ideas about this relationship. The Grinnellian niche (named after Joseph Grinnell), for example, focuses on the idea that the niche of a species is the habitat it occupies, the Eltonian niche (named after Charles Elton) focuses on the role a species plays in its community (e.g., is it a nitrogen fixer that enriches soil or an apex predator that regulates herbivore density), and the Hutchnisonian niche (named after G. E. Hutchinson) focuses on the multivariate space or hypervolume occupied by a species where each axis concerns an environmental factor and biotic interactions shape the hypervolume (for a recent review, see Colwell and Rangel 2009). Leibold (1995) synthesized these various niche concepts into one in which species requirements and their per capita impacts on the environment constituted the two main dimensions of an organism's niche. This idea reappeared in the context of species traits classified as those traits that reflect organismal responses to environmental change and those that impact the environment (Lavorel and Garnier 2002). Another manifestation of the return of the niche is the *periodic table of niches* recently proposed by Winemiller et al. (2015). This periodic table orders niches by a small number of dimensions much the way the periodic table of the elements orders elements by just two dimensions (number of protons and number of valence electrons). Winemiller et al. (2015) propose that niches are ordered by five dimensions (habitat, life history, trophic position, defense strategy, and metabolism). With such a table, once a species is located in the table by their traits, their basic ecological properties can be deduced, much the way one can deduce the basic properties of elements once located in their periodic table. The response-effect framework described below, serves as an example.

To summarize, the niche concerns six different kinds of environmental factors (not to be confused with Winemiller et al.'s (2015) five niche dimensions): (1) the habitat where an organism lives, (2) what it requires to persist in that habitat, (3) how it is impacted by the species it interacts with, (4) what functional role it plays in its ecosystem, (5) how it responds to environmental change and, (6) how they impact their environment. For the restorationist, one can translate restoring lost biodiversity, functions, and services as restoring the niches of the species lost. Where traits come in is that the six different kinds of factors associated with niches can be codified in species' traits to provide concrete and tractable ways of using the concept of niche to address a variety of environmental issues.

The Response-Effect Trait Framework for Restoration

Of the six different kinds of factors that define an organism's niche, responses to and impacts on the environment may be the most immediately useful for restoration ecology. While different from the five-dimensional approach of Winemiller et al. (2015) (described above), the idea is similar in that it condenses the enormous array of traits and niche dimensions to a tractable, useful set. Laughlin (2014) builds upon the response-effect trait classification scheme captured in Lavorel and Garnier (2002) and developed into a framework by Suding et al. (2008). The framework provides a means for considering how individual changes in biodiversity at the species/organism level can be used to predict community/ecosystem level processes using response and effect traits and relative abundances of species. This response-effect framework is very much in line with McGill et al.'s (2006) call for refocusing community ecology away from population dynamics to traits. The response-effect framework of Suding et al. (2008) is simple in its basic form and can be presented as

$$Y_2 = \sum_{j=1}^{s} f(n_{j1} \times R_j E_j),$$

where Y_2 is future ecosystem function (i.e., target ecosystem function), s is the number of species, n_{j1} is the current density of species j, and Rj and Ej are the response and effect traits, respectively, of species j. Thus, the intrinsic growth rates of traditional population approaches have been substituted for the species-specific responses to environmental change over the time period of interest. Take the densities resulting from those responses and multiply those by their effects on ecosystem function and you have just linked biodiversity to ecosystem function through traits. A lot has been left out, however, such as the fact that responses and effects could involve multiple or sequentially linked traits, response and effect may not co-occur and involve lags, there may be feedbacks among traits, response and effect traits may be correlated with one another (negatively or positively), and interaction networks, which are likely to have complex dynamics, are absent from this basic model.

Laughlin (2014) translates the response-effect framework into a utilitarian framework for restoration—one in which a restorationist is guided through the process of establishing a species assemblage that can meet targets. In his framework (see Cadotte et al. 2015, for a synopsis of the foundation and significance of this framework), targets for biodiversity and function are translated into traits. The restorationist then designs a species assemblage from a pool of available species that can meet these targets. The traits of the species in this assemblage are used to determine who will get through the environmental filters and how interactions will shape distribution and abundance. The effect traits of the resulting assemblage, after filtering and interactions, predict what ecosystem functions/services one will get. If either the biodiversity or ecosystem function target is not achieved, one can adjust the constructed or restored assemblage. This abbreviated description of the framework leaves out the complexities inherent in converting species composition and relative abundances (what managers manage) to trait-based targets. A trait-based target, for example, will have enormous numbers of possible species assemblages that can, theoretically, achieve that target. A number of computational and statistical tools, however, can provide optimal solutions and Laughlin provides real world examples (Laughlin 2014; Laughlin and Joshi 2015). One interesting possibility is that some trait-based assemblies generated by the model might have no analogs in nature, like possibly identifying an optimal prairie grassland assemblage that has no grasses in it.

It is worth keeping in mind that there are a number of simplifying assumptions, however, when adopting the response-effect, trait-based approach in restoration. This approach assumes that

- Modal trait values represent peak performance (Messier et al. 2010; Enquist et al. 2015);
- Trait dispersion reflects lower competition, improves ecosystem function and stability (Schamp et al. 2008);
- The mass or density of an organism governs its influence over ecosystem properties (Suding et al. 2008);
- The trait-based methods for quantifying biotic interactions can substitute for population-based methods (McGill et al. 2006);
- One subscribes to the idea of limiting similarity (Herben and Goldberg 2014);
- One does not necessarily concern oneself with commonness and rarity (discussed above); and
- One is not concerned with spatial complexity, such as metapopulation structure, or the extinction debt (discussed above).

These assumptions, however, are not particularly onerous and they are all backed up by theoretical and empirical studies. Nevertheless, it is always good to be cognizant of the assumptions and limitations underlying different approaches.

Key principles in Biodiversity and Ecosystem Functioning (BEF)

Biodiversity and ecosystems are human constructs—neither exists without the other. It follows, then, that change in one leads to change in the other and the field of biodiversity and ecosystem functioning (BEF) (see reviews by Cardinale et al. 2012; Naeem et al. 2012) provides a few theoretical constructs concerning this linkage useful for ecological restoration (Palmer et al. 1997; Naeem 2006). In natural systems, trait-based processes control the assemblage of species into local communities predominantly through habitat filtering (i.e., limiting assembly to species adapted to local habitat conditions) and biotic interactions. Ecological assembly is a venerable field in ecology and one that has many applications in restoration ecology (see volume by Temperton et al. 2004; chap, 9). In contrast to ecological assembly, BEF typically ignores processes that govern assembly and assumes that one is working with a static assemblage to focus on predicting the influence of biodiversity on the magnitude and stability.

Sampling/Selection versus Complementarity

There is little debate over the fact that changes in biodiversity impact ecosystem processes and properties, but it remains difficult to determine whether effects observed in BEF experiments are the result of *identity effects* or *diversity effects* and whether diversity effects are attributed to *sampling* or *selection* or complementarity effects. Below, I expand upon these concepts.

Identity versus Diversity Effects

BEF researchers consider *identity effects* as that part of a change in ecosystem functioning that is attributable primarily to the identity of the species one is using. They consider *diversity effects* as that part of the change in ecosystem functioning that is due specifically to biodiversity. When the mixture yield (e.g., how much biomass a species produces when grown with other species) is more than what you'd expect from the monocultures, it is called overyielding. When the mixture yield is more than you'd expect from the best monoculture, it's called transgressive overyielding. Whether transgressive or nontransgressive, it means that the species together were able to do something that they could not do in isolation. The underlying cause (identity vs. diversity) has important implications for restoration because targets based on functions or services may be achieved by increasing biodiversity, such as species or functional richness. It is possible, however, that a more targeted effort focused on a few specific species may be all that is needed. If the latter is true, then one needs to know their identity.

Kirwan et al. (2007) provides a simple model for identity and diversity effects, which they expand in a way that clarifies how to separate the two effects. The model starts simply as

$$y = ID + DE + \varepsilon,$$

where y is the yield (or ecosystem function), ID is the identity effect, DE is the diversity effect, and ε is the error term, or the part of the result not explained by identity and diversity effects. ID and DE aren't very helpful in terms of what determines these effects, but Kirwan et al. (2007) expand the formula to

$$y = \textstyle\sum_{i=1}^{s} \beta_i P_i + \alpha M + \sum_{\substack{i,j=1 \\ i<j}}^{s} \delta_{ij} P_i P_j + \varepsilon,$$

where M = total initial abundance (think of M for "mass"), P_i is the initial proportion of i^{th} species, s is the number of species, α is the effect of changing initial abundance on y, $\beta = y$ at average M, β_i is the performance of species i in monoculture, and δ_{ij} = strength of the interspecific interaction, or the effect of species j on species i. While the formula has a lot of terms, it provides a fairly clear sense of what an identity effect is compared to a diversity effect. The identity effect is the first two terms, or that portion of the yield that is expected based on the monocultures, or the biomass expected if each species grew in a pot in isolation of the others, plus the effect of changing biomass on the yield. The diversity effect, however, is the sum of pairwise species interactions on each other's contribution to the yield.

Over some twenty years, hundreds of studies have provided results that have shown that diversity effects are common, but there is significant variability among studies, which is attributable to identity effects (Cardinale et al. 2012). For example, if one increases plant species richness from 2 to 16, mean production is likely to increase and variability in production is likely to decrease, but comparable changes in richness in another study may yield quite different results if the identities of the species are different. This co-occurrence of diversity and identity effects is unfortunate because it limits extrapolating from one restoration study to the next whenever species compositions differ among studies.

Separating Complementarity from Selection in Biodiversity Effects

We now turn to the fact that sometimes the diversity effect is not because of the way species interact with one another, but because of the greater efficiency of use of local resources that multiple species can exhibit. The classic example is that a shallow rooted and deep rooted plant will make better use of the soil than either by itself—no part of the soil is without roots. This is called *niche complementarity*, which roughly concerns how different one species is from another in terms of how it uses resources. Trait dispersion, as described above, is one way to think of complementarity—the more different species are in traits, the more complementary they are. Trait dispersion, or the differences in traits among species, is readily quantified using trait-based indices of functional diversity (Schleuter et al.

2010), and it gives the restorationist a clear means for quantifying and manipulating complementarity. For example, if a restoration target involves increasing an ecosystem function and the services it provides while decreasing the variability in functioning and service delivery, in the absence of time or resources to conduct an elaborate BEF experiment to determine the best species mix, theory and empirical research suggests that the restorationist could focus on maximizing functional diversity. This approach requires having trait data for the species in the community, but such data are easier to obtain than establishing long-term, complex, manipulative studies. If manipulative restoration experiments are an option, they could potentially shed light on which species compositions to use rather than the less precise means of extrapolating from trait data. For example, Oakley and Knox (2013) increased plant species richness in restored plots and found that these higher diversity plots were more resistant to invasion by nonnative plants. Whether the mechanism was complementarity or selection was not clear, but the results guide restoration by suggesting that control of exotic species may be improved by increasing plot diversity independent of the mechanism.

Loreau and Hector (2001) provided a way to disentangle sampling from selection effects, which did much to help resolve the debate over which effect was more prevalent. The method is applied to results from experimental manipulations of plant diversity in which monocultures of all the species are established along with mixtures. If one compares an ecosystem function between adjacent levels of ecosystem functioning, like two versus four species mixtures or four versus eight species mixtures, then the change in ecosystem function between the two levels of diversity, ΔY, can be decomposed into a complementarity effect and selection effect using the formula,

$$\Delta Y = N\overline{\Delta RY}\,\overline{M} + N cov(\Delta RY, M),$$

where N is the number of species in the mixture, $\overline{\Delta RY}$ is the average change in relative yield of the mixtures, and $\overline{M}$ is the average monoculture yields. Relative yields are ratios of yields of a species in polyculture to the yield of the species in monoculture. The first term, to the left of the addition sign, is the complementarity effect, which is positive if the average change in relative yields is positive, meaning that species, on average, did better in mixture than in monoculture. The right-hand term is the selection effect, which is positive if gains in relative yields are explained by the more productive monocultures.

The take-home message is that identity and diversity effects always occur, but if ecosystem functioning changes in predictable ways with increasing (or decreasing diversity), such a diversity effect may be attributable to identity, selection or complementarity effects.

Statistical Averaging and Portfolio Effects

Often, the ecosystem impacts of biodiversity are couched in terms of changes in the magnitudes of functions and services, but stability is also important. In many cases, the reported gains in ecosystem functioning are rather small, quite variable (e.g., some increases in diversity lead to large gains in function while other increases result in small gains), and diminish as one adds more and more diversity. Also, biodiversity effects tabulated for single functions underestimate the full suite of gains across multiple ecosystem functions and services (Hector and Bagchi 2007; Zavaleta et al. 2010; Pasari et al. 2013; Byrnes et al. 2014; Perkins et al. 2015).

Ecological stability is treated in chapter 2, so here I focus on biodiversity's influence on one kind of stability: low temporal variability of an ecosystem. As trait-based approaches illustrate, ecosystem functions are really aggregate properties of the plants, animals, and microorganisms whose collective metabolic activities regulate energy flow and nutrient cycling. May (1974), in his afterthoughts in the second edition of his monograph, recognized that you could have fluctuating populations in a system while the system's properties were far less variable. McNaughton (1977) was, perhaps, the first to provide both the theoretical foundation and some empirical support for the idea that the sum of productivities of all the plants in a highly diverse ecosystem is likely to have lower variability in the face of environmental change than low diversity systems.

Following a number of studies that claimed that biodiversity begat stability, however, Doak et al. (1998) pointed out that the variability of an aggregate property is statistically and inevitably lower than the variability of its constituent species. Tilman et al. (1998) countered that the statistical inevitability was tied to a specific relationship between species variance and abundance, in particular that $\sigma_i^2 = cm_i^z$ where σ_i^2 and m_i^z are the variance and mean abundance of the i^{th} species, respectively, and c and z are constants. Doak et al.'s (1998) statistical averaging is based on the fact that $z = 2$ in the case of pure statistical mechanics, but Tilman et al. (1998) argued that in ecological systems where individual populations have complex dynamics, z can be <1 and be less stable with more diversity. Thus, statistical averaging is not inevitable. More important, Tilman et al. (1998) pointed out that what matters is whether species compensate for one another, meaning that their abundances are asynchronous or inversely correlated with one another such that an increase in one is accompanied by a decrease in another. Compensatory growth or compensation among species is key.

Tilman et al. (1998) referred to Doak et al.'s (1998) statistical averaging as *the portfolio effect*, a more palatable name, based on the business mathematical argument that a portfolio of mixed stocks is more stable, over the long haul, than a stock portfolio made up just a few kinds of stocks. The portfolio effect has been observed in a number of systems (Figge 2004; Hughes and Stachowicz 2004; Koellner and Schmitz 2006; Tilman et al. 2006; Worm et al. 2006; Schindler et al. 2010; Thibaut and Connolly 2013) and is one of several different stabilizing effects that arise from compensatory growth, including *biological insurance* (Yachi and Loreau 1999) and *reliability* (McGrady-Steed et al. 1997; Naeem and Li 1997; Rastetter et al. 1999; Naeem 1998).

CV-Stability

If having lots of species means that when some species are faring poorly, others will take their place, then system performance is insured, reliable, and follows the portfolio effect. These forms of stability are often quantified as the coefficient of variation (CV), or the ratio of the standard deviation to the mean of an ecosystem function. More stable systems have, by definition, lower CVs. For convenience, I'll refer to this as *CV-stability*. An important aspect of CV-stability is that it places values on species that may be locally rare but because of their redundancy with dominant species may compensate for dominant species as they decline when environmental conditions change (Mouillot et al. 2013; Jain et al. 2014).

de Mazancourt et al. (2013) provided an elegant way of teasing apart the different contributions of key ecological processes underlying CV-stability. The model they use approximates CV^2_{NT}, the coefficient of variation for community biomass, to three ecological processes by the following formula,

$$CV^2_{NT} \approx \varphi_e \Sigma^2_e + \frac{\Sigma^2_d}{\overline{N_T}} + \lambda \, \frac{\Sigma^2_o}{n_x} \, .$$

The first term is the environmental component and is the product of the synchrony (φ_e) of species environmental responses, independent of biotic interactions among species, and the mean scaled environmental variance (Σ^2_e). The middle term is the demographic component, which is the ratio of the mean scaled demographic variance (Σ^2_d) and the total community biomass $(\overline{N_T})$. The third and last term is the observation component, which is the product of Simpson's concentration index (the reciprocal of Simpson's diversity index), which measures dominance and the variance observed (Σ^2_o) over the number of samples taken within a plot to estimate the CV of the community biomass. In other words, (with apologies to the authors for leaving out some detail), CV-stability declines (i.e., increases in value) when species show synchronicity in response to environmental variability (i.e., no compensatory growth), exhibit demographic stochasticity, and are dominated by a few species.

What de Mazancourt et al. (2013) did was to translate the mathematical model into a structural equation framework in which the mechanisms underlying CV-stability can be explored quantitatively (fig. 3-4).

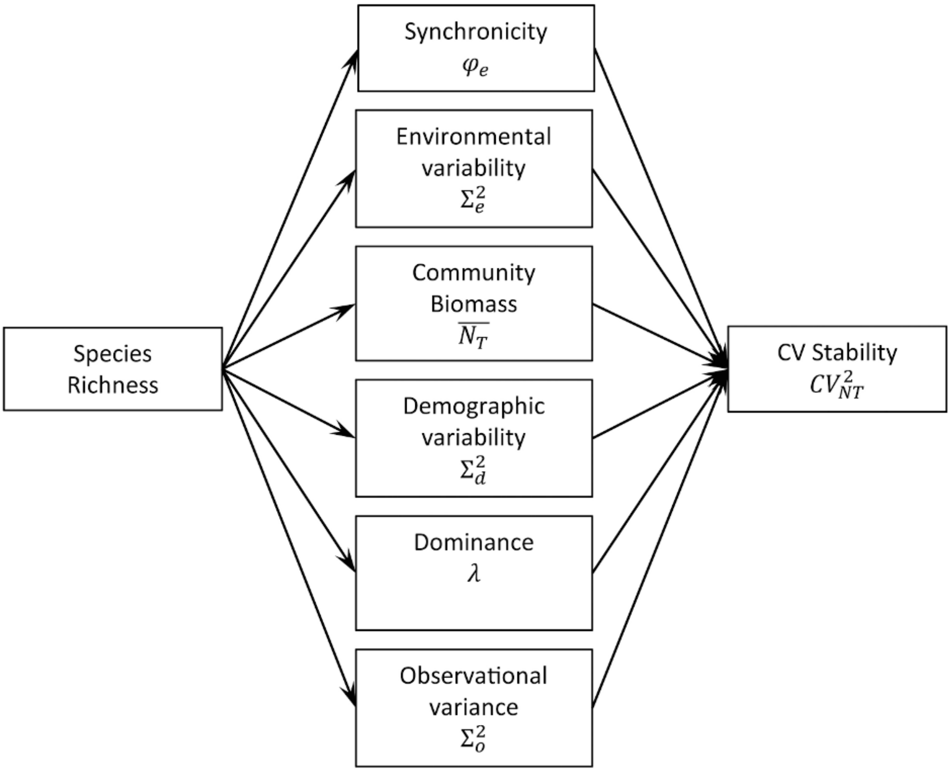

Figure 3-4. CV-stability in the real world.

de Mazancourt et al. (2013) provide a translation of a mathematical model of the coefficient of variation of community biomass, or aggregate property of a community that serves as a measure of an ecosystem function, to a structural equation model that can be used to statistically analyze quantifiable measures of community variation. The model divides CV-stability into three components that capture variation due to synchronicity of species responses to environmental variability, demographic variability, and observational variance. Each box represents a manifest or measured variable. The mathematical term for each measured variable is listed below its name and each is quantifiable. See de Mazancourt et al. (2013) for further explanation and details.

Ecosystem Services

Put simply, ecosystem services are ecosystem functions that benefit humans, but this simple definition belies the enormous scope of ecosystem services that spans virtually all of natural and social science as well as the humanities—well beyond the scope of this chapter. Given its increasing prominence in contemporary BEF literature and in restoration (Montoya et al. 2012), however, it is worthwhile considering three key issues concerning BEF, ecosystem services, and restoration.

First, as emphasized in this chapter, high levels of biodiversity generally enhance the magnitude and stability of ecosystem functions, thus it seems logical to deduce that biodiversity would do the same for services. Logical though this may seem, the lack of robust empirical support for this (Balvanera et al. 2006; Cardinale et al. 2012) suggests caution in assuming that enriching biodiversity through restoration will facilitate meeting ecosystem service-based targets.

Second, Payment for Ecosystem Service (PES) interventions are rapidly becoming the premier mechanism for financing environmental programs to meet their objectives, including restoration projects (Benayas et al. 2009). A recent assessment by social and natural scientists as well as practitioners, however, found that the majority of PES projects do not adhere to one or more fundamental scientific guidelines, which jeopardizes their success (Naeem et al. 2015). For example, in Benayas et al.'s (2009) metanalsysis, PES restoration projects often considered biodiversity itself as an ecosystem service that does not adhere to the basic BEF principle that functions and services are derived from biodiversity, thus biodiversity cannot be a service.

Finally, Kinzig et al. (2011) cautioned that too often market-based mechanisms such as PES may link ecosystem services to other social objectives, such as poverty alleviation, which can imperil PES projects, including restoration projects, from meeting their objectives.

Given these issues concerning functions vs. services and the rise of service-based environmental programs, restorationists may increasingly have to contend with or rely on financing from service-based targets as pressures mount to restore nature to serve humanity. Figure 3-1 illustrates, for example, how shifting the relative delivery of services by ecosystems may be counter to restoration objectives of creating biological assemblages characteristic of reference systems and biophysical properties that attain environmental sustainability (Palmer and Filoso 2009; Palmer et al. 2014).

Closing Remarks

Returning to the bubble analogy at the outset of this chapter, the first thing a restoration ecologist confronts when taking on the task of restoring biodiversity and ecosystem functions and services to a degraded system, is a pattern in species distribution that arose from a complex set of underlying processes. There is, however, abundant theory, and corresponding methods for translating this theory into practice, that can inform restoration on how to make sense of the long list of processes that shape biodiversity and the functions and services it provides. This chapter, focused on biodiversity, touches upon some of the key theoretical constructs that currently provide insight into fundamental ways that nature is structured and how it functions.

There are three challenges, the first being that taking stock of the biodiversity one is confronted with and then designing the diversity of one's target is not a simple unidimensional problem (fig. 3-2, table 3-2). Second, there are a lot of fundamental ecological processes to keep track of and a lot of theoretical constructs that outline how different processes shape biodiversity and the ecosystem processes they regulate, for which this chapter has reviewed just a few (table 3-2). Third, the combinatorics of biodiversity create an overwhelming number of possible assemblages one can construct while restoring an ecosystem.

Meeting these challenges requires taking an increasingly multivariate approach to the restoration of biodiversity and the functions and services it provides. Fortunately, statistical methods, such as structural equation modeling, can provide means for addressing the multidimensional nature of biodiversity, for designing restoration plans that can optimize trait-based functional composition to achieve restoration targets, and for quantitatively assessing how and why biodiversity influences the stability of ecosystem functions. In fact, given the ever shrinking extent of natural habitat, restoration science may find better opportunities to develop both fundamental and use-driven science when larger scales are needed.

There are some interesting issues one needs to consider. First, it is not clear that trait-based ecology, though popular, is actually a substitute for population-based ecology. Like most things in the natural sciences, more than likely both will serve different purposes and have different strengths and weaknesses. Second, ecosystem services is a concept that is forcing the synthesis of the natural and social sciences and this modern trend is strongly shaping restoration ecology. It is high time this synthesis has gotten under way, but to what use we put the outcomes of these efforts, such as payment for ecosystem services, is unclear. From my own perspective, I am not certain that restoration based on ecosystem services can result in sustainable systems (Naeem 2013). Ecosystems collectively harbor millions of species and "serve" the biosphere, but they are being reconfigured to harbor only species that serve humanity across all scales—from local to global. In figure 3-1, can the biosphere function if managed systems became 99% of terrestrial Earth, and restoration and conservation do their best with 1%?

I close, however, with the observation that it is interesting, as the author of a similar chapter (Naeem 2006) almost a decade ago, how dramatically theory has advanced and how theoretical ecologists are well attuned to bringing their findings to the forefront of practice. The progress has been stunning and holds tremendous promise for future developments in our understanding of biodiversity that will facilitate the growth of restoration ecology.

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Chapter 4

Landscape Ecology and Restoration Processes

Jean Paul Metzger and Pedro H. S. Brancalion

Theory and Application

- There is significant empirical evidence supported by a number of theoretical predictions that landscape structure and dynamics affect restoration processes and outcomes.
- A landscape perspective considers the influence of the landscape structure on the local restoration potential as well as the impact restoration may, in turn, have on the landscape.
- A landscape ecology perspective seeks to understand the relationships between process and patterns. To explore those relationships better requires an understanding of the biological mechanisms relating the landscape structure to the restoration.
- A landscape perspective can inform prioritization of restoration sites, enhance and speed ecological recovery, and improve restoration cost-effectiveness.

There is now an increasing and robust set of evidence showing that restoration processes are not only affected by local factors, but also by landscape factors. The landscape context where restoration takes place, characterized by the proximity of species sources, the surrounding land use types, the existence of landscape elements facilitating or impeding movement of organisms, water, and energy, affects restoration outcomes (Leite et al. 2013). Landscape-level factors can be useful to reduce the cost of restoration and to increase its effectiveness. This can be particularly relevant given the global demand for restoration, which aims to restore large land areas, as expressed by the Bonn Challenge, the New York Declaration on Forests, or Aichi Biodiversity Target 15 of the United Nations Convention of Biological Diversity (Menz et al. 2013; Suding et al. 2015).

The proper application of restoration strategies in the context of a given land-

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scape requires a thoughtful understanding of the relationships between restoration processes and landscape structure. Within this context, several questions arise: What is a landscape perspective in restoration? Which are the appropriate spatial scales to capture the effect of landscape structure on restoration processes? How does landscape structure affect restoration processes? Can we estimate landscape resilience? We aim with this chapter to explore these questions and provide a synthesis of the state-of-the-art in the integration of landscape ecology and restoration ecology.

In the first section of this chapter, we explore some definitions and concepts of landscape ecology and present the main theoretical backgrounds to help understand restoration processes using a landscape perspective. In the second section, we present a conceptual framework linking landscape structure and restoration processes. We then explore how restoration can help to improve landscape structure, and finally discuss how a landscape perspective can be used to prioritize sites for restoration projects.

What Is a Landscape Perspective and Why Is It Relevant for Restoration?

Concepts and Terminology

Landscape ecology is a relatively new and emergent science, which has as its main focus the understanding of how ecosystems are organized and transformed across space and the implications of spatial structure and dynamics on ecological processes, considering different spatial-temporal scales (Turner 1989). In brief, it derives from the recognition that "place"—position on the land or seascape—matters. This discipline is part of a paradigm shift in ecology, putting spatial pattern and scale at the center of the ecological debate (Turner 2005). By recognizing that landscapes (and thus the spaces where we live) are by definition heterogeneous, and that this heterogeneity can modulate ecological processes, landscape ecology adds an important element to understanding how land use and land cover changes are affecting the ecological processes and the services that nature provides for humans (see chap. 10).

Landscape can be defined as a "heterogeneous mosaic composed of interacting landscape units, where heterogeneity exists for at least one parameter, for one specific observer and at a particular scale" (Metzger 2001). A landscape can thus be defined at different spatial scales, depending on the focal organisms, and the same piece of land can contain different "landscapes," as organisms with different habitat requirements or dispersal abilities can perceive it differently (fig. 4-1). The landscape is thus a conceptual representation of the space that should make sense for a species or an ecological process. It does not necessarily cover an extensively wide territory or is composed by interacting ecosystems. *Landscape units* can be vegetation units, human land use areas, or habitats of different suitability for a specific species, and in aquatic systems they can be hydrologically similar patches or regions. This representation can be bi- or tri-dimensional, can refer to spatial patterns in terrestrial or in aquatic systems (and it is thus referred as seascapes or aquaticscapes), and can involve visual but also smell or acoustic patterns (smellscapes or soundscapes).

Landscape structure is usually decomposed in two components: *composition* and *configuration*. Composition refers to the assemblage of *landscape units*, and how much of each type of landscape unit is present, while the landscape configuration describes the spatial arrangement of those landscape units (for example, the degree of fragmentation and juxtaposition). The composition of a landscape is a nonspatial attribute (it can be determined without a map), while configuration requires the exact location of each landscape unit in the space. A landscape unit is usually composed of different *landscape elements*, usually patches (relatively small and compact polygons) or *corridors* (linear patches, in some cases defined as patches with length twice the size of the width), and the main landscape unit (e.g., dominant in area or in function) is called the "landscape matrix" (fig. 4-1). Although some landscape units may be critical from a functional perspective but not be the dominant (by area) matrix unit ("hot spots" that drive key ecosystem processes, chap. 10). The matrix is also sometimes referred to as all habitats less suitable for the focal species' reproduction, or less permeable to movement of individuals when compared to the native habitat (Villard and Metzger 2014). Ideally, this simpler patch-corridor-matrix framework should be replaced by a more continuous definition of habitat quality or suitability, considering that each species responds to different environmental factors in a continuous way (McGarigal et al. 2009; Lausch et al. 2015). However, this gradient approach requires a broader set of data and a thorough understanding of species natural history, which is rarely available for restoration projects.

Understanding pattern-process relationships by considering different spatial-temporal scales is a stimulating challenge, which can bring new insights and ideas for different research questions in theoretical and applied ecology (chap. 16). This is the case with ecological restoration as well. In the last fifteen years, the interaction between restoration ecology and landscape ecology has increased, and particularly after 2009 the number of publications on research at the interface of these two fields increased exponentially (for a review, see Leite et al. 2013). The mutual benefits are clear. Understanding the relationships between landscape structure and the different processes involved in restoration allows the optimization of restoration efforts—the position of a restoration site on the landscape can constrain

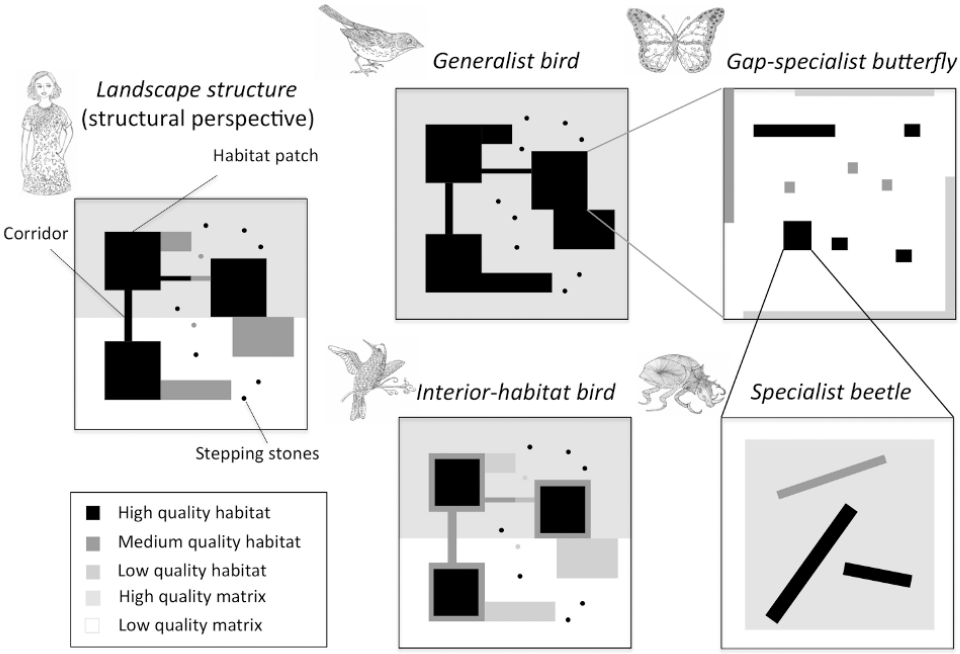

Figure 4-1. The landscape composition and configuration according to different species perceptions. From a structural (and human) point of view, the landscape structure can be defined by identifying habitat patches for a focal group of species, as well as corridors, stepping-stones, and interhabitat matrix areas. However, this perception can change according to the species-specific perspective. A more generalist bird species may not consider differences in habitat and matrix quality, while a more sensitive bird species may avoid habitat edges and be sensitive to habitat and matrix quality. Other species can perceive the landscape at different scales. For instance, the landscape of a butterfly can be a patch of a bird species, and similarly the landscape of a beetle can be a single patch from the landscape of the butterfly. Caption images provided by Maria Paula Correia de Souza.

or enhance the potential for positive ecological outcomes (e.g., chaps. 7, 10, 11, 14), and restoration actions provide exceptional opportunities to test the effects of spatial patterns on ecological processes at larger scales, which is a major challenge when dealing with landscapes at scales relevant for humans.

Local and Landscape Restoration

Ecological restoration consists of human interventions to assist the recovery of an ecosystem that has been degraded, damaged, or destroyed (*sensu* SER 2004). This activity is usually implemented on predetermined landscape areas, where there is an intention to reestablish an ecosystem patch with composition, structure, and functioning similar to those found in non- or less-disturbed, reference patches of the same type of ecosystem. These *local restoration*s can be achieved through different interventions, such as tree planting, protection against human-mediated disturbances, or by managing natural disturbances (e.g., fires, floods). The scale of interventions varies; restoration efforts may also have the goal to transform the whole landscape, not only portions of it. We must therefore distinguish *local restoration*, that is, restoration efforts carried out at site or patch level, from *landscape restoration*.

Landscape restoration describes restoration initiatives that focus on the restoration of landscape structure, dynamics, or function, and understanding the landscape as a mosaic of interactive landscape units. Restoration targets can vary from the reestablishment of historical landscape configurations to configurations representative of least disturbed contemporary landscapes. Like all restoration efforts in which human values and decisions influence goals, landscape restoration generally focuses on improving landscapes to address human demands. However, given the focus of this book—the theory underpinning *ecological* restoration—we focus on landscape restoration that seeks to restore native biodiversity as well as multiple ecological processes, including the reduction of edge effects, reestablishment of biological and hydrological fluxes, and reconnection of fragmented habitats. This can be difficult given that landscapes commonly encompass large areas in multiple land uses and land cover types, each with different degrees of anthropogenic disturbance. The human interventions targeted by landscape restoration can vary widely, although typically include efforts to increase native habitat, enhance connectivity through the introduction of corridors and living fences or the removal of barriers to dispersal, and the installation of more permeable matrix habitats.

However, as the units and boundaries of any landscape depend on the suite of species or processes under consideration, landscape mosaics can be defined at multiple spatial scales. Restoration efforts explicitly undertaken to favor one species or a group of species should be planned to adequately meet the spatial demands for those species. Consequently, true landscape restoration can occur at a wide range of scales, including very local scales, where landscapes cover only some hectares or even some square meters; the smaller scales may apply in cases where focal species or processes use or require very restricted spaces. This decoupling between spatial scales and the incorporation of landscape principles in restoration lies at the heart of why landscape restoration and *large-scale restoration* are not synonymous terms. Landscape restoration is very much about spatial arrangements, not just large spaces.

A *landscape ecology perspective in restoration* encompasses both the actions defined above as landscape restoration for the improvement of landscape structure, functions, or dynamics, as well as local restoration actions that consider the influence of the surrounding landscape structure on restoration outputs (Metzger and Brancalion 2013). Explicit consideration of how landscape structure affects ecological processes involved in restoration can both optimize local-scale restoration actions and enhance effectiveness in transforming the landscape according to the restoration targets, as we will discuss later in this chapter. For local-scale restoration, a landscape ecology perspective will always be important if local factors or constraints are not too limiting, or if the frequency (or intensity) of the disturbance is not too high, preventing any (positive or negative) effects of the surrounding landscape on the local restoration processes. For example, if human-induced forest wildfire is too frequent or if the introduction of pollutants in a local stream is too large, broader scale restoration efforts to improve forest or stream biodiversity will have limited impact unless the local stressors are reduced.

Although it is fundamental to determine the most appropriate scale for restoration, there are few data and research to support such decisions, and probably there is no unique appropriate scale to be considered. A restoration action, from a landscape perspective, will need to evaluate the landscape structure at scales that exert influence on restoration processes. According to simulation models developed by Jackson and Fahrig (2012), the size of a biologically relevant landscape is related to the dispersal distance of the target species, which in turn is related to the body size of the species. The authors suggest that the radius of the landscape should be 4 to 9 times the median dispersal distance (which is usually higher than the size of the species territory) or 0.3 to 0.5 times the maximum dispersal distance of a species. Given that median dispersal distances of species involved in the regeneration/restoration process can varied widely, from 50 to 100 m for some understory bird species (Awade and Metzger 2008), 100s m to several km for aquatic organisms (Radinger and Wolter 2014; Tonkin et al. 2014) to more than 5 to 10 km for some large mammals (Whitmee and Orme 2013), the adequate landscape extent for such kind of analyses can vary from 200 m to more than 90 km. Given this, only a multiscale approach will cover the range of scales relevant for restoration within a landscape perspective.

The paradigm of restoration with a landscape perspective thus goes beyond restoring pieces of the land or even restoring large areas, while ignoring the influence of the landscape structure. We need to move from small-scale “environmental gardening” to large-scale restoration based on landscape ecology principles, as already claimed since the mid-1990s (Naveh 1994; Hobbs and Norton 1996; Bell et al. 1997). This new approach brings new challenges for restoration science and there are immense opportunities for research to better understand the relationships between landscape structure and the processes that influence ecological restoration.

Local and Landscape Resilience

Resilience is usually defined as the capacity of a system to recover after a disturbance (SER 2004). The ability and speed of this recovery depends on the intensity and frequency of the previous disturbance(s), and thus on how intensively the composition, structure, and functioning of the system were altered. Both local and large-scale factors can be involved in this process. In some cases, a favorable landscape context can compensate, at least partially, for low local resilience, or inversely, an ecosystem that was lightly disturbed can have high resilience even if situated in an unfavorable landscape context. For example, a native patch embedded in a large urban matrix will hardly be able to recover the local extinction of a species, even if its quality and the local resilience are high; on the other hand, a highly degraded area (low local resilience) in landscapes with large extents of high-quality habitat cover may be able to recover relatively fast. So the resilience of a site is a combination of factors acting at local and landscape levels, which is not necessarily the sum or product of resilience measured at local and landscape levels.

Landscape resilience can be defined as “the capacity of an entire landscape to recover from previous disturbances” (Cumming et al. 2013). If and how the landscape composition and configuration will contribute to landscape resilience depends on which focal process is under consideration. For example, if restoration is undertaken to recover a species that has been locally extirpated, then landscape resilience will mostly depend on habitat cover and landscape connectivity and, thus, on its capacity to promote or facilitate species recolonization (Pardini et al. 2010). However, if landscape restoration is undertaken to improve or restore the capacity of a landscape to provide high-quality water, then landscape resilience will depend, among other factors, on the composition and native habitat cover in key water recharge regions that will allow the natural process of water percolation and purification while limiting excessive runoff and sediment inputs to water bodies (chap. 14). Or if the focus is on avoiding landslides or soil erosion, native habitat cover should be situated in the most sensitive or susceptible areas to erosion process, such as on steep slopes (chap. 12). One area can thus have different landscape resiliences according to the desired ecological processes.

Theoretical Background of Ecological Processes Acting at the Landscape Level

There is a growing literature that shows that the landscape structure affects several processes that will determine the occurrence, abundance, and persistence of a species and, thus, affect the ecological processes and ecosystem services that those

Table 4-1.

Main ecological theories or hypotheses relevant to understanding restoration processes within a landscape ecology perspective.

Theories and Hypotheses	Main Concepts and Definitions	Implications for Restoration
Island biogeography theory (MacArthur and Wilson 1967)	This theory predicts that the number of species on an island results from a dynamic balance between species extinction, which is related to island size, and species colonization, determined by the distance of the island to the continent (its isolation). The larger and less isolated the island is, the richer its community.	As the size of a restored patch increases and its isolation from a source area (i.e., very large fragment) decreases, the probability it can maintain a large number of species over time is expected to increase.
Metapopulation theory (Levins 1969; Hanski and Gilpin 1997)	A metapopulation is a cluster of local populations spatially isolated in habitat patches but functionally linked through biological fluxes. Metapopulation dynamics are determined by a balance between local population extinction and recolonization. Local population extinction is related to habitat patch size, while local recolonization is related to habitat patch isolation or connectivity. As a consequence, the extinction:recolonization ratio is determined by habitat size and connectivity.	Restored patches situated in landscapes with larger and better connected fragments will be more easily recolonized by local populations from the surrounding landscape and should thus support more stable local populations. Populations present in these restored patches will also have a higher chance of persisting over time, since they will be less vulnerable to genetic drift and inbreeding depression, driven by reproductive isolation.
Metacommunity theory (Wilson 1992; Leibold et al. 2004)	A metacommunity is a set of local communities that are linked by dispersal of multiple potentially interacting species.	Local species interactions as well as populations' birth and death rates will depend not only on local conditions but also on landscape context, especially the arrival of potentially interacting species from the surrounding landscape.
Random placement model (Coleman 1981)	The random placement model is a probabilistic model to explain the spatial distribution of species. According to this model, habitat patches function as "targets" that accumulate individuals passively. Large patches are large targets that accumulate more individuals and, consequently, more species than small patches. Due to its probabilistic particularity, the random placement model has been used as a null model.	Large restored patches have more chance to accumulate species than small restored patches, while large natural remnants may serve as better sources of species to restored patches.

species provide. Understanding those processes that occur at the landscape level is crucial to understanding the mutual benefits of restored areas for landscape functions, and the contribution of landscapes to restoration effectiveness. For this reason, it is useful to summarize the main ecological processes that occur and are affected by the landscape structure. We will focus here on processes that affect species occurrence, for which there is a large body of theories relevant for restoration practice (see also chap. 16).

Area Effect

The area of a fragment is considered to be the main predictor of local species extinction or richness, according to metapopulation and island biogeography theories (table 4-1). The species-area relationship (SAR) is a well-known relationship, first formalized mathematically by Arrhenius (1921), and empirically tested and validated for several taxonomic groups, such as plants, birds, mammals, and insects (Ewers and Didham 2006). Different biological mechanisms can explain this relationship. First, larger areas usually have a higher abundance of resources that can support larger and more stable (less prone to extinction) populations. When resources become less abundant, intraspecific and interspecific competition for access to these resources will increase, and can lead to increased mortality or extinction, respectively. Second, larger patches are generally also more heterogeneous, and thus can potentially contain a larger number of resource types, sustaining species with different habitat requirements (chap. 10). Third, larger areas can support species with larger area requirements or resource demands. And finally, the extinction of particular species can lead to a chain of secondary extinctions, simplifying the ecological network of smaller fragments over time.

Isolation Effects

Isolation is considered a predictor of species colonization or recolonization in theories of fragmented habitats (tables 4-1 and 4-2) and is also related to extinction risk of a species (chap. 7). However, the explanatory power of isolation to predict species richness or extinction is usually lower when compared to area effects, especially for fragmented landscapes (Fahrig 2013). Isolation can be measured in very different ways, as the distance to the closest fragment, the distance to the closest fragment above a certain size (larger, more stable fragments that can act as a source for colonization events by species or individuals), or even a mean distance to all fragments situated within a determined neighborhood of the focal patch (the extension of this neighborhood should be related with the dispersal capacity of the focal species). The higher the isolation value, the lower the number of species that can reach the focal fragment, which then tends to be dominated by species with higher dispersal capacity. As a consequence, isolation is inversely related to the species richness (Steffan-Dewenter and Tscharntke 1999). Additionally, considering metapopulation dynamics, more isolated fragments will have lower recolonization rates, and thus a lower species occurrence over time (chap. 7). In fragmented landscapes, measures of isolation are usually insufficient to assess colonization or recolonization rates, due to the high heterogeneity of the matrix and the existence of barriers and facilitators of species movement throughout the landscape. In these cases, measures of landscape connectivity (see below) are more suitable for inferences about species movement and (re)colonization processes.

Habitat Cover Effects

Recently, Fahrig (2013) suggested that a simple measure of habitat quantity, within an appropriate landscape extent and an adequate definition of a habitat (both depending on the focal species), will be able to represent both fragment size and isolation effects. In fact, Fahrig (2013) argues that patch size and isolation are mainly driven by a sample area effect: the larger the sampled area, the larger is the chance of sampling more species. This hypothesis is in line with the random placement model (table 4-1), which assumes that habitat patches accumulate individuals passively and, thus, landscapes with a large amount of habitat will have more chance to have a large number of species, as a simple probabilistic consequence. According to this reasoning, even small fragments, if situated in landscapes with large habitat amount, will contain (at least temporally) a large number of species, not because this fragment will support those species alone, but because the landscape will allow for the arrival and passage of individuals. Additionally, many landscape attributes or descriptors of landscape structure are correlated with the habitat amount. In particular, as habitat amount increases, the mean size of fragments increases and the mean isolation among those fragments decreases. In other words, the habitat amount synthesizes in a unique value the effects of size and isolation (table 4-2). However, several authors argue that beyond habitat cover, habitat configuration should also be considered, especially when habitat cover is at intermediate to low levels (Andrén 1994; Villard and Metzger 2014; Hanski 2015).

Edge and Cross-Habitat Spillover Effects

Edge effects can be defined as the mutual influences of adjacent landscape units. For instance, at the interface between a forest and a field, there is an effect of the forest on the field, by shading the field and probably reducing its primary produc-

TABLE 4-2.

Key indices for assessing landscape structure in restoration projects (following Leite et al. 2013) and their implications for restoration. This framework is primarily relevant to terrestrial and some marine landscapes; for a landscape ecology treatment of riverine ecosystems, see Poole (2002). The implications are generalizations derived from research and their relevance will vary depending on the species and context.

Indices	Main Meaning and Interpretation (see literature review in Andrén 1994; Fahrig 2003; Ewers and Didham 2006)	Implications and Recommendations For Restoration
Patch indices*		
Patch size	The size of the patch is usually positively related to the amount and diversity of resources, and thus with its capacity to support larger and more stable populations, and more species.	Larger restored patch size (or the sizes of the surrounding patches) is better for restoration processes. Larger patches will potentially recover faster, attracting more species, and sustaining them better over time.
Patch isolation	The isolation of a patch is inversely related to its capacity to receive species from neighboring habitat patches. As a consequence, the greater the isolation, the lower the immigration and recolonization rates, and the lower its richness.	To take maximum advantage of neighboring patches to provide species and individuals for a restored patch, less isolation enhances restoration. Reduced patch isolation favors the genetic viability of populations reintroduced through active restoration.
Patch shape	Patch shape indices are usually related to the balance between edge and interior habitat areas. More elongated or irregular patches will have a higher proportion of edge habitats, and thus will be more disturbed or affected by the matrix.	More regular patches, less affected by edge effects, are usually better for restoration purposes.
Habitat indices**		
Habitat cover	The amount of habitat in a landscape is considered the most important metric for predicting the capacity of the landscape to sustain habitat-dependent species (Fahrig 2013). Habitat cover is usually related to other metrics; it is positively related to mean habitat patch size and habitat connectivity, and inversely related to habitat patch isolation.	Higher habitat cover is better for restoration. The main challenge is to define an adequate landscape scale (extent) that considers the multiple species and processes involved in restoration actions. Generally, habitat cover should be considered at multiple spatial scales.

Table 4-2. *continued*

Indices	Main Meaning and Interpretation (see literature review in Andrén 1994; Fahrig 2003; Ewers and Didham 2006)	Implications and Recommendations For Restoration
Patch density	The number of habitat patches divided by the area of the landscape is the patch density; it is usually considered as a measurement of spatial fragmentation (high density means high fragmentation). The ecological significance of patch density depends on habitat cover. If cover is high, a large number of patches means low isolation among habitat patches; if cover is low, patches will be distant. High patch density also means a high density of habitat edges per unit area, and thus a large portion of the habitat under edge effects.	There is no simple recommendation in this case. A large patch density can be good for restoration because patches are closer to each other, but it could be due to the large areas under edge effects. This index should not be interpreted without considering other landscape metrics.
Connectivity	The capacity of the landscape to facilitate biological movements (Taylor et al. 1993). It is a species-specific measurement that will depend on the interaction of landscape structural measurements (e.g., density of corridor and stepping-stones, matrix permeability) and functional dispersal attributes of the species (e.g., their capacity to move in the matrix, use corridors and stepping-stones). If correctly measured, landscape connectivity is also a measurement of how much habitat is available or accessible in the landscape, and thus it is a functional measure of habitat amount.	Higher connectivity is generally better for restoration since connectivity is often positively correlated with species arrival and with the availability of resources in neighboring patches. So, high connectivity also means high capacity of the landscape to provide the same kind of resource in different neighboring patches (i.e., landscape supplementation, *sensu* Taylor et al. 1993). Connectivity integrates information of habitat amount and arrangement with species dispersal ability and should thus be the single best landscape indicator for potential restoration success (Tambosi et al. 2014). It is the primary metric that takes into account the matrix and corridor effects on species movement. However, parameterizing functional connectivity measurements for all species involved in the restoration process is a major challenge.

Table 4-2. *continued*

Indices	Main Meaning and Interpretation (see literature review in Andrén 1994; Fahrig 2003; Ewers and Didham 2006)	Implications and Recommendations For Restoration
Landscape indices**		
Landscape composition	Landscape composition is usually represented by the relative proportion of different landscape units (e.g., land use and land cover or ecosystems types). It is a nonspatially explicit measurement (the spatial location of the landscape units is not considered).	There is no simple recommendation with respect to restoration since the most favorable landscape composition varies with species. High landscape richness means high capacity of the landscape to provide different kinds of resources (i.e., landscape complementation), favoring species that need more than one type of habitat to survive. However, if landscape richness increases at the expense of habitat amount, then the most sensitive habitat-dependent species may be impaired.
Landscape heterogeneity	Heterogeneity is one of the primary indicators of landscape structure. It can be measured by diversity indices, such as the Shannon-Wienner index, which do not consider the spatial arrangement of landscape units. Alternatively, indices such as contagion and interspersion metrics (McGarigal and Marks 1995) can take into account the spatial complexity in their arrangement.	Higher landscape heterogeneity is usually related to a higher landscape complementation, but also with higher overall fragmentation and greater edge effects. As with landscape composition, the best configuration or heterogeneity will depend on the species considered.

* Usually refers to the restored patch.

** Habitat and landscape indices should be measured at an appropriated landscape extent around a restored patch (see Jackson & Fahrig 2012) or, in the case of a *landscape restoration*, should encompass the focal landscape and the surrounding areas that can affect this focal landscape.

tivity or increasing soil moisture, and there is an effect from the open field on the forest, facilitating the entry of light, wind, and so also modifying the temperature and humidity at the forest edge. The most studied and known edge effect is the influence of an open matrix on forests, which is usually limited to less than 100 m, but can reach more than 500 m depending on the ecological process and local conditions (Benchimol and Peres 2015). The consequence of these edge effects can be drastic, increasing the mortality of some species or inversely providing or aggregating new resources for other species, thus leading to significant changes in species composition from other forested areas. These compositional changes can, in turn, lead to functional modifications such as reducing the capacity of vegetation in forest edges to store carbon, inhibiting or promoting the passage of some species and thus acting as a selective filter in the landscape. Forests can also positively affect the adjacent landscape units, acting as a source of species that can provide ecosystem services, such as crop pollination and pest control, a source of nutrients or water, or acting as a site for acquisition of food (chaps. 11–14). The movements of species or resources from one habitat (landscape unit) to another are called *cross-habitat spillovers* or *spatial subsidies* (Blitzer et al. 2012; Schriever et al. 2014). In the case of restoration areas, those movements can occur in both directions, from adjacent habitats to restored habitat (affecting the restoration process), or from restored areas to neighboring areas, thus creating a functional effect of restored areas at the landscape level.

Connectivity Process

Despite an expected positive relationship between area and species richness, there are examples in the literature of nonsignificant or negative relationships (Ewers and Didham 2006). Usually, this is because the relationship is masked or altered by other attributes of the landscape, such as the matrix quality. Landscape connectivity, defined as the capacity of the landscape to facilitate biological fluxes (Taylor et al. 1993) is a species-specific attribute because it depends on the interaction between structural characteristics of the landscape and the dispersal capacity of the species under consideration. The landscape structural characteristics that influence connectivity include the spatial position of habitat patches (i.e., average habitat isolation), the quality of the matrix (which can be structurally evaluated by an analysis of the physiognomic or compositional similarity with the main habitat type), the density of stepping-stones (defined as microhabitats dispersed in the matrix that can be used to facilitate movement in inhospitable areas), or the density, quality, and width of corridors (fig. 4-1). From a functional point of view, connectivity will depend on the capacity of a species to cross gaps among habitat patches, to use the matrix or other linking elements of the landscape (corridors, stepping-stones), or to pass through some biological barriers (such as roads or large rivers). By combining information on habitat amount, configuration, and dispersal abilities of species, it is possible to evaluate the amount of habitat that is available or accessible for a particular species (Saura and Rubio 2010). Connectivity or habitat availability/reaching potential measurements can thus go a step further from a simple habitat amount evaluation, by incorporating the functional properties of species dispersal abilities. However, adequate information on species movement is not usually available for all species of interest, and in this case habitat amount can be used as a pragmatic proxy of habitat availability.

Landscape Complementation and Supplementation

Landscape composition and complexity also affect species distribution, particularly for those species that require different types of resources or that need resources that are located in more than one patch of the same type. *Landscape complementation* is the capacity of the landscape to provide different kinds of resources, usually located in different landscape units. Organisms like some amphibians, require completely different resources or even habitat types during different life stages and will only survive when all requirements are present in the landscape. For the resources to be functionally available requires both a particular landscape composition and adequate spatial arrangement and heterogeneity (table 4-2). *Landscape supplementation* is a similar concept but refers to the capacity of the landscape to provide the same kind of resource in different neighboring patches; it can supplement insufficiently abundant resources in one patch. The species that need this resource must be capable of moving among several patches to obtain the needed resources. Landscape complementation and supplementation are important processes occurring at the landscape level that can affect species dispersal and the interactions of local communities and metacommunities (Miyashita et al. 2014) (table 4-1).

Linking Landscape Structure and Restoration Processes

How does landscape structure affect restoration processes and determine its outcomes? How do restoration interventions influence landscape structure and spatial ecological processes? Both questions are intrinsically tied to each other, as a consequence of the mutual influence between restoration and landscape structure. We propose a framework to represent how landscape structure may be affecting key ecological restoration processes, which in turn affect the composition, structure, and dynamics of local landscape units as well as the entire landscape (fig. 4-2). This framework can help to guide restoration design, so that restored areas may act as new structural elements in the landscape to improve its functions.

As already discussed, the preexistent landscape structure as determined by its composition and configuration (particularly the size, shape and distribution of habitat patches, ecological corridors, and stepping-stones) has a major influence on ecological processes operating at different spatial scales and, consequently, influences the restoration process at a site. In parallel, the implementation of site-

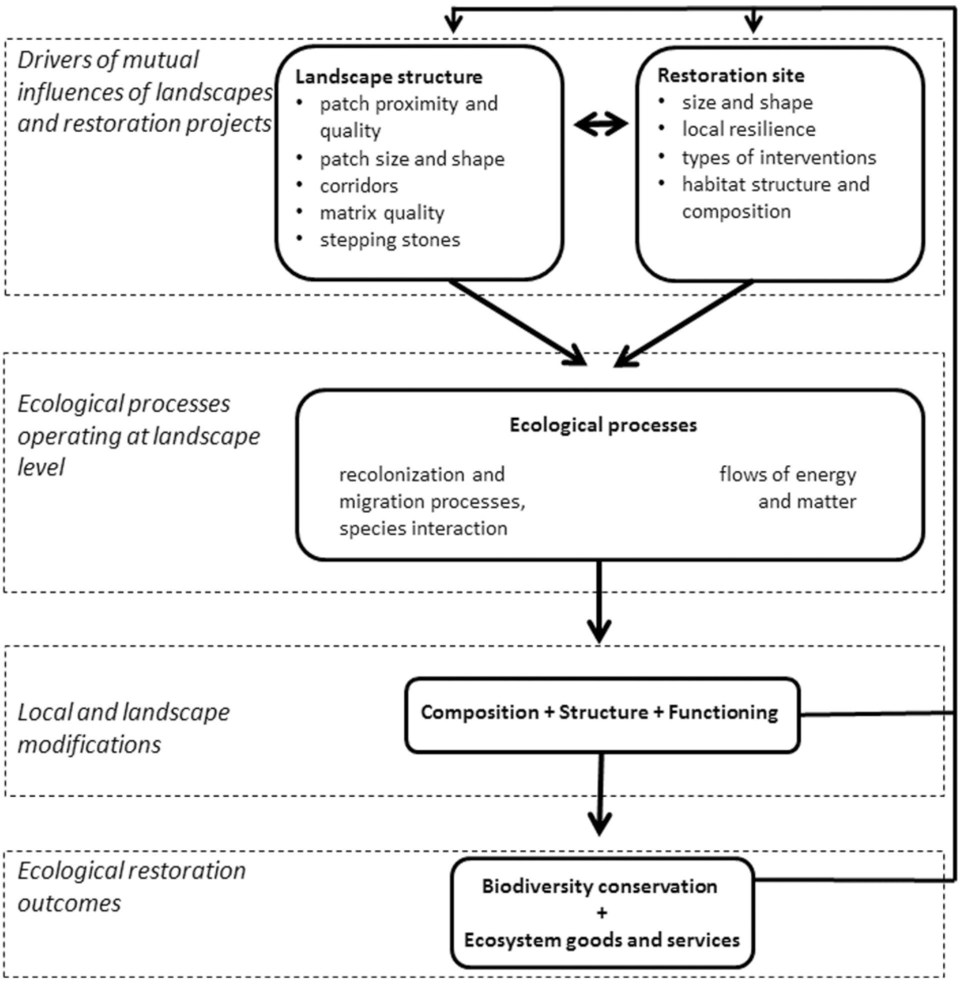

Figure 4-2. A framework for understanding the mutual interaction between landscape structure and ecological restoration.

scale restoration changes the structure of its landscape (Holl et al. 2003). Such changes are mainly driven by the biophysical characteristics of restored sites, which are largely determined by the following: (i) their size and shape, which affects the edge-to-area ratio and habitat quality; (ii) local resilience, which influences the potential for site regeneration; (iii) restoration interventions, which modify the initial biophysical conditions; and (iv) structure and composition, which influences ecological processes operating among the restored site and remaining habitat patches.

Several ecological processes operating at the landscape level are thus mediating the interaction between landscape structure and restoration site. These are mainly manifested as biotic processes (species recolonization, migration, and interaction) and abiotic fluxes (flows of energy and matter). The biotic and abiotic processes controlled by landscape structure may have both positive and negative effects on restoration processes, such as controlling the arrival of rare mammal species in savannas, the invasion of grasslands by exotic trees, the regulation of the flows of organic matter in streams, or the spread of pollutants that may cause population declines or species extinctions. At the same time, restoration interventions may also influence migration, recolonization, and species interaction, since species colonizing restoration sites may enhance biophysical properties over time, thereby facilitating biological flows. For example, the reintroduction of trees in pasturelands by restoration plantings increases shading and, thus, facilitates movements of forest understory birds in the landscape. Meanwhile, restoration interventions may also impact the flow of energy and matter as a consequence of modifications of the physical structure of a site (Liu et al. 2014). For instance, removing dams is a common intervention for stream restoration, which modifies not only the ability of fish to disperse upstream but modifies nutrient and sediment fluxes within the whole catchment (Oliver et al. 2014; Magilligan et al. 2016).

The shifts in ecological processes resulting from the mutual interaction between landscape structure and restoration will drive changes in the composition, structure, and functioning of both restored areas and landscape. Landscape structure and restoration site characteristics may favor recolonization processes and, consequently, restoration sites (or landscapes) can gradually become more biologically similar to the remaining habitat (or the reference landscape) in terms of taxonomic, functional, and phylogenetic composition. Thus, restoration sites may become more species rich and host higher conservation-value species. Once the newly colonizing species become a permanent or transient part of the community, they may change its structure. Big trees in forest ecosystems, beavers in streams, elephants in savannas, and species forming coral reefs in seas are a few of the many examples of how species change the structure of the ecosystems where they occur (Romero et al. 2014). Changes in ecosystem composition and structure will influence its functioning, as predicted by biodiversity and ecosystem-functioning theory (chaps. 3, 9). In the other direction, biotic and abiotic changes in ecological processes mediated by modifications in landscape structure impact species migration and the flow of energy and matter in landscapes, thus potentially affecting the ecological attributes of the remaining habitat patches (chap. 13).

From a biodiversity conservation perspective, restoration of fragmented landscapes increases landscape connectivity, which should support higher biodiversity levels over time (Brancalion et al. 2013). This holds true, because well-planned restoration that takes into account species dispersal ability can improve functional connectivity, which enhances recolonization potential and over time reduces extinction risk for species sensitive to habitat fragmentation (Crouzeilles et al. 2015). However, the relative importance of within-site vegetation attributes and landscape context attributes that can influence colonization and persistence at restored sites may change over time, often due to vegetation succession (Gould and Mackey 2015).

From an ecosystem goods and services perspective, restored or rehabilitated landscapes can provide better ecological conditions for supporting populations of native species, including many with economic importance for humans. For example, forest restoration projects can be designed to reduce edge effects and favor the arrival of late-successional woody tree species that grow to a larger size and are long-lived that may favor carbon sequestration and climate change mitigation (Brancalion et al. 2013; Pütz et al. 2014).

Finally, the benefits for biodiversity conservation and ecosystem goods and services provisioning to society will impact the implementation of future local and landscape restoration projects, which will further impact the structure and functioning of other landscapes submitted to this kind of manipulation.

Using Restoration to Improve Landscape Structure and Dynamics

Restoration is currently considered one of the main strategies to avoid species extinctions, mitigate climate change problems, and improve the offer of a wide range of supporting and regulating ecosystem services (Rey Benayas et al. 2009; chaps. 1, 5, 15, 17). However, the same restoration intervention performed in different locations of the landscape can result in distinctly different ecological benefits (Villard and Metzger 2014). While the selection of an appropriate restoration area will first depend on the main restoration goal there will always be differences among sites in their restoration potential. The use of a landscape ecology perspective is fundamental to the selection and spatial distribution of restored areas. This is most obvious in habitats that are directionally structured, such as river networks where landscape structure and tributaries upstream may inhibit restoration at points lower in the river network (Palmer et al. 2014; chap. 14). The importance of landscape context for restoration-site selection is critical to achieving restoration goals (Tambosi et al. 2014; Torrubia et al. 2014).

Landscape restoration can be accomplished by changing the landscape structure, introducing or removing landscape elements, or by modifying its dynamics including controlling or regulating human or natural disturbance regimes. Landscapes can be structurally manipulated and restored by the following methods: (a) creating new habitat patches, ecological corridors, or stepping-stones areas; (b) reducing edge effects in patches; (c) increasing patch area/improving its shape;

and (d) increasing matrix permeability (fig. 4-3). From a biodiversity perspective, structural interventions in landscapes can be particularly useful for increasing species migration and recolonization processes, which are essential for avoiding species extinctions and supporting the successional development of the ecosystem undergoing restoration at the landscape level. At the same time, restoration of habitat patches may also favor some ecosystem functions, like soil protection, water purification, and pollination, thus favoring the provisioning of ecosystem services to society (Mitchell et al. 2013). Reducing edge effects in patches is particularly useful for avoiding local extinctions at the patch level, since it improves the habitat quality for disturbance-sensitive species, improving the ecosystem services depending on better vegetation structure, like carbon sequestration (table 4-3). Despite these many potential benefits, it is important to keep in mind that habitat or connectivity may not be the factor limiting ecological recovery. Extensive empirical evaluations of river and stream restoration projects have shown that restoration of in-stream habitat typically has little effect on biodiversity recovery largely because most degraded streams have poor water quality (Palmer et al. 2014). Similarly, it does not matter how much habitat is restored if hunting or fishing is the primary factor limiting populations (Peres 2010).

Landscapes can also be manipulated and restored by acting on their temporal dynamics. Humans have modified the natural or desired disturbance regimes in many ecosystems. The composition, structure, and dynamics of ecosystems and landscapes depend on the historical regime of disturbances that have shaped them over time. Impacts on the frequency, magnitude, and duration of natural disturbances may bring negative effects for biodiversity conservation, since they may modify the habitat characteristics making them less suitable for endemic species, while increasing the vulnerability to biological invasions (Suding et al. 2004). For instance, the protection of savannas and temperate grasslands from natural fires, as done by past “conservation” initiatives, has threatened biodiversity and led to colonization by trees, which excludes endemic open-land species. In some cases, natural disturbances have been amplified by human-mediated interventions, such as allowing overgrazing in native grasslands (Wu et al. 2014) and the eruption of bark beetles in North American forests (Raffa et al. 2008). Another example is the modification of flooding regimes in streams caused by dams, where seasonal floods are important for establishing river channel deposits, serving as spawning cues for some species, and as essential conditions for reproduction of some aquatic species (Quiñones et al. 2015). The above-mentioned disturbances can thus be manipulated by restoration interventions to shift the disturbance regime closer to that of historic or least-disturbed systems and thus favor the persistence of native species, the recolonization of locally extinct native species, and the enhanced provision of some ecosystem functions with special importance for human well-being.

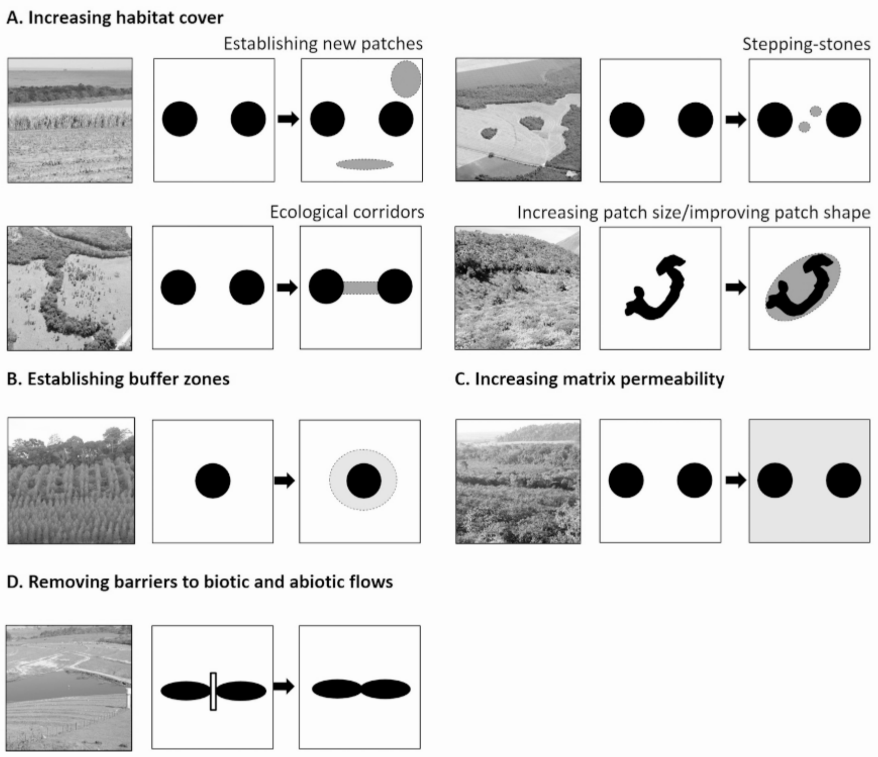

Figure 4-3. Options of structural landscape interventions for local and landscape restoration—(A) increasing habitat cover, which can be done by creating new habitat patches, implementing ecological corridors and stepping-stones, and increasing patch size/improving shape; (B) reducing edge effects by establishing protective barriers at the borders of habitat patches; (C) increasing matrix permeability, and (D) removing barriers to biotic and abiotic flows. The first image of each example illustrates a real situation where such structural interventions apply, and the second and third images are, respectively, schemes of a hypothetical situation before and after local and landscape restoration interventions. The white quadrants represent the original matrix, the black shapes represent habitat remnants, the dark gray shapes with dashed line borders represent restoration sites, the light gray forms new land uses with structure more similar to that of habitat patches, and the white rectangle a barrier established by human intervention in landscapes.

TABLE 4-3.

Main landscape structural interventions for local and landscape restoration (see fig. 4-3).

Structural Interventions	Purpose	Key Issues to Consider	Restoration Examples
Increasing habitat cover			
Establishing new habitat patches and stepping-stones	To reduce the gap distance between isolated habitat patches that were previously united.	Habitat cover in the landscape and matrix permeability: the role of stepping stones is optimized at intermediate habitat covers (reduced cover: distances too great to be crossed in the matrix; high cover: stepping-stones may be useless due to suitable landscape structure) and in a more permeable matrix (Uezu et al. 2008).	Establishing woodland islets within agricultural landscapes to support biodiversity conservation and ecosystem services provisioning (Rey Benayas et al. 2009).
Ecological corridors	To reestablish natural habitat continuity between patches to allow species movement without having to cross nonhabitat zones or to restore connectivity required for critical ecological processes.	Habitat cover in the landscape, corridor width and structure—the role of ecological corridors is optimized at intermediate habitat cover (Baum et al. 2004), and if the corridor is wide enough to mitigate edge effects and mimic the structure of the habitat patches to be reconnected, in order to avoid abrupt changes in environmental conditions (Lees and Peres 2008).	Restored riparian buffers in Brazil preventing water courses pollution by herbicides and being used by forest-dependent bird species to move among remnants in a low permeable matrix (Bicalho et al. 2010; Silva et al.).
Increasing patch size/ improving patch shape	To reduce the edge-to-area ratio in remaining habitat patches.	Patch shape and invaginations: elongated shapes increase the proportion of edges and thus restoration actions should prioritize the increase of patch area in a direction that makes it more circular if edges are disadvantageous for the species. Invaginations have also to be filled by restoration in order to increase the proportion of core zones (Brancalion et al. 2013).	Restoration interventions to increasing patch size/improving patch shape.

TABLE 4-3. *continued*

Structural Interventions	Purpose	Key Issues to Consider	Restoration Examples
Establishing buffer zones around habitat patches	To establish buffer zones between habitat patches and the matrix to mitigate edge effects.	The structural similarity between the habitat patches and the land uses to be implemented in the buffer zones: the higher this similarity, the greater the effectiveness in reducing edge effects (see review in Ewers and Didham 2006).	The establishment of agroforests around remaining forest fragments for conserving a threatened tamarin species (Cullen Júnior et al. 2001).
Increasing matrix permeability	To modify and manipulate matrix units to reduce their resistance to physical and biological fluxes	Matrix permeability is positively associated with the structural similarity between matrix units and the focal native habitat consider for restoration (Donald and Evans 2006).	Establishing commercial tree plantations or implementing silvopastoral systems over pasturelands in landscapes previously occupied by native forests can increase landscape connectivity in Colombia (Calle et al. 2012).
Removing barriers to biotic and abiotic flows	To remove undesirable landscape or anthropogenic elements hampering the natural flow of species and energy-matter in the landscape.	The proper identification of the barrier and of its level of interference in biotic and abiotic flows, as well the impact that removing such barriers may have in species already adapted to the new environmental conditions (Bednarek 2001).	Blowing up dams in streams to recover salmon populations in California, United States (Quiñones et al. 2015).

Taking Advantage of Landscape Structure to Prioritize Sites for Restoration

Restoration actions are usually expensive and need to be optimized. For this reason, several restoration optimization frameworks were recently proposed in order to reduce the costs and increase its benefits. This optimization can be achieved by defining how and where restoration should be done. There is a wide variety of ways to do restoration, going from very expensive and labor-intensive interventions ("active restoration") to less intensive actions, such as ceasing or avoiding human-mediated disturbances to facilitate natural regeneration ("passive restoration") (Barral et al. 2015; Gonzalez et al. 2015). Choosing the appropriate form of intervention will depend on the level of degradation and resilience of the considered system (Holl and Aide 2011), and thus the optimal intervention will vary for different locations. Here, we will see how landscape structure and dynamics can be used to optimize restoration actions.

Prioritization Models/Frameworks Considering Landscape Structure

The speed of ecosystem recovery can be affected by the surrounding landscape structure, as previously explained. Restoration optimization considering the landscape structure has been particularly developed for biodiversity conservation purposes in order to (i) improve biological fluxes in the landscape thereby increasing recolonization or immigration processes (see previous section); (ii) reduce the risks of local extinctions; and (iii) safeguard or recover landscapes containing greater biological diversity.

Several frameworks or methodologies have been proposed for prioritization; some are focused on biological data, while others rely on landscape structural data. For the first, methodologies are usually expansions of conservation algorithms called "systematic conservation planning"; here the optimization of biological attributes (e.g., total or endemic species richness, protection of endangered species) is balanced with the costs of land protection (actual land or opportunity costs; see examples in Thomson et al. 2009; Crouzeilles et al. 2015). In these cases, landscape structure typically plays a secondary role in prioritization and may be used as a tie-breaking factor for areas with similar biodiversity relevance or used to improve the proximity or potential connectivity among selected areas. Such frameworks usually demand high levels of biological data and do not consider an explicit relationship between landscape structure and restoration processes.

More recently proposed methodological frameworks are based on landscape structure and concepts of resilience (Tambosi et al. 2014; Rappaport et al. 2015), considering resilience as the capacity of a landscape to rebound from local extinctions through immigration at the landscape scale. In those frameworks, sites with higher connectivity and more habitat are generally considered best for restoration, but, based on data obtained in the Atlantic forest from Brazil (Pardini et al. 2010; Banks-Leite et al. 2014), a better cost/benefit should be achieved in landscapes with intermediate habitat amount and connectivity (and thus with intermediate landscape resilience). Tambosi et al. (2014) propose that landscapes with high habitat amounts (>60%) will usually have high connectivity and resilience and, thus, will be able to maintain biological integrity through autogenic processes, reducing the need for restoration actions. On the other hand, in highly degraded landscapes with low habitat cover (usually <20%), landscape resilience and connectivity are low, the most sensitive species have already disappeared, and restoration investments should be too high, with limited chances of avoiding species extinctions. Landscapes with intermediate conditions of habitat amount, connectivity, and resilience should be the best cost/benefit areas for restoration actions.

Prioritization Models/Frameworks That Incorporate Landscape Dynamics

Landscape structure alone is not always sufficient for determining optimal restoration areas, because landscape change can occur quickly relative to the subsequent biological responses, such as species extinction (Rappaport et al. 2015). Recently degraded landscapes can often still support ecological processes and assemblages, but over time this will be less and less possible unless actions are taken. This suggests that, the longer a habitat has been degraded, it may be less preferable during site selection. Sites only recently disturbed may have a higher probability of recovery.

Lags in biological response to landscape disturbance are particularly well documented for species extinctions (Diamond 1972; Brooks et al. 1999). The time taken for a community to reach a new equilibrium after disturbance is known as relaxation time, and the number of species predicted to go extinct as the community reaches this new equilibrium is referred to as its “extinction debt” (Tilman et al. 1994). If restoration occurs before this extinction debt is paid, then activities will be more effective in maintaining species within the landscape, and it should be easier to avoid extinction than to promote recolonization.

Knowing past landscape dynamics helps in identifying potential extinction debts and in using prioritization frameworks (Rappaport et al. 2015). Based on the framework presented from Tambosi et al. (2014), a low resilience landscape might be automatically excluded from consideration as a restoration candidate, but when we consider landscape history, the now deteriorated landscape can be recognized as a formerly high-resilience landscape subjected to recent degradation. Given the potential of a lagged biological response, such a landscape might warrant consideration under certain scenarios and objectives (Rappaport et al. 2015). Actually, time lag in biological response can represent an opportunity to avert species loss and the “payment” of outstanding extinction debts (Metzger et al. 2009).

Understanding landscape dynamics can also be relevant to identifying areas that are regenerating naturally and thus, where restoration will be less costly. This is particularly relevant in regions where native habitat regeneration is higher than native habitat loss and habitat amount is increasing. This phenomenon is well documented for some forest habitats (e.g., “forest transition”) and has been responsible for the increase in forest cover in Europe and Central America (Meyfroidt and Lambin 2011). One of the main explanatory hypotheses for this phenomenon is that socioeconomic transformations in society lead to urbanization and a massive migration of people from rural regions to cities (Rudel et al. 2005). Agricultural activities are then concentrated in mechanized lands, with reduced labor requirements, while steep slopes, rocky soils, and other marginal lands previously used for agriculture and cattle ranching are abandoned and can be recolonized by native plant species.

By tracking historical nonhabitat to habitat transitions, it is possible to identify important drivers of landscape regeneration, such as relief; previous and current land uses; proximity to other remnants and water courses; and distance from cities, roads, or ecosystem types (Ferraz et al. 2014). Knowledge about the relative contribution of each of these factors can contribute to the development of maps prioritizing regions with high regeneration probabilities. By selecting those sites, passive restoration strategies can be favored, while expensive interventions typical of active restoration—like weeding and direct seeding in terrestrial ecosystems, and channel modification and species reintroduction in freshwater ecosystems—are avoided. In other words, considering the probability of natural recovery may allow us to take advantage of nature’s natural healing tendencies, a contribution that will be crucial to meet ambitious restoration goals worldwide (Chazdon 2014). This would also increase restoration cost-effectiveness and improve the economic viability of payments for ecosystem services schemes associated with restoration (Birch et al. 2010).

Closing Remarks

Restoration is affected by different ecological processes related to the fragment area and isolation, habitat amount, edges, cross-habitat spillover, landscape connectivity, complementation and supplementation, abundance and movement of individuals, and to abiotic fluxes (flows of energy and matter). In turn, those ecological processes are modulated by the landscape structure, particularly by the composition and heterogeneity of the landscape; the amount, arrangement, and connectivity of the focal habitat; and the spatial arrangement of existing and restored patches. As a result of the relationships between restoration processes and landscape structure, the outcomes of ecological restoration and the speed of recovery can vary widely across space and time. Recognizing and understanding these relationships can be a powerful instrument to optimize restoration benefits while reducing costs. At the same time, restoration provides unique opportunities for landscape ecologists to manipulate landscapes in a controlled manner and test hypotheses about how changes in landscape structure can affect ecological dynamics and functioning. Much remains to be learned at this interface between landscape ecology and restoration ecology, but the result of this research will certainly be crucial to achieve the ambitious global demands for ecological restoration and, thus, to avoid future species extinctions and safeguard the provision of key ecosystem services for human well-being.

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PART II

Ecological Theory and the Restoration of Populations and Communities

Chapter 5

Population and Ecological Genetics in Restoration Ecology

Christopher M. Richards, Donald A. Falk, and Arlee M. Montalvo

Theory and Application

- Genetic diversity holds the key to populations and species to persist through changing environments.
- Genomic data is connecting the ecology with the genetics of adaptation in many diverse species and will play a role in restoration practice.
- The integration of genetic diversity data with spatial and environmental models of species ranges provides new ways to assess the way landscape features influence the rates of connectivity and adaptation in current and future conditions.
- Conservation planning under climate change scenarios requires a recalibration from restoration targets based on historical conditions to those that anticipate adaptive potential.

Genetic diversity is the basis for adaptive evolution in all living organisms. Heritable differences among individuals influence how they interact with the physical environment and other species, and how they function within ecosystems. Genetic composition affects ecologically important form and function of organisms, including body size, shape, physiological processes, behavioral traits, reproductive characteristics, tolerance of environmental extremes, dispersal and colonizing ability, phenology, disease resistance, and many other traits (Lewontin 1974; Hedrick 1985; Booy et al. 2000). Genetic diversity within a species thus provides the means for responding to environmental uncertainty, and forms the base of the biodiversity hierarchy (Stebbins 1942; Noss 1990; Reed and Frankham 2003). To overlook genetic variation is to ignore a fundamental force that shapes the ecology of living organisms.

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Genetic variation thus also holds the key to the ability of populations and species to persist through changing environments over evolutionary time (Frankel 1974; Lande and Shannon 1996; Crandall et al. 2000; Stockwell et al. 2003). The magnitude and pattern of adaptive variation is critical for the long-term persistence of a species, whether endangered or widespread (Allendorf et al. 2010).

Restoration ecologists are often faced with practical consequences of this variation when selecting plant and animal sources for restoration projects. Ecological genetics is thus fundamental to the design, implementation, and expectation of any restoration project, whether or not consideration of the genetic dimension is explicit. For these and many other reasons, genetic variability merits increased attention in restoration practice and research (Rice and Emery 2003; Allendorf et al. 2010; Havens et al. 2015).

In this chapter we outline genetic considerations that are important to the design, implementation, and long-term outcome of restoration in natural habitats. We begin by reviewing how genetic variation is measured and assessed at the levels of individuals and populations. We conclude by highlighting not only how the scale of genomic data has changed analytical approaches, but also how these data are being integrated with spatially explicit models of species distributions and landscape ecology to address key issues in ecological restoration practice, particularly those related to global climate change (Neale 2012; Hamann and Aitken 2013; Williams et al. 2014; Mijangos et al. 2015).

Measuring Genetic Diversity

In order to achieve desired outcomes for restoration projects, metrics of heritable genetic variation can be used to select, deploy plant materials, and monitor establishment. The two basic categories of variation are the *genotype* (the genomic sequence of an individual) and the *phenotype* (the measurable appearance of a trait). Genetic differences exist among individuals, and most populations differ genetically. A *population* is defined as a group of potentially interbreeding individuals that share a common ancestry or gene pool.

The most practical and accessible biological characteristics for restoration are phenotypic variations. Phenotypes interact directly with the local environment, are the objects of selection, and determine reproductive fitness. These traits can be represented by variation in morphology (e.g., root architecture, plant height, branching pattern), physiology (e.g., disease resistance, drought tolerance), and development (e.g., time to emergence and flowering) and many other properties. Often these traits are not discrete or categorical states, but vary in a continuous distribution of phenotypes in a segregating population. A fundamental challenge in quantitative genetics is to distinguish variation in continuous phenotypes caused by genetic and environmental (nongenetic) components respectively (Lynch and Walsh 1998). Partitioning the observed variation in a trait permits evaluation of the relative importance of heritable variation in shaping morphology and other complex traits. Many organisms, however, display a wide variety of phenotypic responses to the environment that are ecologically important but not heritable (*phenotypic plasticity*). This flexibility in phenotype may in itself be adaptively important, and may have a genetic basis (Lande 2014).

The acquisition and analysis of multivariate phenotypic data has become a high priority for agriculture breeding but also provides insights into the evolutionary origins of plant adaptation (Houle et al. 2010; Furbank and Tester 2011). The underlying variation and genetic basis of traits is often referred to as *genetic architecture*. Interest in the architecture of complex traits, their evolutionary adaptive value, and the distribution of quantitative genetic variation in the wild has a long history in evolutionary biology (Clausen et al. 1940; Stebbins 1950; Mather and Jinks 1982; Slate 2005; Anderson 2016). The measurement of heritable phenotypes is directly applicable to defining seed transfer zones where local adaptation may play an important role in population persistence (Hufford and Mazer 2003; Willis and McElwain 2013). Quantitative genetic approaches can generate useful and testable predictions for the evolutionary dynamics of phenotypes subject to selection under changing environmental conditions, such as may be encountered in both disturbed or restored ecosystems, especially in a context of changing climate (chap. 17).

With recent technological advancements and the availability of numerous fully sequenced genomes, emphasis is shifting from the analysis of neutral markers (DNA variation conveying no functional value to adaptive diversity) toward analyses on the genomic scale, which include functionally relevant loci; however, neutral markers still have value in measuring important parameters such as population history, inbreeding, and gene flow. The expansion of molecular approaches has been facilitated by increased computing speed, cost-effective molecular genotyping, and improved technologies for sequencing whole genomes (table 5-1). Data on “the genes that matter” may ultimately play an important role in the management of germplasm resources and restoration ecology by determining the heritable component of ecologically important traits such as growth rate and tolerance for drought or extreme temperatures (Mitchell-Olds 1995; van Tienderen et al. 2002; Howe et al. 2003; Hoffmann and Sgrò 2011).

Several comprehensive reviews have examined current and future impacts of genomic data in the field of conservation genetics and our understanding of the genetic basis of adaptation (Bonin 2008; Allendorf et al. 2010; Frankham, 2010; Ouborg et al. 2010; Williams et al. 2014). The use of genomic polymorphisms extends population genetic inference beyond summary estimates of inbreeding and

Table 5-1.

A comparison of marker systems for evaluation genetic variation

In this table, *genic* refers to markers located in defined regions such as a particular gene, whereas *anonymous* markers are uncharacterized, with an unknown distribution in the genome. *Dominance* of the marker system determines whether (as in a diploid organism) the allelic state of both parental alleles (codominant) or just one (dominant) can be retrieved. *Transferability* denotes how readily markers developed in one species can be used in another. The *potential for estimating selection* is related to whether the marker affects a character under selection (as distinguished from neutral variation). Many marker systems exploit variation in noncoding (presumably neutral or nearly so) regions of the genome, so their variation is independent of selective traits. The *information* criterion of a marker indicates whether the marker gives information about the genotype (both alleles), the haplotype, which is the linear ordered arrangement of alleles found on one (haploid) chromosome, or phenotype. The *development* of these markers varies from technically difficult (requiring specialized equipment and significant investment) to logistically difficult (requiring field space and plot management). *Genomic coverage* denotes to the number of loci that can be reasonable handled in a single study. Abbreviations: RFLP=Restriction Length Polymorphism, AFLP=Amplified Fragment Length Polymorphism, SSR=Simple Sequence Repeat, SNP=Single Nucleotide Polymorphism

Feature	Allozymes	RFLP	AFLP	SSR	SNP	Quantitative Traits
Source of marker information	Genic protein	Anonymous or genic DNA	Anonymous DNA	Anonymous or genic DNA	Genic DNA	Multigenic Morphology and physiology
Dominance	Codominant	Codominant	Dominant (in practice)	Codominant	Codominant	Variable
Transferability	High	Moderate	High	Variable	Variable	High
Potential for estimating selection	Limited	Limited	Limited	Limited	Moderate to high	High
Information	Molecular phenotype	Genotype	Molecular phenotype	Genotype	Genotype, haplotype	Phenotype
Ease of development	Moderate	Technically difficult	Moderate	Technically difficult	Technically difficult	Logistically difficult
Genomic coverage	Low	Moderate	High	Moderate	High	High

drift, helps identify specific genetic loci under selection, and clarifies key relatedness measures and inbreeding (Allendorf et al. 2010). These characteristics will be critical in understanding the genetic basis of adaptive differentiation important in making decisions about resources to use in restoration.

Patterns and Processes of Genetic Structure

The genetic profile of populations typically varies from place to place across a species' range. Differences among populations may arise as the result of chance occurrences, such as the genetic composition of dispersing individuals that create a new population (*founder effect*), or changes in allelic frequencies that result from chance mating and reproductive success in very small populations (*genetic drift*) (Hedrick 1985). Differences among populations can also arise deterministically (i.e., by natural selection), especially if the environment subjects individuals to different selection pressures for survival and reproduction.

Populations can diverge in their genetic composition, especially when there is little gene flow among them (e.g., limited dispersal of seeds, vegetative propagules, pollen, or limited movement of animals across physiographic barriers). Indeed, "populations" are defined as much by patterns of mating and gene flow (historical and current) as by the physical distribution of individuals, although the two are often closely related (Slatkin 1987).

In a restoration context, it is important to distinguish the *census population* (the number of individuals counted) from the *effective population size* (N_e, which is the number of individuals that contribute genes to succeeding generations (Lande and Barrowclough 1987). This number is typically smaller than the number of individuals in a population census, because not all individuals reproduce, and progeny numbers vary (Nunney and Elam 1994). Effective population size and the components of an organism's life-history and breeding system that influence it are important considerations in collection strategies and the management of small remnant or restored populations).

Differences among populations are commonly quantified by the use of statistics such as Wright's inbreeding coefficient (F_{ST}) and Nei's coefficient of gene differentiation (G_{ST}) (fig. 5-1). These indices reflect how heterozygosity is partitioned within and among populations, based on differences in allele frequencies (Wright 1969; Holsinger and Weir 2009). In hierarchical measures such as F_{ST}, G_{ST}, and Q_{ST}, the subscript "ST" indicates the variation in subpopulations compared to the total variation in all the populations combined (but see Edelaar et al. 2011). A value of 0 means that variation is distributed randomly in space, that is, all of the variation observed is due to differences among individuals within populations, and none to differences among populations. In contrast, the maximum value 1 means that all the variation at loci measured is due to differences among populations, and individuals within populations are identical to each other (fig. 5-1). Genomic-level analyses have led to increased understanding of genetic structure of populations and the development of new analytical methods (Hedrick 2005; Weir et al. 2006; Jost 2008; Merimans and Hedrick 2011; Whitlock 2011) that account for dominance and differences in diversity among markers. Quantitative traits can also be examined to reveal hierarchical structure (i.e., within and among subpopulations). The proportion of quantitative trait variance that occurs among populations relative to that for all populations combined is called Q_{ST} (Merlia and Crnokrak 2001).

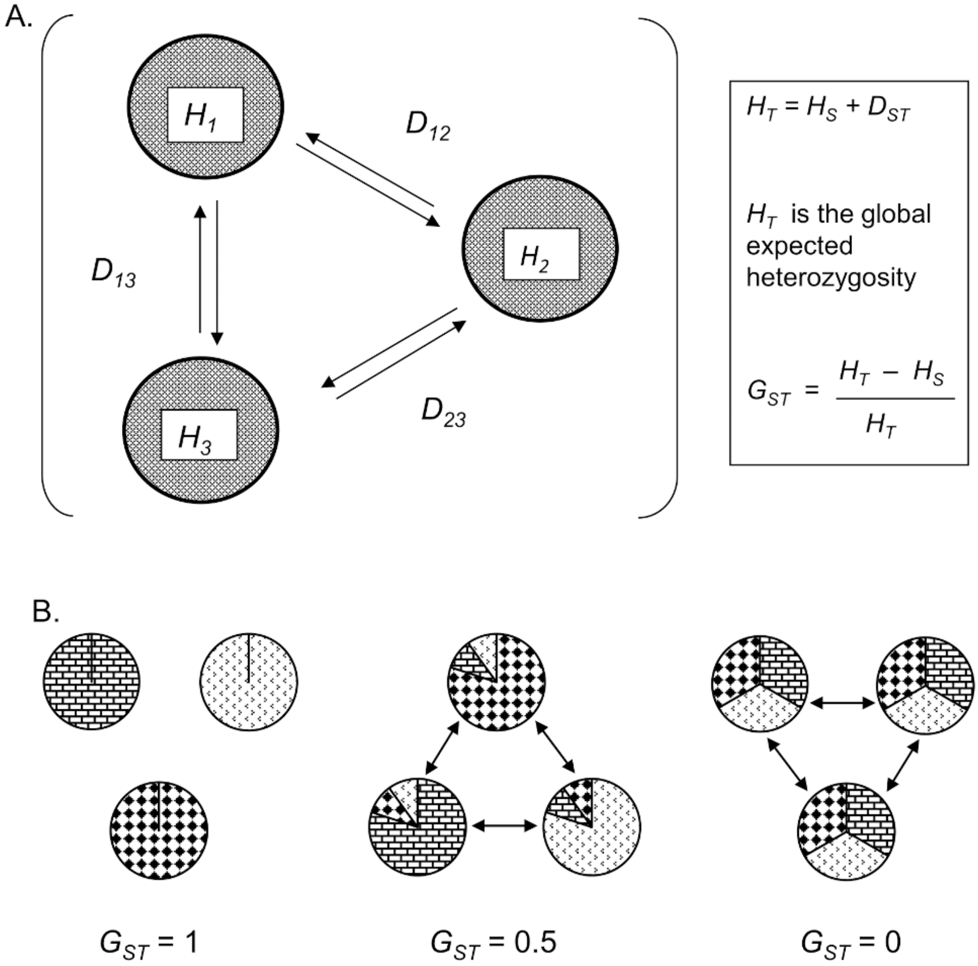

Figure 5-1. Hierarchical nature of population structure, based on Nei (1973).

A. The observed heterozygosity (H_i) for each of three subpopulations is used to calculate the gene diversity (D_{ij}), also sometimes called among population divergence, for each pair of subpopulations. Mean population divergence is D_{ST}. The average expected heterozygosity of the subpopulations is H_S, and the expected heterozygosity for the pooled subpopulations is H_T. Adapted from Meffe and Carroll (1994).

B. Resulting population structure for three hypothetical populations based on one locus with three alleles, with no gene flow, low gene flow, and high gene flow (*left* to *right*). Most studies would utilize data from multiple loci.

Although these descriptive statistics of differentiation and diversity are focused on predefined populations, population boundaries are not always clear. Genotypic clustering approaches have been developed to construct natural groupings directly from the data using models to maximize an equilibrium parameter (like random mating frequencies) in the data set. These clustering methods rely on minimizing the linkage disequilibrium (the nonrandom association of alleles at different loci) that occurs in a mixture of individuals from different populations (Pritchard et al. 2000; Huelsenbeck and Andolfatto 2007; Corander et al. 2008; Duchesne and Turgeon 2009; François and Durand 2010). The development of these assignment methods has shed new light on the boundaries between genetic lineages, enabled the identification of the origins of specific individuals, and has provided new insights into the patterns of dispersal and gene flow.

The emerging field of landscape genetics utilizes features of population genetics, spatial statistics, and ecology (Manel et al. 2003; Storfer et al. 2007; Storfer et al. 2010). Research in this area seeks to develop spatially explicit models that correlate a genetic lineage with topological features in the landscape. The field extends the application of population genetics by creating realistic and heterogeneous migration matrices (pairwise gene flow among populations) with specific information about the configuration and suitability of the intervening habitat (Ewers and Didham 2006; McRae 2006). These approaches test how landscape structure influences genetic subdivision and migration (Storfer et al. 2010) and can inform decisions about genetic resource choices especially when coupled with information about how projected changes in climate might shift locations of suitable habitat for species (Hoffmann et al. 2015; Prober et al. 2015).

Interest in species range distributions has a long history in the fields of biogeography and ecology (chap. 16). The niche can be thought of as the multidimensional set of environmental (abiotic) and biotic conditions in which a species is able to persist (Hutchinson 1957; Colwell and Rangel 2009; Wiens et al. 2010). The retention of niche related traits that are shared among closely related taxa is generally referred to as *niche conservatism* and has important implications for how species respond geographically to the changes in climate and ultimately how restoration is conducted (Jackson et al. 2009). Qualitative descriptions of range occurrences have yielded to more quantitative methods to predict the environmental envelope for individual species (Elith et al. 2006; Franklin 2010; Elith et al. 2011).

Advances in species distribution modeling (SDM) to quantify the realized environmental niche of a species have influenced how we quantify species responses to environmental heterogeneity (Guisan et al. 2013). SDM has become a critical tool for predicting where suitable habitat for species may exist in the future under a range of climate change scenarios (Keith et al. 2008). Indeed, the prospect of climate change has sparked a renewed interest in evolutionary responses to temporal variation (Parmesan 2006; Hoffmann and Sgrò 2011; Shaw and Etterson 2012). Combining SDM and landscape genetics has improved understanding of how species ranges influence patterns of diversity and differentiation. These data have also been used to evaluate fitness and extinction risk in rapid climate change (Urban 2015; Anderson 2016). Understanding both the historic and future habitat suitability may play a role in restoration planning (Vitt et al. 2010; Aitken and Whitlock 2013; Hoffmann et al. 2015).

Sampling Diversity

The genetic diversity of organisms in a restoration site is limited initially by the diversity of the original sample. While other alleles may enter the project area over time (by migration of individuals, dispersal of gametes, or additional reintroduction measures), the starting pool of genetic diversity will govern the performance of a reintroduced population for a period of time.

Various guidelines have been developed for sampling wild populations of plants and animals for breeding and reintroduction (CPC 1991; BGCI 1994; Guerrant 1996; IUCN/SSC 1998; Guerrant et al. 2004; Rogers and Montalvo 2004; Hoban and Schlarbaum 2014). These and other strategies for collecting propagules vary in their purposes and conclusions: some focus on seed collection for long-term banking, while others address the needs of plant material for reintroduction of populations or restoration of habitats. Many sampling guidelines derive in part from early work by Marshall and Brown (1975); subsequent variations emphasize different aspects of collection, such as multilocus diversity and efficiency in collection cost per return in diversity captured (Falk 1991; Volk et al. 2007). Most strategies seek to capture all alleles in a population with a frequency greater than some value (commonly 5%) with a probability of 95%. Although the purposes of collections vary, most guidelines address certain common sampling issues:

1. How many individuals will be sampled from each population?
2. How many populations will be sampled to create the source pool?
3. What is the probability of a collected sample surviving to establishment?

Number of Individuals to Sample within Populations.

The underlying theoretical basis for sampling multiple individuals within a population is that populations are rarely truly *panmictic* (that is, with completely randomized breeding). In plants, a large proportion of mating occurs between neighboring individuals, even when pollination occurs via an animal vector. In animal populations, a wide range of behavioral adaptations commonly concentrates breeding success in a few individuals. The result is that populations are not genetically homogeneous. Multiple individuals need to be sampled to capture a population's genetic diversity adequately.

Volk et al. (2007) reviewed a range of sampling strategies published over the previous thirty-five years and found general agreement when sampling goals are taken into account (e.g., the level of genetic diversity desired, allele frequencies, probability of capture). These sampling strategies represent a minimum collection, however, and the restorationist must also consider the viability and potential attrition of field-collected material through to eventual propagation or reintroduction (see below). For species that are locally rare, large seed collections may be prohibited if they would potentially interfere with the dynamics of the source population; in these cases spreading out sampling effort over multiple years can reduce the impact on population reproductive potential (CPC 1991).

Number of Populations to Sample

In most species, the cumulative amount of genetic variation captured increases as successive populations are added to the sample. However, since populations have some degree of similarity ($0 < G_{ST} < 1$), each additional population added to a sample collects some alleles that are new to the sample, and some that are already present from previous samples. As the number of populations sampled increases, the *marginal diversity rate* decreases (that is, fewer and fewer novel alleles are captured), and the *cumulative diversity function* approaches an asymptote. For a pool of populations sampled at random, there is a point where further sampling across populations provides little or no additional genetic benefit (Falk 1991; Neel and Cummings 2003; McGlaughlin et al. 2015). The number of populations at which this occurs is related strongly to the measure of differentiation among populations, G_{ST}. When G_{ST} is high, populations are more differentiated from one another, so more populations need to be sampled to capture the maximum total diversity. When G_{ST} is low, populations are relatively similar, so sampling from only a few will capture most of the diversity that exists.

Beyond these general patterns, and given the great variability within and among organisms, there are few absolute rules for the number of populations to sample that apply to all taxa of restoration interest. Recent studies by Hoban and Strand (2015) and Hoban and Schlarbaum (2014) employed a simulation approach using simple genetic structures to evaluate the efficiency of sampling methods. Simulation studies have an advantage in isolating specific parameters of interest without confounding effects (Hoban et al. 2012, but see Guerrant et al. 2015). Results from these simulations suggest that tailoring sampling designs to species' life history features can improve collection efficiency. Simulation approaches open up a new avenue of predictive modeling and sampling design specific to the target species.

In the end, what counts in a reintroduced population are the numbers of individuals and their diversity (Harper 1977; Menges 1991; Guerrant 1996; Primack 1996; Montalvo et al. 1997; Leimu et al. 2006). Almost certainly, fewer than 100% of samples (seeds, cutting, eggs, adults) collected in the field will survive to establishment in a restoration site. Attrition occurs at every step along the way: during collection, transportation, storage, propagation/curation, and outplanting/release (Guerrant 1996; Walters et al. 2005, 2013). High initial mortality rates are frequently observed in reintroduced populations, often continuing for several years (Brown and Briggs 1991; Howald 1996).

Population Genetics and Restoration Practice

Environments that vary in time and over space are often described in terms of the *natural* or *historical range of variability* in weather, disturbance events, resource availability, population sizes of competitors, and so forth. (Morgan et al. 1994; White and Walker 1997; Swetnam and Betancourt 1998; chap. 17). In a completely stable physical and biological environment, species may benefit more by maintaining a narrow range of genotypes adapted to prevailing conditions, and allele frequencies may eventually attain equilibrium (Rice and Emery 2003; Pritchard et al. 2013). By contrast, if the environment is patchy, unpredictable over time, or includes a wide and changing variety of diseases, predators, and parasites, then subtle differences among individuals increase the probability that some individuals and not others will survive to reproduce, that is, individuals will vary in *fitness* when traits influencing survival or reproduction are exposed to selection (Adondakis and Venable 2004; Siol et al. 2010).

Identification of Conservation Units

Restorationists are concerned not only about the degree of variability in materials to introduce, but also their geographic distribution and phylogenetic lineage. The most common approach is to specify an ecogeographic range within which source material should be collected (Bower et al. 2014; Jones 2014; Basey et al. 2015; Havens et al. 2015; Prober et al. 2015). This approach is based on the assumption that populations near one another and growing in similar conditions will be more similar. If a population is "genetically local" to a site, it would presumably be adapted to the site and compatible with existing populations of the same species at the site (McKay et al. 2005; but see Jones 2013).

Geographic proximity and genetic similarity, however, are not always highly correlated (McRae 2006; Storfer et al. 2010). Some geographic areas (e.g., California and the Sky Island bioregion of southwestern North America) are highly heterogeneous in topography, soils, and climate at relatively small spatial scales, while other areas (e.g., shortgrass prairies and high plains) are more homogeneous over large spatial scales. Montalvo and Ellstrand (2001) found that the cumulative fitness of crossed populations was affected significantly by genetic distance and environmental factors, but not correlated with geographic distance in a heterogeneous landscape (fig. 5-2).

Combining genetic and environmental data, Reeves and Richards (2014) were able to examine a barrier to gene flow that was not apparent by geographic distance alone (fig. 5-3). When clustering individual genotypes using a Bayesian method (Pritchard et al. 2000), they found that the assignment split coincided exactly with a region of highly unsuitable habitat based on environmental distance or resistance (McRae 2006).

Climatic zones or measures of environmental distance may be better predictors of fitness than genetic distance or geographic distance, especially if there is a *clinal* (continuous gradient) in variation in an adaptive trait (Montalvo and Ellstrand 2000, 2001; Frichot et al. 2013). Furthermore, there are no simple distance rules that apply equally to all species, because species vary in gene flow among populations, population size, and the resulting distribution of diversity (G_{ST}). For some species (e.g., self-fertilizing plants in small, isolated patches of habitat, or fishes in isolated stream reaches), each site may reflect a unique local adaptation, and the geographic range of suitable genotypes can be very small (a few km^2). Other species with higher rates of gene flow (for example, those with wind dispersed pollen and seeds) and those with larger effective populations, are generally less differentiated over the landscape and can be collected across wider ranges.

Mix or Match? The Genetic Impact of Translocations

Just as the initial species planted have strong effects on restoration outcomes (chap. 9), the starting pool of genetic variation is a critical element in the design and implementation of a restoration project, but opinions differ on how much explicit attention should be given to the genetic component. For example, the primary goal for a population-level restoration project may be variously (1) reintroduction of a species that has been extirpated; (2) restoration of critical habitat components (such as nesting structure or food plants) for a species of interest; (3) demographic or genetic augmentation of an existing but reduced population; or (4) planting “ahead of the curve” to anticipate climate-driven shifts in suitable climate. Genetic variation is relevant in all of these contexts. Restoration experiments may

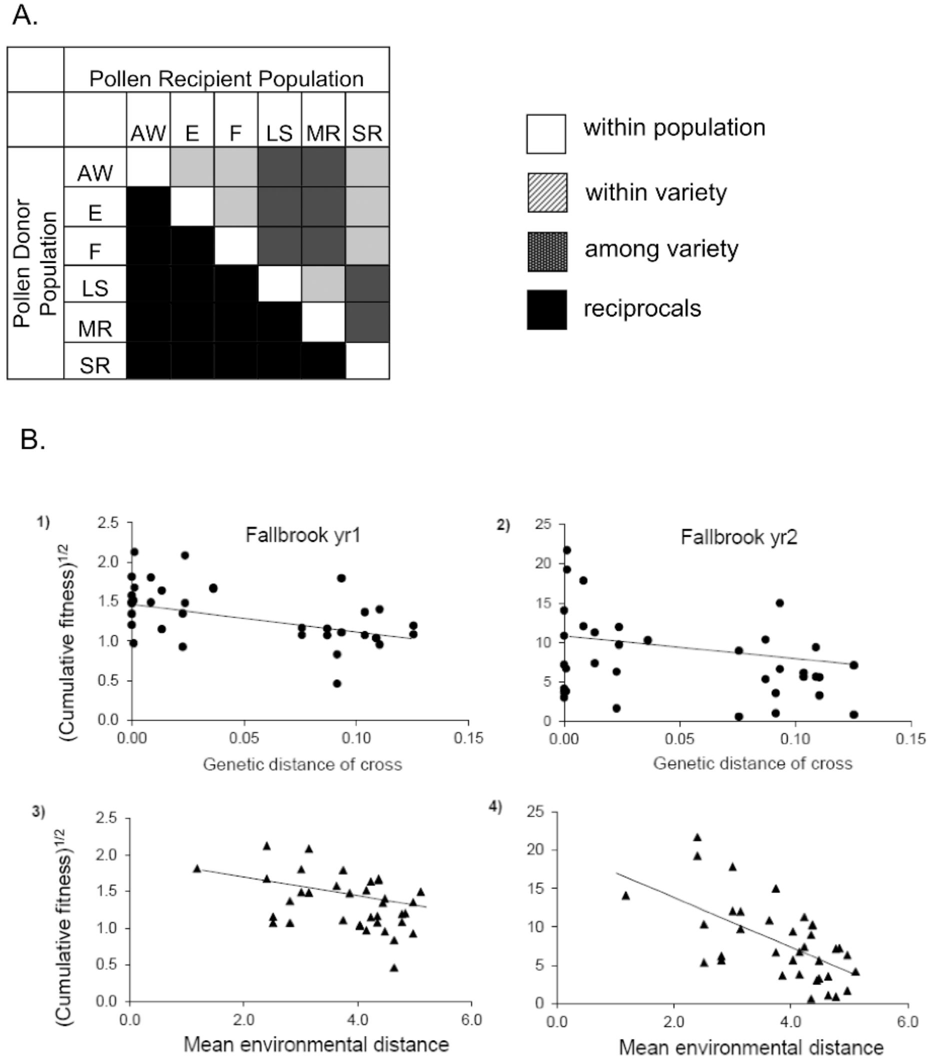

Figure 5-2. Outbreeding depression and local adaptation in *Lotus scoparius*.

A. Experimental crossing design used to test for outbreeding depression. Plants from populations listed across the top of the diagram served as mothers, while other plants on the vertical axis served as fathers. The cells below the diagonal represent the reciprocal of those crosses shown above the diagonal.

B. Cumulative fitness of progeny planted at one of two common gardens, plotted as a function of genetic distance of the crossed parental populations (1 and 2), and as a function of the mean environmental distance of the parental source sites to the common garden site (3 and 4). For each variable, data are shown for the juvenile phase (1 and 3) and at maturity (2 and 4). In this study, genetic distance and mean environmental distance significantly predicted success of hybrids, whereas geographic distance was not a significant predictor of fitness. Figures adapted from Montalvo and Ellstrand (2001).

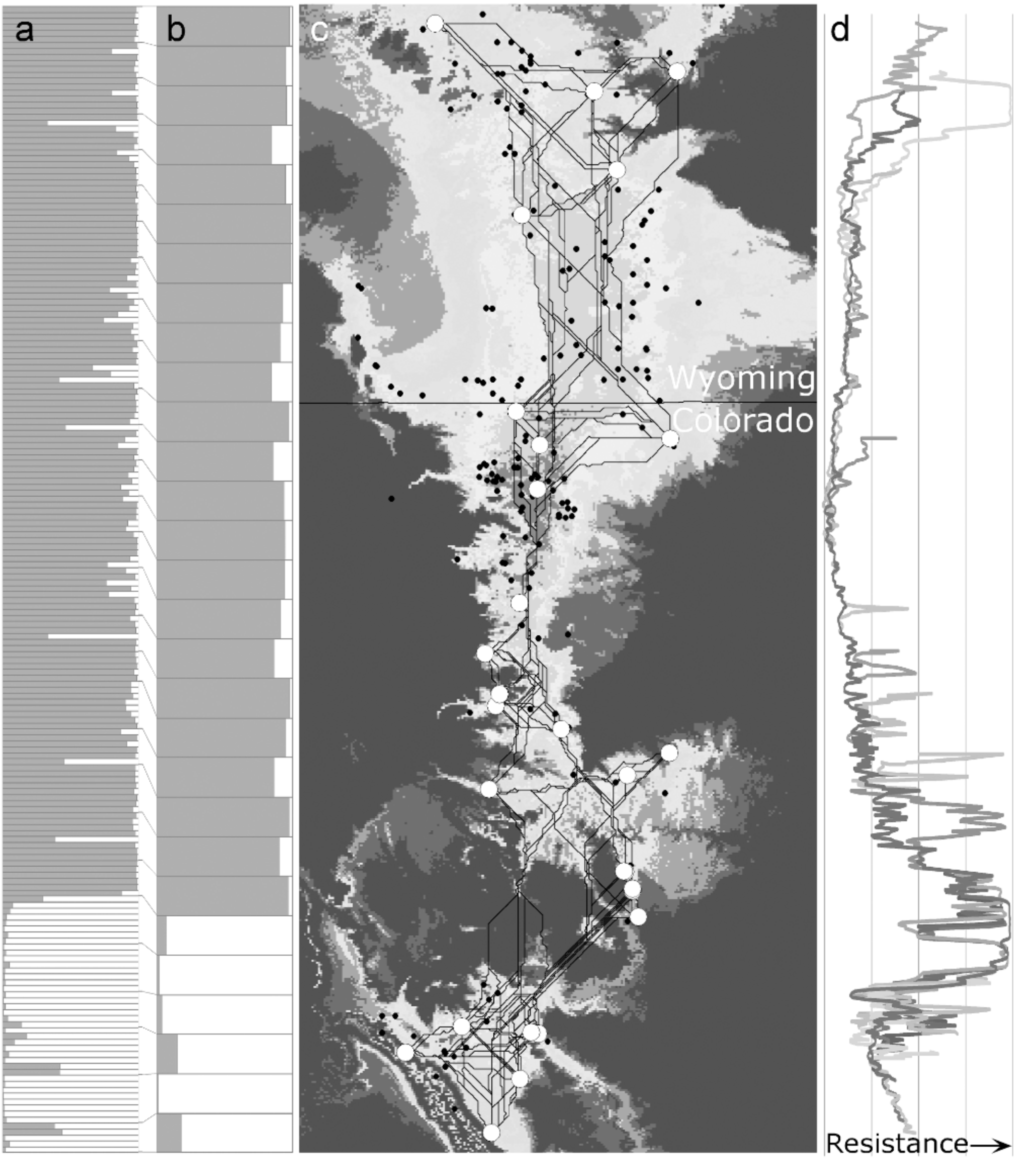

Figure 5-3. Combining genetic and spatial data.

White circles are samples for genotyping at 16 SSR loci for *Helianthus pumilus* in its native range from southern Wyoming into central Colorado. Black dots are historic species occurrences used for SDM development. Lines mark least cost paths inferred between sampled populations across the habitat suitability surface where the habitat suitability is high with warmer coloring. A. genetic discontinuity, visualized in STRUCTURE assignments of populations to two clusters (*left* panel), is coincident with a region of unsuitable habitat in the niche model (*center* panel), where resistance to migration is high (*right* panel). Adapted from Reeves and Richards (2014).

prove useful in testing the effect of combining propagules from multiple populations. Studies have shown that the immediate local population can be wanting in genetic diversity, and that sometimes augmenting the local gene pool can be highly beneficial (Havens et al. 2015). However, careful strategies are needed to mix or match populations in a way that will increase fitness and evolutionary potential while minimizing risks (Aitken and Whitlock 2013; Hoffmann et al. 2015; Prober et al. 2015; Waller 2015).

Since few reintroductions can replicate past populations exactly, questions about genetics are often pragmatic: "How similar is this source population to the population we wish to augment?" "Should we combine material from multiple source populations?" "Which is the more immediate threat: genetic, demographic, or environmental stochasticity?" These are difficult questions with few general answers (table 5-2) (Clewell 2000). In the case of a wilderness manager restoring a high-quality reference site, the goal might be complete fidelity to the historic distribution of genotypes. This standard can be difficult to achieve, however, and also ignores the possibility that populations are not at genetic equilibrium. By contrast, the highest priority for a restoration project in a severely degraded ecosystem may be to establish a functional plant community for which tolerance of extreme conditions may be paramount, especially if changing climate is a factor (Stockwell et al. 2003; chaps. 16 and 17).

Homozygosity at key gene loci is a common result of *inbreeding*, which is mating among closely related individuals. Populations that are small, isolated, or subdivided into small groups because of restricted dispersal can be particularly susceptible to inbreeding and *inbreeding depression*, which reduces overall fitness of organisms with low heterozygosity. If populations that have been fixed for different alleles are crossed, *heterosis* (increased vigor of hybrids) in progeny may indicate inbreeding depression in the parental population (Keller and Waller 2002). Such increases in fitness are known as *genetic rescue*, which occurs when new genetic material is added to inbred populations (Hedrick 1995; Richards 2000; Ingvarsson 2001; Tallmon et al. 2004; Whiteley et al. 2015; Frankham 2015; Hufbauer et al. 2015).

Heterozygosity is not always beneficial, and inbreeding does not always have adverse effects on the fitness of populations (Waser 1993; Byers and Waller 1999). In some circumstances, a population may be so well adapted to local circumstances that introducing alleles from other populations actually reduces its performance once populations hybridize (the extrinsic or ecological form of *outbreeding depression*) (Waser 1993; Tallmon et al. 2004). Alternatively, isolated populations may have diverged and become so genetically distinct, even if adapted to similar environmental conditions, that they suffer chromosomal mismatches, cytoplasmic incompatibilities, or loss of coadaptation when hybridized (the intrinsic, or genetic forms of outbreeding depression) (Templeton 1994; Fenster and Galloway

Table 5-2.

Types of population-level restoration

Restoration materials can be native to a project site or brought in from elsewhere. If a species is not native to a project site, genetic appropriateness of the plant material can differ compared to when a species is resident or connected to nearby resident populations by gene flow. Introduction, reintroduction, and augmentation may involve both rare and common species. See Falk and Holsinger (1991), Gordon (1994), and Rogers and Montalvo (2004) for discussion.

Term	Definition
Type of restoration	
Introduction	Species or genotypes not presently at the project site, and not known to have existed there previously, are established at a site. Species may or may not be native to broader geographic area.
Reintroduction	Reestablishment of species or genotypes not presently at the project site, but which did occur there in the past (population was extirpated and reestablished).
Augmentation	Individuals of a species are added to a site where the species occurs presently (also called *restocking*).
Type of restoration material	
Resident	Species, populations, or genotypes native to a local site. These can be extracted from a local site for onsite restoration or augmentation.
Translocated	Genotypes collected offsite for planting or release at a project site within the natural range of the species. Differs from usage in Gordon (1994).
Introduced	Species, populations, or genotypes collected offsite and introduced to a project site outside their historical range.

2000; Montalvo and Ellstrand 2001; Galloway and Etterson 2004; Walisch et al. 2012). The reduction in fitness due to these genetic incompatibilities can depend on multiple factors, including relatedness of hybridizing populations, genetic architectures, and environmental conditions (Edmands and Timmerman 2003; Rogers and Montalvo 2004; Walisch et al. 2012; Aitken and Whitlock 2013).

There is no one best choice of seed sources for restoration (provenancing) that circumvents all risks of inbreeding depression, outbreeding depression, habitat fragmentation, and shifts in habitat suitability caused by climate change. Many different collection strategies are possible, ranging from strictly local to various types of composite mixtures, and decisions need to be based on what is known about a particular plant and a weighing of probable risks. Progress has been made in modeling the risks to different types of populations along a provenance strategy continuum and in providing decision frameworks for their use (Walisch et al. 2012; Breed et al. 2013; Havens et al. 2015; Hoffmann et al. 2015; Prober et al. 2015).

The gene pools of many remnant native populations have been seriously eroded, such that what persists today is a small remnant of the original diversity. Small gene pools are more prone to inbreeding, as well as random genetic change from drift. Populations that formerly exchanged genes regularly may have also become genetically isolated by habitat fragmentation and other dispersal limitations (Schwartz 1993; Young and Clarke 2000; Gustafson et al. 2004). In such cases, a credible argument can be made to bring together genetic material from several nearby populations, in effect replacing the natural (but now disrupted) processes of gene flow (Tallmon et al. 2004; Bouzat et al. 2009; Whiteley et al. 2015; Frankham 2015). In addition, some restoration sites may be so heavily disturbed (i.e., mine tailing reclamation areas) that the most geographically local population is no longer the one best adapted to the new growing environment (Stockwell et al. 2003; chap. 16). In such circumstances, inclusion of diverse genotypes may increase the chances that at least some plants will survive. (Case Study Box 5-1).

Restoration Genetics in the Context of Climate Change

For restoration ecology, the theoretical rate of evolution under equilibrium conditions may be less important than the more dynamic rates of species divergence under scenarios of projected climate change (Neale 2012; chap. 15). In many regions, current climate projections to 2100 involve increases in mean temperature fifty times faster than at any time in the previous 5,000 years (Parmesan 2006; Stocker et al. 2013; chap. 17). Such rapid environmental change will almost certainly drive the displacement of populations from their current locations; major species range shifts, and selection for traits such as drought resistance. If (and this is by no means certain) their seeds or pollen are dispersed into the new location, the population can “migrate” across the landscape over generations (McLachlan et al. 2005; Kremer et al. 2012; Corlett and Wescott 2013). By contrast, populations with a narrower range of genotypes may lag in their adaptive rate relative to climate change and fail to survive and reproduce as conditions become less favorable locally (Wilczek et al. 2014). Such populations are more likely to become *extirpated* (locally extinct).

Conservation planning under climate change scenarios requires a recalibration from restoration targets (including the genetic component) based on historical conditions to those that anticipate change and adaptive potential (chaps. 15, 17). This will require predictions of genetic responses derived from evolutionary theory (Etterson et al. 2016). For example, seed and hardiness zones may no longer be viewed as absolute barriers to movement of propagules, especially experimentally (Broadhurst et al. 2005). Adapting to climate change will require an ever-increasing integration of scientific approaches, including spatial modeling, population genetics, and climate forecasting. Sampling for restoration projects

Case Study Box 5-1
Restoration Genetics of the Hawaiian Silverswords

The Hawaiian Islands are known for their spectacular globally endemic plants, perhaps none more than the silversword alliance (Asteraceae). Along with Darwin's finches and African cichlid fishes, the silverswords and related genera are the result of one of the best-documented episodes of adaptive radiation, which began with a single colonizing founder 5.2 ± 0.8 MYA, most likely a perennial herb from western North America. The alliance now constitutes a monophyletic lineage of thirty-three known species in three genera (*Argyroxiphium*, *Dubautia*, and *Wilkesia*). Many of these species are endemic to a single island and limited in population size. As a consequence, they are highly threatened by a variety of causes, particularly browsing and trampling by nonnative ungulates, competition, and altered fire regimes from introduced exotic plants, loss of native insect pollinators, and seed and seedling predation by alien rodents and slugs.

The Mauna Kea silversword (*Argyroxiphium sandwicense* subsp. *sandwicense*) of Hawaii Island is an alpine species that was formerly common at high elevations (2,600–3,800 m) on the slopes of Mauna Kea, the highest volcano in the Hawaiian Island chain (fig. 5.4). Nonnative ungulates (initially sheep, but over time also mouflon sheep and goats) were introduced by European explorers beginning in the 1790s. By 1820 ungulates had reached the subalpine zone, and by the 1930s there were more than 40,000 exotic animals grazing the slopes of Mauna Kea. As a result of heavy grazing pressure, silversword populations plummeted until only about 100 known individuals remained in the 1970s, and about 40 by the mid-1990s, limited to crags and cliffs that sheep could not reach.

Silverswords are long-lived monocarpic plants, living fifteen to forty-five years before flowering only once and dying. In 1973, botanists collected seeds from two plants that flowered in the remnant population. The Hawaii Division of Forestry and Wildlife used these as the basis of a propagation effort that eventually resulted in over 800 outplanted individuals by the late 1990s. However, the inclusion of only two maternal founders in this initial reintroduction created a severe genetic bottleneck. Compared to the remnant natural population, the outplanted population had significantly reduced polymorphism at sampled loci, possibly including those that regulate self-incompatibility. Only three loci were detectably polymorphic in the outplanted population compared to eleven polymorphic loci in the remnant natural population, which appears to contain levels of genetic variation at random amplified polymorphic DNA (RAPD) loci comparable to the closely related and more abundant Haleakalā silversword (*A. sandwicense* subsp. *macrocephalum*) on the island of Maui. A later study using microsatellite loci found a similar reduction in number of effective alleles per locus, expected heterozygosity, and proportion of polymorphic loci in the reintroduced population (fig. 5.5).

The discovery of two flowering plants in the remnant population in 1997 allowed the inclusion of additional maternal founders. Flowering plants were hand pollinated to maximize outcrossing over the spatial extent of both the natural and outplanted populations. Over time additional remnant individuals have flowered and been sampled and used for crossing and F_1 outplants. Since 1999, more than 11,000 seedlings have been outplanted by the Hawaii Division of Forestry and Wildlife and its partners.

Case Study Box 5-1 continued

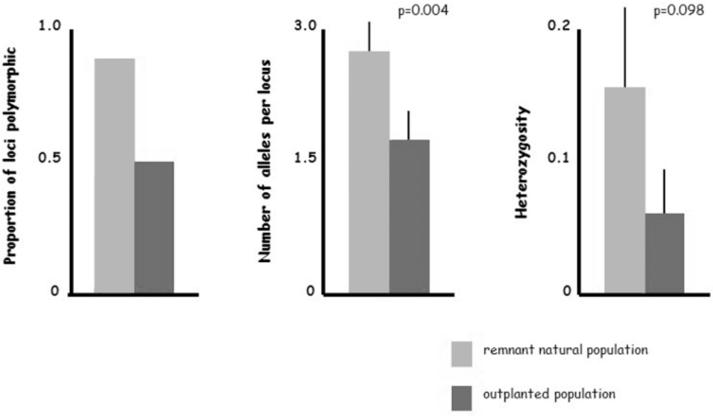

Figure 5-4. Proportion of loci polymorphic (*left* panel), observed number of alleles per locus (center panel), and observed heterozygosity (*right* panel) in the remnant natural (gray bars) and outplanted (black bars) populations of the Mauna Kea silversword (*Argyroxiphium sandwicense* subsp. *sandwicense*). Figure courtesy of R. Robichaux; data from Friar et al. 2000.

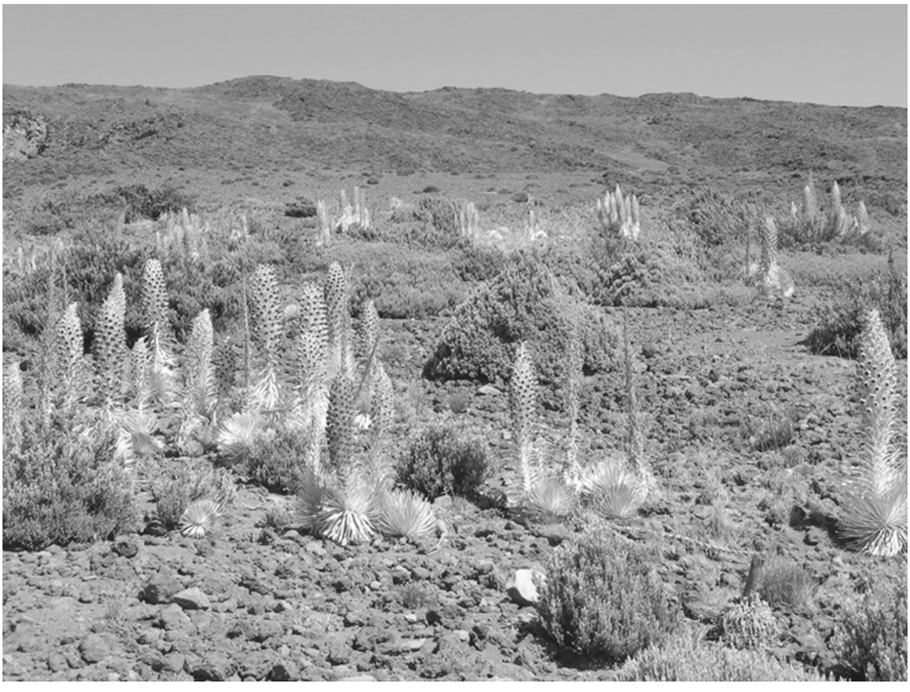

Figure 5-5. Outplanted population of the Mauna Kea silversword (*Argyroxiphium sandwicense* subsp. *sandwicense*) in subalpine, shrubland habitat on the upper slopes of Mauna Kea volcano on the Island of Hawaii. Photograph courtesy of R. Robichaux.

Case Study Box 5-1 continued

A similar effort with the Kaʻū silversword (*A. kauense*) in Hawaii Volcanoes National Park on Mauna Loa has resulted in more than 20,000 outplanted seedlings derived from 169 founders being reintroduced into restored habitats, with the genetic pedigree of every seedling documented. These species-level reintroductions have been closely linked to landscape restoration at large scales on federal, state, and private lands.

Reintroduction and restoration programs often focus on demographic parameters (population size, age, and sex ratios) but neglect equally important elements of genetic diversity. Genetic bottlenecks associated with population reintroduction based on a relatively small number of founders could impair population adaptability to changing environmental conditions as well as expose the population to inbreeding depression, especially in self-incompatible species. Conservation efforts for the Hawaiian silversword alliance over the past twenty years are a leading global example of the importance of including genetic considerations in population- and species-level reintroduction and restoration programs.

References: Carr 1985; Falk and Holsinger 1991; Falk et al. 1996; Friar et al. 2000; Robichaux et al. 1997, 1998; Baldwin and Sanderson 1998; Friar et al. 2000; Schluter 2000; Baldwin 2003; Purugganan and Robichaux 2005; R. Robichaux, pers. comm.; Robichaux et al., forthcoming.

will have to be informed by species-specific vulnerability assessment (Williams et al. 2008; Havens et al. 2015). Meeting these challenges will require a new focus on diversity (rather than relying strictly on local ecotypes) to develop genetic variation able to respond to environmental changes. New approaches, including assisted gene flow and assisted migration, are changing a field once focused on maintaining the status quo to one contending with rapid change (Havens et al. 2015; Aitken and Whitlock 2013; St. Clair et al. 2013; Williams and Dumroese 2013; chap. 17).

For example, in a study of blackbrush (*Coleogyne ramosissima* Torr.), a desert shrub found in southwestern North America, researchers refined seed transfer guidelines to incorporate expected climate change after coupling the results of a genecological model based on common garden tests of many populations across a range of environments (provenance tests), with predictive niche modeling that incorporated the overlap among six contrasting climate models (Richardson et al. 2014). Furthermore, with a focus on expected range changes in regionally common species that are key contributors to the structure of communities, others have been working to identify and integrate networks of interacting species and their environments to predict the broader impacts of environmental change (Ikeda et al. 2014). Such studies are too consuming to achieve for most species or specific restoration projects, but as studies accumulate, informative patterns may emerge among species that share distribution and life-history attributes.

Closing Remarks

In the most general terms, any restoration practitioner or scientist should be aware of the degree of genetic diversity with which s/he is working. Restoration researchers, planners, and managers should understand how plants and animals they use were generated, by asking the collector, propagator, or breeder how the material was obtained, and what steps were taken to ensure the presence of a suitably wide range of genotypes. While clonally produced flats of thousands of identical plants may offer short-term advantages of predictable response to current growing conditions (as they do for agricultural crops), such populations may be less likely to persist in the face of disease, competition, and environmental variability. Of course, knowing the methods by which individuals or material was produced provides genetic information only by inference; it is uncommon to have good genetic data ahead of time for reintroduction efforts (Robichaux et al. 1997, 1998).

The differentiation of populations across the range of a species remains at the heart of the genetic dimension in restoration ecology. Species distribution models are providing testable hypotheses for assessing the geography of genetic diversity. Despite the search for universal and simple rules, population genetics shows us that species vary in their dispersal rates and distances, and hence in rates of gene flow and the degree of genetic differentiation among populations. These differences are often correlated closely with life-history attributes particular to each species. This leads us to conclude that the most relevant guidelines for restoration ecology will often be species-specific. If populations are highly divergent, reflecting either the neutral effects of isolation and small population size, or the diversifying effects of selection, the restoration ecologist must seek to understand this variation.

Can restoration ecology contribute to basic research in population genetics? We have argued that population and ecological genetics are important sources of ideas and information for restoration. We also maintain that restoration ecology has a great deal of unique value to offer to the field of population genetics in return (chap. 1). Restoration ecology is particularly well configured to contribute empirical tests of genetic drift, founder events, breakup of coadapted gene complexes and maladaptation, inbreeding and outbreeding depression, reduced gene flow, adaptation to climatic and environmental extremes, and small effective population size, all of which are possible outcomes of the restoration process itself. These are all promising areas of research in restoration genetics.

Several progressive strategies are being explored, such as the BLM's National Seed Strategy for Rehabilitation and Restoration 2015–2020 (http://www.blm.gov/wo/st/en/prog/more/fish__wildlife _and/plants/seedstrategy.html), involving federal agencies, the Plant Conservation Alliance, and others to organize networks of native seed collectors, farmers, nurseries, seed storage facilities, and restoration ecologists to figure out how to put "the right seed in the right place at the right time."

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Chapter 6

Ecophysiological Considerations for Restoration

Sarah Kimball, Jennifer L. Funk, Darren R. Sandquist, and James R. Ehleringer

Theory and Application

- Ecophysiological traits can be used to determine tolerances to environmental conditions and to estimate rates of nutrient cycling.
- Measurements of traits related to light, water, and soil nutrient acquisition may help practitioners select plant palettes for restoration projects.
- Trait differences between native and nonnative species may be used to assemble invasion-resistant communities.
- Comparing ecophysiological traits between plants in restored and intact communities provides an additional metric for defining the success of restoration projects.

Plant restoration activities can be positively or negatively affected by changes in the abiotic or biotic environment from that of the pre-disturbance condition, such as invasion by nonnative species and changes in aboveground microclimate, soil structure, or soil nutrients. A thorough understanding of the ecophysiological mechanisms of adaptation that describe the potential for a plant to persist in a habitat allows a more accurate assessment of the impact of an altered environment on future plant performance and restoration outcomes. This feature of plants is often referred to as *tolerance*. Plant species vary in their capacity to tolerate different biotic and abiotic stressors, and this tolerance can be the basis for why some species are capable of reestablishing themselves quickly in a restoration setting, whereas the reestablishment of other species proceeds more slowly, if at all. Individual plants also vary in the rate at which they take up carbon, nitrogen, and water, and these differences will influence rates of nutrient cycling and other ecosystem functions. Ecophysiological traits that influence ecosystem functioning are referred to as *effect* traits (Suding et al. 2008).

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This chapter describes how measurements of ecophysiological traits can explain a plant's tolerance to variations in abiotic and biotic conditions and its capacity to cycle nutrients in ecological systems. We describe the basic light, water, and soil nutrient requirements of plants, as well as plant responses to variation in the availability of these requirements. We also describe how commonly measured ecophysiological traits can be used to predict restoration outcomes, to assess the success of restoration projects, and to aid in the design of restoration projects.

Ecophysiological Measurements

Measurements of ecophysiological traits can provide valuable information to restoration practitioners and researchers (Taiz and Zeiger 1998; Cornelissen et al. 2003; Lambers et al. 2008). Trait measurements may be used to assess the health of individuals, the quality of the environment, the environmental tolerance of species (their ecological niche), and the role of a species within the community (McGill et al. 2006; Violle et al. 2007; Fortunel et al. 2009). When average species trait values are weighted by their abundance to calculate community-weighted mean trait values, they can also provide information on ecosystem-level processes such as nutrient cycling (Diaz et al. 2007; Lavorel 2013). Trait data can help with decisions regarding necessary site preparation, selections of species to add to the landscape, and methods for removing invasive species (Kimball et al., 2015). Measurements may also be used to assess ecosystem processes, something that is increasingly suggested as a measure of the progress or success of restoration projects (Benayas et al. 2009; Wortley et al. 2013).

Several ecophysiological traits are routinely measured to determine tolerance and rates of nutrient cycling (table 6-1). Commonly measured leaf-level traits include instantaneous photosynthetic and transpiration rates, typically measured with portable gas exchange systems containing infrared gas analyzers, or IRGAs. With an IRGA system, it is possible to measure the rate at which carbon is fixed (photosynthesis) and water is lost (transpiration) under ambient or manipulated conditions. The ratio of carbon gain to water loss is a measure of drought tolerance or water-use efficiency (WUE). Many IRGAs allow users to alter the CO_2 concentration available to plants, leaf temperature (within a small range), and available light, making it possible to collect response curve data from which critical maximum and minimum values, as well as optima and thresholds, can be determined (Farquhar et al. 1980; Harley et al. 1992). Leaves can also be collected and processed to determine carbon content, nitrogen content, and stable carbon isotope ratios. The ratio of heavy to light stable isotopes of carbon in a leaf is correlated with long-term intrinsic WUE (Farquhar et al. 1989).

Measurements at the branch or whole-plant level, including growth rate and

Table 6-1.

Some frequently measured physiological traits, common abbreviations, units of measurement, and how they are measured, followed by what high values of such traits can indicate in terms of environmental conditions (compared among sites), environmental tolerances (compared among species), the ecological niche (for a given species), and effects on ecosystem processes (using community-weighted metrics across species).

Trait	Units	Measured	Environment	Tolerances	Niche	Ecosystem Processes
Maximum photosynthetic rate (A_{max})	µmol CO_2 m^{-2} s^{-1}	Gas exchange system with infrared gas analyzer	Favorable	Suitable for environment	Competitor	High C cycling
Water-use efficiency (WUE)	µmol CO_2 mol^{-1} H_2O	Gas exchange system with infrared gas analyzer	More xeric	Ability to tolerate dry conditions	Stress tolerator	Low water cycling
Midday water potential (Ψ_{md})	MPa	Pressure chamber	Mesic	Lower ability to tolerate dry conditions	Less stress tolerant	High plant water flux
Relative growth rate (RGR)	g g^{-1} day^{-1}	Size through time	Favorable	Suitable for environment	Competitor	High NPP; High C cycling
Leaf longevity (LL)	days	Mark leaves and revisit	Less favorable	Greater stress tolerance	Stress tolerator	Low nutrient cycling
Specific leaf area (SLA)	g m^{-2}	Determine leaf area, divide by dry weight	Favorable	Suitable for environment	Competitor	High nutrient cycling
Root mass ratio (RMR)	g root g^{-1} plant	Harvest plants, separate roots, dry and weigh	More stressful	Ability to tolerate dry conditions	Stress tolerator	More even water cycling throughout year
Leaf N content (leaf N)	mg g^{-1}	Grind up leaves and analyze content	More N available for uptake	Higher growth potential or greater cold tolerance	Colonizer	High N cycling
Intrinsic water-use efficiency ($\delta^{13}C$)	‰	Grind up leaves; analyze stable isotope ratios (send to stable isotope facility)	Xeric	Ability to tolerate dry conditions	Stress tolerator	Low water cycling

leaf longevity, require marking individual plant modules and returning to take measurements through time, or by performing sequential harvests of individuals in the same population through time (Hunt et al. 2002). Harvesting an individual plant and measuring leaf, stem, root, and reproductive material enables determination of biomass allocation patterns, such as root:shoot, specific leaf area (SLA, the ratio of leaf area to leaf mass), and root mass ratio (RMR, the ratio of root mass to total biomass). Predawn and midday water potential measurements on stems can be collected with a pressure chamber, providing information on soil water availability and plant water stress, respectively (Slatyer 1967).

Many traits are typically correlated, leading ecologists to search for the ideal mix of non-redundant traits that provides information about where species fall along different trade-off axes (Westoby et al. 2002; Reich 2014). For example, a global analysis of six leaf traits from 2,548 plant species identified trait correlations that differentiated species with short leaf lifetimes, fast gas exchange rates, and high nutrient concentrations from those species with long leaf lifetimes, slow gas exchange rates, and low nutrient concentrations (Wright et al. 2004). Some studies suggest that parallel trade-offs occur belowground. For example, specific root length (SRL) indicates greater absorptive root length per unit biomass, so it may be the belowground analog of SLA. Species with a high resource acquisition strategy might have high SRL, high root respiration rate (Tjoelker et al. 2005), and low root lifespan (Eissenstat et al. 2000; McCormack et al. 2012). Many studies measure belowground biomass allocation (table 6-1), such as RMR and root-to-shoot biomass ratio (R:S), to assess species' responses to water and soil nutrient availability (Drenovsky et al. 2008; Funk and Zachary 2010). However, root-to-shoot and other allocation ratios may not be good predictors of resource acquisition (Aerts and Chapin 2000). For example, species may achieve high water uptake with a low root allocation but high SRL, suggesting that morphological and physiological traits should be examined in concert. Similarly, while the global pattern of leaf trait correlations suggests that only a few key traits need to be measured, some community types (such as those dominated by herbaceous species) show different patterns of leaf trait correlations (Funk and Cornwell 2013). Thus, measurements of multiple traits are likely necessary to provide the most useful information for restoration.

Ecophysiological Requirements and Stressors

Understanding the environmental conditions required for plants to persist may be critical to the success of restoration projects. Below, we describe the importance of light, water, and soil nutrients, providing examples for how these abiotic requirements and stressors influence plants in restoration settings.

Light

Photosynthesis is the basic process whereby the simultaneous capture of carbon dioxide from the atmosphere and of photons from the sun results in the formation of the organic compounds used as the building blocks of growth in plants (Lambers et al. 2008). In general, neither of these two essential substrates for photosynthesis differs in concentration between pristine habitats and disturbed sites undergoing restoration. What may differ, though, is the light profile within the vegetation, which may be altered due to physical disturbance or invasion by nonnative species with different phenology, growth rate, or maximum height than natives. Since plant species differ in their light tolerances and preferences, it is important to consider whether light availability at a site matches the needs of plants to be restored (Baltzer and Thomas 2007).

Photosynthetic light saturation can occur at light levels that are as low as 5%–20% of midday sunlight for leaves of understory plants or shade leaves of large trees (Givnish 1988; Funk and Lerdau 2004). Two factors that determine the light level at which photosynthesis does not increase further are stomatal conductance and leaf protein content (typically estimated by leaf nitrogen content). Each of these factors respond to the plant's growth environment (e.g., soil nutrient availability, vapor pressure deficit), with the upper limits often well correlated with leaf life expectancy (Reich et al. 1999). Stomatal conductance is a measure of how open the stomatal pores are that allow the inward diffusion of CO_2 for photosynthesis. Since stomatal pores also control the outward flux of water, water stress (described below) tends to result in reduced stomatal conductance (to prevent water loss) and consequently lower photosynthetic rates. The same applies for protein content. Since the majority of leaf protein is associated with photosynthetic activity (Evans 1989), reduction in leaf protein content will reduce photosynthetic rates, particularly under water stress. The successful establishment of plants in a restoration setting will thus depend on a sufficient supply of nutrient resources to build plant tissues and support photosynthetic activities, and adequate water supplied to leaves to maintain stomatal conductance and the inward diffusion of CO_2.

Exposure to light levels far greater than those experienced during development, such as for greenhouse plants transplanted to the field, or shade plants exposed to higher light levels than they might experience under more natural conditions, can create a significant challenge for plants in a restoration context. *Photoinhibition* (a reduction of photosynthetic rates at high light levels) can occur when leaves are exposed to sunlight above the light saturation point, as shown in figure 6-1 (Adir et al. 2003; Demmig-Adams 2003). The effects of photoinhibition can include a reduction in photosynthetic capacity and loss of chlorophyll (bleaching), potentially causing leaf mortality and leading to reduced plant establishment. The excess light energy absorbed beyond light saturation can oxidize and damage cellular components unless a mechanism is available to dissipate this energy. Some species have evolved protective mechanisms, such as xanthophyll, that can minimize the damage to leaves caused by excess light availability (Adir et al. 2003; Demmig-Adams 2003; Adams et al. 2004). Sometimes light levels are too high for these protections to be effective, as for plants that naturally grow in shade but are exposed to high light during transplanting, or plants exposed to water stress and high temperature conditions.

In sites needing restoration, shade-loving plants may need to be shaded during establishment, and this can occur by planting next to existing "nurse plants" that facilitate establishment (Butterfield and Briggs 2011). High light levels in disturbed sites can also be problematic due to increased competition from fast-growing, shade-intolerant invasive species (Cabin et al. 2000; Loh and Daehler 2008; Chen et al. 2013). Working in a disturbed Hawaiian rainforest, Funk and McDaniel (2010) found that shading with mesh screens reduced the growth of invasive grass species and increased survival and growth of native woody seedlings.

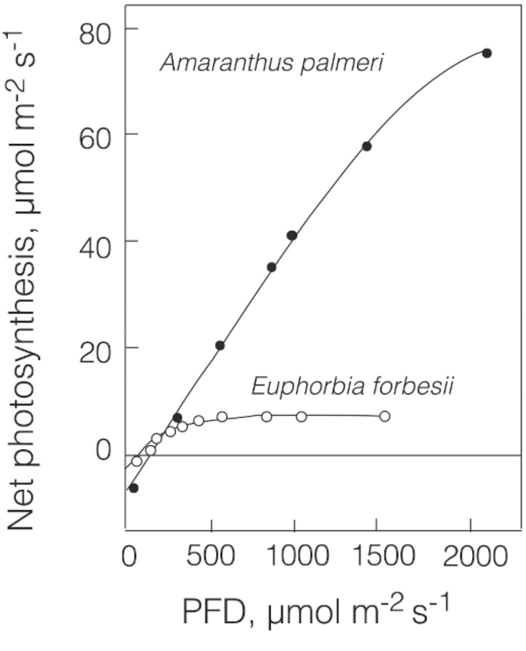

Figure 6-1. The response of photosynthesis (µmol/m^2/s, as measured with an infrared gas analyzer) to changes in light availability (Photon Flux Density in µmol/m^2/s) for two C_4 species adapted to different light conditions. *Amaranthus palmeri* is a desert annual, adapted to high light environments. *Euphorbia forbesii* is a shade adapted species from the forests of Hawaii. Note the correlation between maximum photosynthetic rate and sunlight level at which photosynthesis saturates. Modified from Pearcy and Ehleringer (1984).

While shading structures might not be feasible on large scales, reestablishing the canopy through seeding or planting of fast-growing native species can lower light levels and promote the growth of slower-growing, shade-tolerant native species. Restoration practitioners may also be challenged by systems that receive too little light. The recruitment of native tree seedlings in a seasonally dry forest in Hawaii was suppressed due to shading by alien fountain grass (*Pennisetum setaceum*), demonstrating that restoration, especially by natural recruitment, must be preceded by removal of fountain grass (Cabin et al. 2000). Similarly, native shrub establishment in a California coastal sage scrub community was inhibited when fast growing annuals shaded the shrub seedlings. The authors concluded that some type of weed maintenance (e.g., mowing, manual pulling) and planting of native perennials without native annuals is required for native perennial establishment in that system (Kimball, Lulow et al. 2014).

Solar radiation also affects microclimate variation that contributes to the small-scale topographic heterogeneity influencing natural and restoration success of both plant and animal systems (chap. 10). For example, plants may experience a microclimate in which air and leaf temperatures near the soil surface can be significantly hotter during the day and significantly cooler at night than those experienced at greater heights (fig. 6-2). During the day, the sun's energy is absorbed by the soil surface, potentially raising surface temperatures to dangerously high levels on sunny days. A portion of the surface heat is transferred to the air by convection, raising the air temperature nearest the surface, and creating an air temperature profile that is hottest near the ground (fig. 6-2). Metabolic activities, such as rates of photosynthesis and respiration, are a function of leaf temperature, so we would expect the highest rates to occur in leaves nearest the soil surface. However, near-surface temperatures can also exceed critical maximum temperatures, thereby posing a thermal stress, especially for establishing seedlings, since their rooting depths, water transport capacities, and carbon reserves are likely to be lower than for mature, established plants. Environmental variation also influences plants at a larger scale, such as through slope aspect and steepness. Slopes that receive more solar radiation will be warmer and drier, and this will influence plant performance (Kulpa et al. 2012). For example, when identical methods were used to restore native plant cover to a highly degraded site in California, cover on the north-facing slope was significantly higher than on the south-facing slope three years after seeding and planting (Kimball et al., 2015). Although native grass and forb establishment was impacted by slope aspect, native shrubs were able to establish fairly well on both slopes, indicating practitioners in this system may have greater success restoring shrubs than other functional groups on south-facing slopes (fig. 6-3).

Leaf temperatures often can be elevated 1°C–10°C above air temperatures (Funk and Lerdau 2004; Lambers et al. 2008). Leaf temperatures will rise until

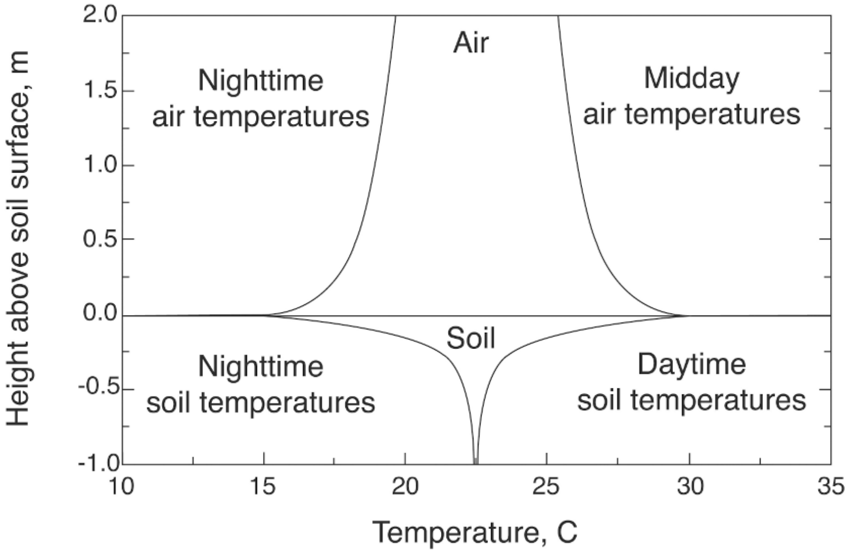

Figure 6-2. Microclimate profile of air temperature as a function of height above the soil surface during midday and nighttime conditions.

the energy absorbed by a leaf equals the energy dissipated by re-radiation, convection, and transpiration. If leaves are able to transpire at a high rate or if leaves are small so that convection rates are potentially high, then leaf temperatures may be similar to air temperatures. However, seedlings with large leaves near the surface, or leaves not able to dissipate heat through transpirational cooling, will have higher temperatures than that of the adjacent air. Over time, these elevated leaf temperatures can result in dehydration and leaf mortality. In restoration settings, seedlings are frequently planted with tree guards to reduce herbivory, but an experimental study in Australia found that plastic tree guards increased leaf temperature and mortality, while guards constructed out of shade cloth created a more favorable microclimate for seedling establishment (Close et al. 2009). Adding shading structures, utilizing existing nurse plants, or reestablishing canopy trees can also promote favorable microclimates: they reduce the net energy load incident on the seedling (Loh and Daehler 2008; Funk and McDaniel 2010).

At the critical stage of seedling establishment, spring nighttime conditions at the soil surface in some habitats can also represent a thermal stress. This is because at night the coldest part of the microclimatic profile on a bare surface is at the soil surface (fig. 6-2). Here energy is lost by re-radiation; the radiative loss from the soil is greater than the absorption of infrared radiation from a nighttime sky, resulting in low soil and leaf temperatures. During early spring conditions in temperate regions, frost may develop at the soil surface as a result of this thermal imbalance.

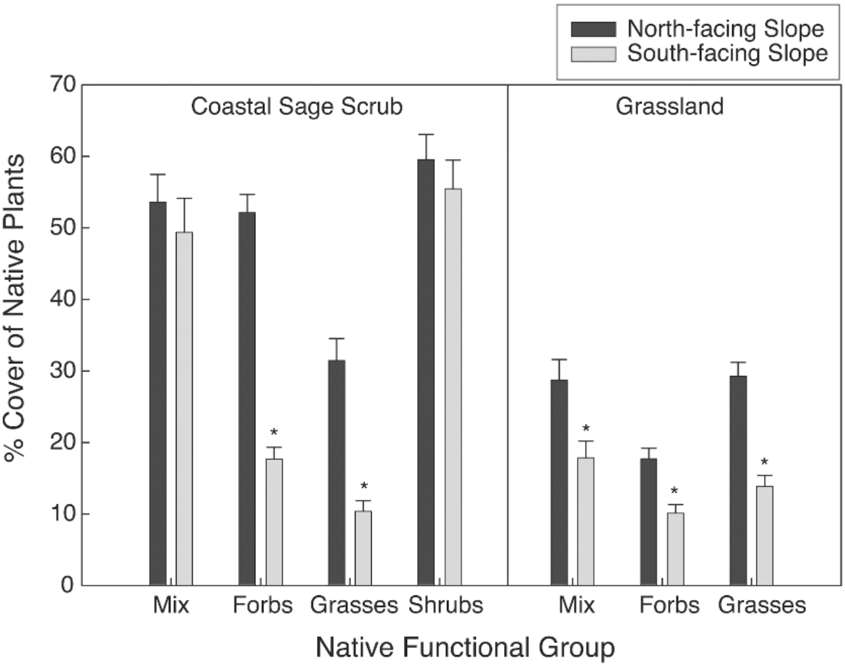

Figure 6-3. Post-restoration % cover of native plants on North- and South-facing slopes. Identical methods were used to restore native coastal sage scrub and grassland species on each slope, but aspect had a significant effect on the establishment of grasses and forbs. * indicates cover on S-facing slopes was significantly lower than N-facing slopes for that functional group of plants. Data are from the West Loma Ecological Restoration Experiment (described in case study box 6-1).

Cold tolerance can be a major limitation to seedling establishment in restoration of shrub (Hou and Romo 1998) and tree seedlings (Gurney et al. 2011), making it important to select cold hardy species. Tissues of emerging seedlings at the soil surface are most vulnerable to freezing stress, which can often be avoided by leaf and bud tissues that are raised 5–10 cm above the soil surface. Frost damage to seedlings may be minimized by adding protective structures or by planting seedlings under the canopy of existing nurse plants to prevent radiative heat loss from the soil (Scowcroft and Jeffrey 1999; Curran et al. 2010).

The capacity to use light is also influenced by biochemical differences among the three major photosynthetic pathways: C_3, C_4, and CAM (Taiz and Zeiger 1998; Sage and Monson 1999). However, owing to slow growth rates and relatively low abundances of CAM species worldwide, only C_3 and C_4 photosynthesis are particularly relevant to restoration activities in most cases. C_3 photosynthesis is the ancestral pathway common to all taxonomic lines (Ehleringer and Monson 1993; Sage and Monson 1999). C_4 photosynthesis is a modification of the C_3 pathway that spatially restricts the C_3 photosynthetic cycle to the interior portions of a leaf thereby preventing *photorespiration*, a process that occurs when rubisco (ribulose bisphosphate), the key enzyme in the first step of carbon fixation, combines with atmospheric oxygen rather than CO_2. C_4 plants tend to have higher photosynthetic rates relative to C_3 plants because they lack photorespiratory activity. They can also have higher growth rates, particularly in warm climates. Not surprisingly, many of the most common invasive species on disturbed sites in temperate to tropical regions possess C_4 photosynthesis. C_4 grasses, including species in the genera *Andropogon* and *Pennisetum*, have been particularly well studied and can have significant impacts on rates of nutrient cycling and fire frequency (D'Antonio and Vitousek 1992; Reed et al. 2005; Litton et al. 2008). Restoration in communities invaded by C_4 grasses can be stymied by high fire tolerance and nitrogen use efficiency of C_4 grasses, rendering common management practices, such as fire and reduction of soil nutrient availability, less effective (Stevens and Falk 2009).

Water

The acquisition of water via belowground plant structures may be significantly altered in a restored habitat, owing to effects on both water availability and plant function (i.e., uptake and transport). The former is primarily a hydrological issue, influenced by soil properties, soil salinity, and climate (Sperry 2000). However, ecological effects such as differences in rooting depths and structures (Schenk and Jackson 2002), competition for water by neighboring plants (Ehleringer et al. 1991), and hydraulic redistribution of water from deep to shallow depths (Burgess et al. 1998) can also play an important role in altering the availability of water resources. The absence of canopy trees has also been shown to increase leaf-to-air vapor pressure difference, which leads to increased transpiration of remaining plants, and hastens drought and water stress in the system (Lambers et al. 2008). This negative feedback can lead to slow but pronounced changes in species function and composition, resulting ultimately in type conversion to a relatively more xerophytic flora, an alternative state that may be resilient to restoration (Suding, Gross, and Houseman 2004). For example, in the Hawaiian dry forest, conversion to nonnative grasses has led to competition with natives for water, making it difficult to establish native trees in restoration projects (Cabin et al. 2002). Alternatively, removing canopy species can benefit native recruitment in systems experiencing drought. The removal of invasive canopy species in tropical systems, which reduce soil water availability through high rates of transpiration and rainfall interception, can lead to higher soil water availability for establishing native species despite higher midday vapor pressure deficit (Michaud et al. 2015). Similarly, in the southwestern United States, canopy thinning results in higher access to water by native Ponderosa pines because the practice allows more snow to reach the soil surface, increasing soil moisture recharge (Kerhoulas et al. 2013).

Water acquisition can be increased by mycorrhizal associations (found in many species) and by specific plant adaptations, including hydraulic lift (generally defined as the movement of soil water through root systems from areas of high water availability to areas with lower water availability) and direct interception of moisture, such as fog (Lambers et al. 2008). Facilitating the maintenance or recovery of these biotic contributions to resource enhancement may be particularly crucial to restoration. For example, hydraulic lift by key tree species within eastern deciduous forests can enhance water availability in the upper soil layers, not only to the tree species itself, but also to many forb and herbaceous species in the tree's immediate proximity (Dawson 1993, 1996). Fog-water interception and subsequent fog drip caused by redwood trees in the coastal forests of northwestern California have been shown to contribute substantial portions of the monthly water consumption by understory species (Dawson 1998). In the absence of these tall trees, summer soil moisture input for understory and shrub species would be nil since rainfall is absent during the summer in this ecosystem. Water that condenses onto redwood foliage can directly enter the leaf, which is where the water is most needed (Burgess and Dawson 2004).

Following uptake, the transport of water through a plant is achieved by the presence of a water potential gradient from the site of water uptake (the soil) to the site of water loss (air). Commonly referred to as the soil-plant-air continuum (SPAC), this water transport mechanism is largely passive, driven by leaf-level transpiration, but because transport depends on the maintenance of this gradient, it is critical that management of each end-member (soil and air) accompany restoration of the transport medium (plant). Although the SPAC gradient is passively derived, the actual water fluxes are regulated by biotic factors such as stomatal function and hydraulic architecture, and environmental factors such as the leaf-to-air vapor pressure difference (Sperry 2000; Sperry et al. 2002; McDowell et al. 2010).

Leaf stomata have the greatest effect on regulating water fluxes from plants (Jones 1998). Stomata are sensitive to both plant water status and relative humidity, and generally close during periods of water stress (Kozlowski and Pallardy 2002; Sperry et al. 2002). There is no single stomatal response exhibited by all plants to humidity and water-deficit stresses; rather, stomatal pores of different species exhibit a wide range of sensitivities. Cultivated and noncultivated populations of the same species can also exhibit differences in rates of stomatal conductance and carbon fixation, potentially influencing the competitive environment in restoration settings (Lambert et al. 2011).

Rates of stomatal conductance also reflect environmental conditions, including moisture levels in the air and the soil. The California native shrub, *Salvia api-*

ana, exhibited lower stomatal conductance during the first year of growth when seeded with native forbs than when seeded in a mix of native shrubs without forbs (case study box 6-1; Bell et al., forthcoming). These results suggest greater water usage by the herbaceous forbs compared to perennial shrubs, and demonstrate how the selection of plant palette can influence water use (fig. 6-4). Determining the abiotic goals of a restoration project in advance (for example, increased versus decreased amounts of surface water flow) will allow practitioners to select plants with ecophysiological traits that help achieve those goals.

Differential rooting depths, such as that found between shrubs and herbaceous species, and variable sensitivities of stomata to humidity describe a fundamental water-relations challenge in restoring species within arid ecosystems. Facilitation by shading to alter the microclimate can be a viable mechanism permitting species with differing rooting depths to become established. Maestre et al. (2001) established three desired shrub species (*Medicago arborea*, *Quercus coccifera*, and *Pistacia lentiscus*) in a Mediterranean restoration setting using the tussock of *Stipa tenacissima* (alpha grass) to facilitate establishment. In this case, it is likely that the differential use of soil moisture in surface and deeper soil layers by the grass and shrubs species, respectively, afforded an opportunity to both reduce the radiation load on developing perennials and avoid competition for water at depth. With better knowledge of the differential rooting depths for water uptake of juvenile

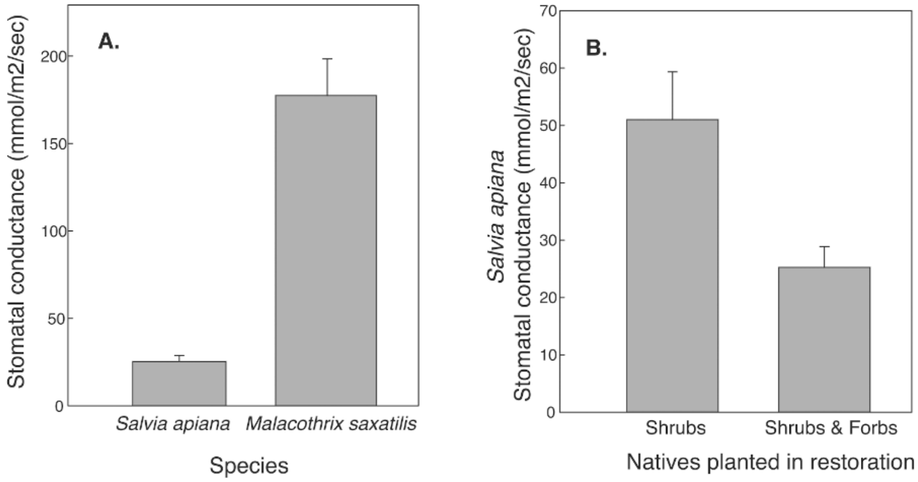

Figure 6-4. A. Stomatal conductance values for the shrub, *Salvia apiana*, and the herbaceous forb, *Malacothrix saxatilis*, measured in the same restoration plot in coastal sage scrub (Santa Ana Mountains, CA). B. Conductance values for the shrub, *Salvia apiana*, when planted with other native shrubs and when planted with a mix of shrubs and forbs.

Case Study Box 6-1
The West Loma Ecological Restoration Experiment

By Sarah Kimball, Travis E. Huxman, and Megan Lulow
Collaboration between UC Irvine's Center for Environmental Biology,
the Irvine Ranch Conservancy, and OC Parks

Santa Ana Mountains, CA: Different combinations of native Coastal Sage Scrub and Grassland species were added to the landscape, which was initially dominated by Eurasian grass and forb species. Restoration was conducted in strips with functional groups (shrubs, forbs, and grasses) seeded alone or in combination to determine the mixture of natives with community-weighted traits that best limit subsequent invasion by nonnative species.

Case Study 6-1. Student interns with the Center for Environmental Biology collect plant density data on the top of the South-facing slope at the West Loma Ecological Restoration Experiment. In the background, blocks restored to coastal sage scrub and native grassland on the North-facing slope are visible.

Test of theory: Incorporation of ecophysiological traits that may be used to assemble invasion-resistant communities (hypothesis of limiting similarity). The limiting similarity hypothesis predicts that communities are more resistant to invasion when they contain natives with traits similar to the most common invasive species.

UC Irvine's Center for Environmental Biology collaborated with the Irvine Ranch Conservancy and OC Parks to test this hypothesis by restoring natives with a diversity of trait combinations. Trait measurements were conducted on native and nonnative species, and community-weighted trait values were related to the abundance of nonnative species in the different plots.

Expected outcome: Plots with the highest functional diversity values and with community-weighted mean values most similar to abundant nonnatives would be more resistant to invasion by nonnative species.

Case Study Box 6-1 continued

Progress: In the first year, invasibility did not differ among seed mixes, but each native functional group had greater establishment in plots with lower native diversity. After three years of growth, shrub-only plots were less invaded, which appeared to be related to these plots containing natives with greater cumulative water extraction capacities that suppressed invader performance.

References: Fargione et al. 2003; Emery 2007; Kimball et al. 2014b; Kimball et al. 2015; Bell et al. forthcoming.

and adult perennials, it is possible to devise irrigation routines that increase the probability that perennials will become established in a restoration setting.

Over the past few decades, it has become clear that plant hydraulic architecture plays a fundamental role in governing the flow of water through plants (Maherali et al. 2004; McDowell et al. 2011). Given that water in the xylem is held under tension, low soil moisture availability and high evaporation demand can cause xylem within plant stems and roots to lose its conductive ability (i.e., cavitate), resulting in a disruption of water flow from the soil to the transpiring leaf surfaces. Different plant species have contrasting "vulnerability" curves, which describe the relationship between the plant water potential (a measure of water stress) and xylem cavitation (a measure of the plant's ability to move water between roots and leaves) (fig. 6-5). The xylem tissues transporting water between roots and shoots of species from more mesic habitats tend to cavitate at higher plant water potentials (Maherali et al. 2004). The steep changes in cavitation that can occur over a narrow water potential range underscores the importance of maintaining adequate soil moisture or selecting less vulnerable species during the development and establishment of plants in a restored community.

Variation of water availability, uptake and transport, and the factors that affect them in restoration settings should follow patterns similar to those found under natural conditions. Specifically, in light of the altered soil conditions typical of most projects, future restoration efforts would benefit from designs that explicitly incorporate the ecological importance of water relations, especially if the restoration objectives include efforts to recover some semblance of a normal or sustainable hydrological cycle. Indeed, because water availability is found repeatedly to be the resource most limiting to plant and ecosystem production (Knapp and Smith 2001; Huxman, Smith et al. 2004), recognizing the factors that govern water acquisition and transport is critical to restoration programs. The choice of native plants in restoration projects can influence local hydrologic processes such as runoff. For example, restoring a heavily grazed site from nonnative, invasive

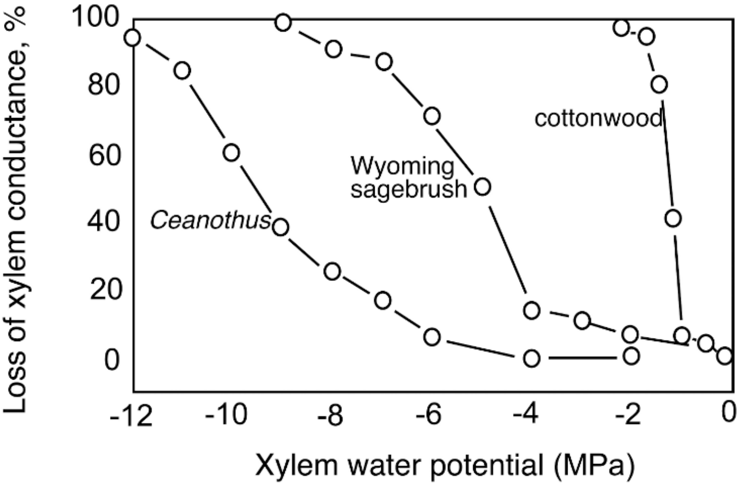

Figure 6-5. Vulnerability curves for three contrasting perennial species, showing loss of xylem conductance (xylem embolism) within the plant hydraulic system as a function of plant water potential. Modified from Sperry (2000).

grasses to grassland would likely result in greater surface flow of water than restoring the same area to shrubland. In mixed communities, plant species often exhibit pronounced differences in rooting properties, with root density and effective rooting depth for water uptake varying within the soil profile (Dawson and Ehleringer 1998). Additionally, rooting zones differ between juvenile and adult plants for many perennial species (Donovan and Ehleringer 1992, 1994). As many restoration projects involve planting perennials as seedlings, there may be increased competition for water during the initial year of plant establishment, when the young perennials have similar root depths to annuals and perennial grasses (Eliason and Allen 1997; Schenk and Jackson 2002; Bell et al., forthcoming).

The timing of rain events, in addition to the total amount of precipitation, has important implications for plant fitness (Huxman, Snyder et al. 2004; Kimball et al. 2012). Since patterns of precipitation are expected to change in response to increasing atmospheric CO_2 levels, this becomes important to consider when selecting plant palettes for restoration. Rare plants are increasingly being transplanted beyond their current ranges to match predicted future climate predictions (Kreyling et al. 2011). Measurements of ecophysiological traits can be a key tool in identifying environmental preferences, and such knowledge could be applied to restore sustainable plant communities for future climatic conditions. While this idea has been identified in academic studies for both plant and animal communities (Laughlin 2014), we are unaware of any management projects that are actively restoring communities for future climatic conditions. Extreme events are likely to increase in frequency along with climate change, and this suggests careful selection of restoration sites (chap. 17). Steep slopes, for example, present challenges to plant growth due to continual erosion, but such slopes may become even more difficult to restore during years with large rain events (Bochet et al. 2009).

Soil Nutrients

Most plants take up nutrients through their roots, specifically through root hairs that probe the aqueous soil environment surrounding a root. A common practice in restoration settings is to supply some of the critical macronutrients for plant growth—particularly calcium, iron, magnesium, nitrogen, phosphorus, and sulfur—as fertilizer (Bloomfield et al. 1982; Bradshaw 2004). Mineral nutrients, such as nitrate and ammonium, are highly soluble in soil water and have a relatively high diffusion rate in a water solution, facilitating their uptake. The uptake of nutrients by roots is an active energy-dependent process, in contrast to the uptake of water, which is a largely passive process. The uptake of minerals is facilitated by their solubilities, but this also makes these same minerals highly leachable from soils, especially in high-precipitation environments such as rain forests (Paul et al. 2010; Marschner 2012). Of the mineral elements extracted from the soil, nitrogen is the element needed in highest concentration within leaves as an essential component of proteins (particularly the photosynthetic enzyme rubisco), pigments, and nucleic acids, which explains why high additions of nitrogen are particularly important (Bradshaw 1983, 1984). Many pioneer species that establish readily in restoration settings are nitrogen-fixers, including rhizobial and actinorhizal plant species (Macedo et al. 2008). These plants have evolved mutually beneficial relationships with soil bacteria that convert atmospheric nitrogen into ammonium, which the plant uses in exchange for carbon. While some restoration efforts use nitrogen-fixing plant species to help replenish soil nutrient availability following disturbance (Griscom and Ashton 2011), they can be problematic invaders that impede restoration efforts, particularly in nutrient-poor soil (Funk 2013).

Often the root surface area and lateral extension of root hairs are inadequate to provide sufficient uptake of all essential nutrients available in the soil. This is particularly true for phosphorus, an essential element that has a low solubility and low diffusivity in the soil water solution. Thus, associations with mycorrhizal fungi are essential to establishment and nutrient (especially P) uptake by most higher plants (Bolan 1991; Jeffries et al. 2003). Fungal hyphae are able to extend up to several orders of magnitude farther away from the root than can root hairs, creating such a wider effective mineral-uptake domain that many plants fail to grow or have significantly reduced growth rates in the absence of their symbiotic mycorrhizal partners (Allen et al. 2003). Disturbance processes (e.g., strip-mining activities, atmospheric nitrogen deposition, or desertification) often disrupt plant-microbe symbioses, requiring that seeds or transplanted seedlings on restoration sites be provided a fungal or bacterial inoculum (Egerton-Warburton and Allen 2000; Requena et al. 2001; Siguenza et al. 2006). Areas dominated by nonnative species show decreased numbers of the mycorrhizae required by natives. The reduction may be due to weaker associations between mutualists and nonnative plants or due to exudation of allelopathic chemicals by the nonnatives that are toxic to the soil micro-biota (Callaway and Ridenour 2004; Vogelsang and Bever 2009). In many restoration cases the microbial symbionts can be provided to the system by collecting and reserving the surface soils during the initial disturbance process, then adding back this soil during restoration. If pre-disturbance soils are not available, mycorrhizal inoculum may be collected from nearby sites dominated by natives and added to the restoration site along with native seeds or plants (Renker et al. 2004). Using local innocula results in higher increases in mycorrhizal colonization than inocula from commercial sources (Maltz and Treseder 2015).

In contrast to nutrient limitations, many ecosystems are receiving excessive nutrient additions through fertilizer runoff and atmospheric deposition (Vitousek et al. 1997). Increased soil fertility can cause problems for some restoration efforts because nutrients stimulate the growth of invasive species (chaps. 8, 12) with more competitive resource acquisition traits such as high SLA and A_{max} (table 6-1). In addition, increased soil nitrogen may limit the growth of native pioneer species that associate with N-fixing bacteria (Kimball, Goulden et al., 2014). Many studies have attempted, with some success, to reduce soil N availability by adding carbon, typically in the form of sugar or sawdust, to the soil (Zink and Allen 1998; Corbin and D'Antonio 2004; Suding, LeJeune, and Seastedt. 2004). Adding carbon stimulates microbial activity and N immobilization, and has been demonstrated to suppress the growth of fast-growing invaders and promote the growth of stress-tolerant natives. For example, sugar addition to a California desert system invaded by the annual grass *Schismus barbatus* reduced biomass of the invader relative to natives when applied in years where rainfall patterns stimulated early germination of the invader (Steers et al. 2011). However, when a large, early-season rainfall event stimulated the germination of both *S. barbatus* and native species, N immobilization resulting from sugar addition suppressed the growth of all species, including natives. Additionally, these treatments may need to be applied every year as the microbial population turns over and N is returned to the soil (Steers et al. 2011), making this application most effective under certain conditions (e.g., dry years) and for restoration of small areas.

Disturbed sites in need of restoration often also differ from more natural habitats by an abundance of toxic elements in the soil (Antonovics and Bradshaw 1970; Bradshaw 1984; Wong 2003). The three most common mineral-related challenges to restoration are highly saline soils, soils with altered pH levels, and high-metal-toxicity soils. The physiological impacts of these three stressors on plants are as different as the solutions applied in restoration. Altered soil pH levels have multiple effects on plant roots. Directly, pH can have a negative impact through the effect of excess H^+ or OH^- on membrane integrity and ion uptake systems. Indirectly, pH can influence the solubility of metals that are toxic to plants. Heavy-metal tolerance in plants is often fairly specific and limited to a single metal instead of species being tolerant of a wide range of heavy metals (Shaw 1990). For instance, aluminum toxicity (Al^{3+}) occurs in acidic soils and is a major constraint on plant growth in all but calcifuge ("chalk-escaping", "acid-loving") species, which hyperaccumulate aluminum (Jansen et al. 2002). The presence of Al^{3+} generally reduces root elongation and uptake rates of essential cations such as calcium and magnesium (De la Fuente-Martinez and Herrera-Estrella 1999). Zinc, cadmium, copper, iron and other metals can also have negative effects on plant metabolism when present in the soil in high concentrations (Shaw 1990; Rout and Das 2003). Plants with physiological traits that resist or tolerate soils with high metal concentrations, or metallophytes, are typically endemic to areas with high metals in the soils, and are often the best species to use in restoration of such sites (Whiting et al. 2004). For example, *Stanleya pinnata* and *Astragalus bisulcatus* both accumulate selenium when grown in soils that are toxic to most plant species (Freeman et al. 2006).

Traits and Restoration

Early in this chapter, we introduced commonly measured ecophysiological traits and described what they tell us about tolerances to environmental conditions and rates of nutrient cycling (table 6-1). These traits, and their combinations, are particularly useful predictors for restoration success, and provide valuable information for planning. For example, in a Ponderosa pine forest, old growth trees were subjected to thinning and burning treatments in an attempt to return the forest to pre-fire-suppression conditions. Measurements of leaf gas exchange, leaf nutrient content, water potential, and resin flow were used to assess the success of these methods, and indicated that restoration treatments increased the health of old growth trees (Feeney et al. 1998). Comparing traits of native and nonnative species can reveal useful methods of controlling invasions. For example, measurements of several traits in a Hawaiian system demonstrated that natives were more shade-tolerant than nonnatives, indicating the possibility of planting taller natives or adding artificial shade structures to prevent invasion (Funk and McDaniel 2010). Recognizing trait combinations of common natives and nonnatives in a system can also be useful when deciding the plant palette to use in active restoration. This is based on the hypothesis of limiting similarity, and the concept of competitive exclusion, which state that no two species that occupy the same ecological niche can coexist indefinitely (Macarthur and Levins 1967; Abrams 1983). In natural systems, there is evidence that communities are more resistant to invasion when they contain natives that have traits similar to potential nonnative invaders (Fargione et al. 2003; Emery 2007), suggesting that restoration practitioners should consider planting natives with traits similar to the most common invasive species (Funk et al. 2008; Drenovsky et al. 2012). There are problems in practice, however, since planting diverse natives can limit establishment through increased competition among fast- and slow-growing native species (Kimball, Lulow et al. 2014). Additionally, planting different types of natives together prevents the use of selective herbicides to control nonnative species following planting (Kimball, Lulow et al. 2014). Nonetheless, there is strong support of the limiting similarity hypothesis from experimentally assembled communities, suggesting that the theory shows promising applicability to restoration contexts (Price and Partel 2013).

Ecophysiological traits may also be useful to assess the success of restoration projects in terms of the ecosystem functions or services provided by the restored system. With billions of dollars spent annually on restoration, there is an increasing need to define metrics for success. Rates of carbon, water, and nutrient cycles have been proposed as a preferred metric in restoration (Palmer et al. 2005), and these processes may be determined through measuring ecophysiological traits of all species in the community and calculating community-weighted trait mean and functional diversity (FD) values (Diaz et al. 2007). FD values provide information regarding community-level processes, such as community assembly and function, and are valuable for assessing the health of restored communities (Cadotte et al. 2011). Other measurements taken at the community level, such as net primary productivity, and measurements of functional diversity across multiple trophic levels would further aid in assessments of ecosystem processes as indicators of restoration success (Lavorel 2013).

Closing Remarks

In the most idealized study design, plant ecophysiological performance and metrics of system functioning (such as net primary production) in a restored setting should be compared to measurements in a reference system (Morgan and Short 2002). Such studies provide the best opportunities for identifying performance expectations and ultimately attaining restoration goals (Feeney et al. 1998; Ruiz-Jaen and Aide 2005). Field-based comparative experiments are likely to offer the greatest insights for restoration, but in the past, this research tended to be time-intensive and technologically expensive—burdens that often precluded adequate sample sizes. However, improved technological capabilities over the past three decades, such as lightweight portable gas-exchange systems and compact data loggers, have made field ecophysiological assessments much more rapid and tractable (table 6-1). In addition, the use of proxies, such as stable isotopes, that correlate well with long-term, integrated ecophysiological function, provide a relatively easy means by which to monitor plant performance and predict restoration outcomes (Adams and Kolb 2004; Roden et al. 2005; McDowell et al. 2010). Careful selection of which ecophysiological variables to monitor, and on which species, also helps to refine such studies; variables should be based on the stresses that are expected to have the greatest impact on plant survival (e.g., water potential in an arid system or light response in high light environments) and for those species that best represent the reference ecosystem. Simple proxies, such as leaf area and stem elongation can provide a decent integrated evaluation of stress response, but if certain ecosystem functions such as water or carbon fluxes are an objective of restoration, more sophisticated measurements may be necessary. In all cases, however, ecophysiological trait values that match the expected ranges seen in reference plants should be included in the performance standards of a restoration project.

It is clear that all plant species do not exhibit the same sets of physiological response curves or stress tolerances, because these responses reflect the evolved species niche space (Sultan et al. 1998; Reich et al. 2003; Kimball et al. 2012; Gianoli and Saldana 2013). Thus, changes in the state of aboveground microclimate conditions and belowground resource states are likely to produce different species responses that might be predictable once the basic ecophysiological traits of the key species are characterized. Restoration involves not only understanding the role of the physical environment as a driver of plant performance, but also an appreciation of the biotic feedbacks that influence plant performance directly. In this context, the restoration of plant communities may benefit from ecophysiological research on animal and microbe communities (Reynolds et al. 2003; Tylianakis et al. 2008). An understanding of these basic ecophysiological mechanisms of adaptation and physiological environmental responses can shed fundamental insights that inform the practice of ecological restoration, as well as help guide restoration ecology research and restoration experiments. Furthermore, because restoration settings often pose unique environmental challenges to plants, ecophysiological studies in these settings may also provide significant new insights about plant ecophysiological function.

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Chapter 7

Implications of Population and Metapopulation Theory for Restoration Science and Practice

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Theory and Application

- Using Population and Metapopulation theory to guide restoration design can improve restoration success, whether increasing desirable or decreasing undesirable species.
- Models are best constructed from long-term information about vital rates and good estimates of dispersal and colonization.
- Understanding environmental drivers of spatial and temporal variation in population vital rates is fundamental for determining suitable habitat for restoration.
- Restoration can help rescue populations and reduce local extinction risk and increase metapopulation persistence.
- Population and Metapopulation models based on sound statistical and geospatial analyses can aid evaluation of the benefits, costs, and outcomes of management scenarios.

Those who have tried to restore viable self-sustaining populations to the wild are left with a sense of humility and wonder at the complexity of ecological systems. Although restoration may have a deceiving appearance of simplicity, many early attempts at restoring populations met with low success (examples in Falk et al. 1996) or have not been monitored long enough to know their status (Dalrymple et al. 2012). Experience has taught us that establishing viable, self-sustaining populations—one of the stated objectives of restoration ecology—can be extraordinarily difficult and require a great deal of time (Albrecht et al. 2011).

In a broad sense, a population comprises actually or potentially interbreeding individuals of a species living in a geographical area (Mills 2013). Variation of demographic factors, for example, number of living individuals, their ages, growth, and reproduction from year to year determine growth, stability, or decline of a

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population. Understanding how populations change in response to spatial and temporal environmental, genetic, and demographic variation is the study of population dynamics, which is central to planning any restoration effort or recovering any rare species. Interactive factors influencing population persistence are complex. Most native species lack even basic research for estimating birth rates, death rates, rates of population increase, and habitat occupation, yet such information is essential for developing effective, reliable recovery, and restoration plans (Schemske et al. 1994; Maschinski, Albrecht et al. 2012).

Species may have multiple natural populations. Restoration practitioners may need to create more than one population of a rare species in multiple locations to secure regional persistence. A set of discrete populations of a species within a geographical area that may exchange individuals through migration, dispersal, or human-mediated movement is known as a metapopulation (Akcakaya et al. 2006). The dynamics of a metapopulation arise from the finite lifetime of populations (Hanski and Gilpin 1991), their colonization and extinction and the processes that can facilitate interaction between them.

Theoretical population and metapopulation models are important tools for evaluating restoration success. They have become integral to the legal protection of rare species and habitats (Schemske et al. 1994; Dreschler and Burgman 2004) and for control of invasive species (Ramula et al. 2008). Models have become widely used for conservation management and they also have relevance for restoration planning (Possingham et al. 2000). Developing reliable models that help evaluate the most promising restoration strategies is essential (Dreschler and Burgman 2004).

Theoretical constructs from population and metapopulation analyses can help provide testable hypotheses for restoration projects, which may in turn help refine theory. In the face of increasing threats of habitat fragmentation and climate change, it is critical that restoration efforts include a research agenda and an experimental component. Here, we briefly highlight key principles of the major theories of population and metapopulation biology of relevance to restoration, and note the challenges of each. We illustrate some of the limitations and potential of using population and metapopulation theory in restoration science and practice.

Population Models

Population models are fundamental tools for understanding the dynamics and persistence of populations (Soule 1987; Beissinger and McCullough 2002; Brigham and Schwartz 2003; Crone et al. 2011). Rather than predicting the absolute fate of a population, models are heuristic tools for estimating the *relative* viability of populations under variable management or experimental regimes (Doak and Mills 1994; Possingham et al. 2000; Brigham and Thomson 2003; Crone et al. 2013).

Models can be used to compare population dynamics in natural versus restored habitats (Bell et al. 2003), under scenarios of projected future conditions (Maschinski et al. 2006), or for risk assessment (Madden and Van den Bosch 2002). In that sense population models provide a perfect theoretical platform from which restoration plans can be derived.

Matrix modeling is an effective approach to approximate population dynamics (Caswell 2001; Morris and Doak 2002). Matrix population models can be deterministic or stochastic, spatially structured or nonspatial (Beissinger and Westphal 1998), and stage or age-structured (Dennis et al. 1991; Crone et al. 2013). They can be used to address restoration questions about the number of individuals and populations needed and the type of propagule that should be used for a successful reintroduction (Knight 2012), and whether the restored population is sustainable. Matrix models form a framework for exploring potential effects of different restoration strategies (Ball et al. 2003) and can serve as a foundation for complex statistical and geospatial analyses.

Matrix and other population models require that individual growth, reproduction and survival are measured over a discrete interval and then summarized as a projection matrix: $n(t+1) = An(t)$, where $n(t)$ and $n(t+1)$ are population vectors that contain the number of individuals in each life stage at times t and $t+1$, respectively and A is the population projection matrix. The matrix contains transitions summarizing changes for individuals that stay the same, grow, shrink, go dormant, or reproduce (table 7-1). Collectively, these changes (birth, growth, maturation, etc.), describing the movements of individuals through the life cycle, are called the vital rates (Caswell 2001). The time interval can range from months to a single year or multiple years depending on the population ecology of the species in question. The biology of the species and the researcher's questions determine the nature of matrix A and the possible population models that a practitioner can build (Caswell 2001; Ellner and Rees 2006). The matrix eigenvalue, or lambda (λ), provides an estimate of the population growth rate between time t and $t+1$ (Caswell 2001). A population with $\lambda = 1$ is stable, $\lambda < 1$ indicates population decline, and $\lambda > 1$ indicates population growth. In a restoration context, there may be species for which increased abundance is a desired future condition, whereas the opposite may be true for undesirable species.

Although early matrix models were deterministic, models now incorporate stochasticity (Lande 2002) and analysis of extinction probability or quasi-extinction, defined as a population dropping below an arbitrary threshold assigned by the modeler (Burgman et al. 1993). Shaffer (1987) first introduced and defined the primary categories of stochasticity that influence population viability: *demographic stochasticity* resulting from events in the survival and reproduction of individuals; *environmental stochasticity* caused by changes in weather, resource supply, and populations of predators, competitors, and so forth; *natural catastrophes*, such as

Table 7-1.

Example of a stage-based matrix. The first column, first row indicates the proportion of seeds that remained in the seedbank between 2012 and 2013. The first column second row indicates the proportion of seeds in the seedbank in 2012 that germinated and became seedlings in 2013. No seeds became juveniles or adults between 2012 and 2013 (zeroes are in the third and fourth rows). The second column indicates the proportion of seedlings alive in 2012 that became juveniles (0.19) in 2013. The third column indicates the proportion of juveniles alive in 2012 that remained juveniles (0.16) or became adults (0.21) in 2013. The fourth column indicates the contribution of adults alive in 2012 to the seedbank (16.4) and to seedling stages (1.07) and the proportion that remained alive until 2013 (0.7). See Caswell (2001) for details about matrix development.

2012–2013				
	Seedbank	Seedling	Juvenile	Adult
Seedbank	0.65	0	0	16.4
Seedling	0.09	0	0	1.07
Juvenile	0	0.19	0.16	0
Adult	0	0	0.21	0.7

floods, fires, droughts, which are extreme manifestations of a fluctuating environment (Lande 1993); and *genetic stochasticity* caused by changes in the genetic make-up of populations due to inbreeding, genetic drift, or founder effects. All of these factors have stronger influence on small populations than on large populations (Shaffer 1987; Menges 1998), because larger populations are better buffered against stochasticity. Knowing that uncertainty plays an important role in population dynamics calls for testing the performance of founding populations with varying genetic diversity and densities in habitats that vary in quality, level of disturbance, or other factors (Kephart 2004; Sheller et al. 2006).

Environmental stochasticity is likely to have important effects on all populations; while demographic and genetic stochasticity will likely play their greatest roles in small populations (Shaffer 1987; Lande 1993; but see Lande 1995; Kendall and Fox 2002). Populations with modest growth rates and delayed reproduction tend to be influenced more strongly by demographic stochasticity (Menges 1998). Populations that have a mean per capita growth rate larger than variance will have greater persistence under environmental stochasticity, but regardless of initial population size, a population with negative long-run growth rates will have a high probability of extinction (Lande 1993).

During the last decade, we have witnessed remarkable improvements in our ability to deal with complex data associated with restoration, management, and conservation problems. An increasing recognition of the simultaneous and frequently synergistic or hierarchical effects of multiple environmental factors, including social and economic stressors, on the persistence and abundance of species (Cressie et al. 2009) has led to the development and implementation of more flexible, robust analytical and modeling approaches. These methods include, among many others, Bayesian modeling and integral projection modeling (IPM), which may be integrated with geospatial data. Below, we address applications of these models to population dynamics that have relevance to restoration.

To understand the factors that influence variation in vital rates, new types of models have promise. When change in vital rates can be associated with a continuous state variable (size, age, etc.), IPMs are appropriate (Rees and Ellner 2009). They are particularly suitable for small data sets (Ramula et al. 2009). These models can incorporate variation of vital rates (survival, growth, and fecundity), covariates (predation, environmental stressors, time since disturbance, density, etc.) and effects of year and location. For example, using spatial integral projection models (SIPMs), Jongejans et al. (2011) estimated the spread rate of different sized rosettes of the invasive monocarpic thistle *Carduus nutans* in New Zealand and identified the plant sizes that are crucial management targets for control. To control spread, managers should target seedlings that grow to become small reproducing plants, while controlling local population densities will require targeting plants that survive and grow for one or more years and then produce many seeds. Restoration of a desirable species could use this same modeling tool.

Bayesian modeling is particularly appropriate for complex analyses that may involve multiple years, variable ecological data, and nested factors, while providing separate estimates of measurement error, genetic or environmental variation (known as process variability), and model uncertainty (Kruschke 2011). Bayesian networks can represent correlative and causal relationships graphically and probabilistically (McCann et al. 2006). They are also effective tools to evaluate costs and benefits of management alternatives under adaptive frameworks (Marcot 1998). This approach combines empirical data with expert understanding to define explicitly complex relationships including uncertainty. For example, conditions leading to Carolina willow (*Salix caroliniana*) supplanting numerous native herbaceous species along the Upper St. Johns River in Florida have led to considerable restoration investment. Wilkinson et al. (2013) extended a state-transition, dynamic, Bayesian network model that integrated a structured demographic model, GIS spatial data, and a seed dispersal model to evaluate the influence of environmental and management factors on temporal changes in willow abundance across the whole upper basin (fig. 7-1). Combining data from ecological experiments and expert observations, they parameterized this population model (Nicholson et al. 2012; Quintana-Ascencio et al. 2013; Castro Morales et al. 2014) and used it to evaluate costs and benefits of willow removal.

Elasticity Analysis

Elasticity analyses measure the proportional change in population growth (λ) given small changes in stage-specific vital rates (Caswell 2001). Elasticity values

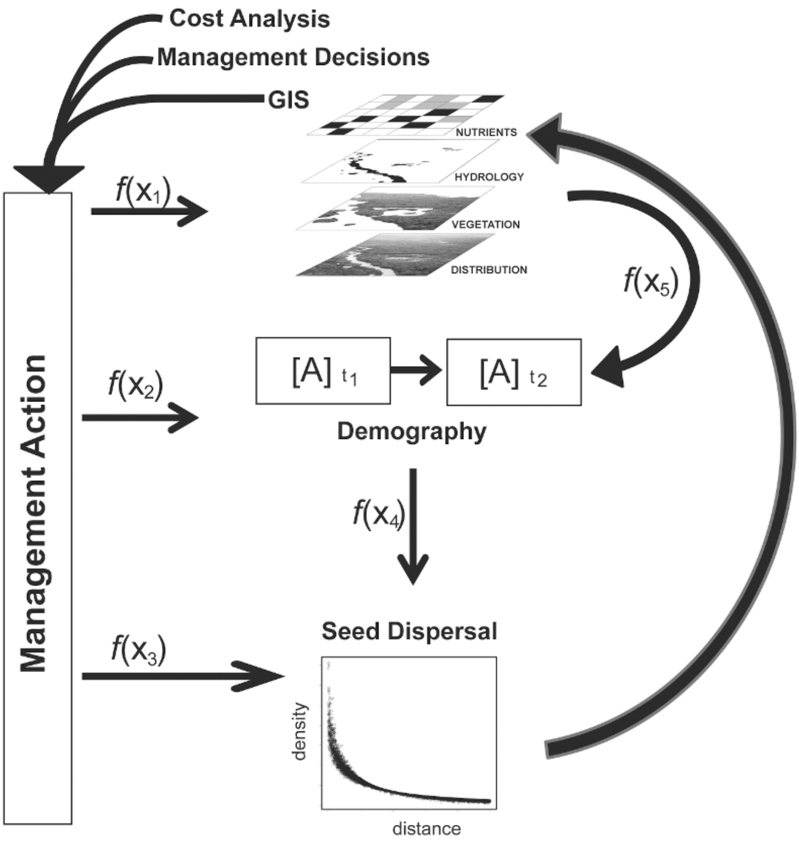

Figure 7-1. Schematic of a Bayesian Network modeling approach that integrates spatially explicit environmental data, a structured demographic model, and seed dispersal model to evaluate the influence of management actions on target species abundance over time (Nicholson et al. 2012). Such integrated approaches can be used interactively to assess costs and inform future management actions.

can be used to identify the life stage that has the strongest effect on population growth given the matrix structure (Silvertown et al. 1996). Thus, elasticity analysis, together with an evaluation of the actual variation of the vital rates and their impact on each other, can be used to assess what life stage will have greatest promise or will be most limiting for building and sustaining a restored population. Conversely, they can also aid decisions about invasive species control (Morris et al. 2011) or harvesting rates, especially if coupled with life table response experiments (Schmidt et al. 2011).

It is important to be aware of underlying assumptions that generate elasticities and recognize that elasticity analyses may not always provide accurate predictions. Vital rates with high elasticities do not necessarily correspond to the life history stages that are currently limiting population growth or that are the most productive targets for management (Brigham and Thomson 2003; Schwartz 2003). Most models assume that transition elements are independent, while in reality transitions may be correlated. For example, improving reproduction may negatively impact subsequent survival or growth. Some elements may vary widely across years, such that selecting the highest value life stage for a restoration in one year may not hold for another year (Silvertown et al. 1996). Population transitions with high elasticities tend to have low variation across years or sites (Pfister 1998; see Pico et al. 2003); therefore, changes in these life stages may have little impact on population growth. For example, long–lived species often have the largest elasticity values for surviving adults, yet the major threat for species' persistence may result from lack of recruitment (Schwartz 2003). Restoring a population with adults may not only be the technically most difficult and resource-intensive approach, but it also may not improve the species' conservation status in the long term.

For example, elasticity analyses of the federally endangered Upper Sonoran shrub, *Purshia subintegra*, indicated that vegetative and reproductive adult survival had the greatest contributions to population growth (table 7-2; Maschinski et al. 2006) suggesting that adult plants would be the best life stage to use for reintroduction. However, reintroductions comparing whole plants and seeds showed seeds to be the most successful propagule after five years (fig. 7-2; Maschinski et

TABLE 7-2.

Elasticities for Purshia subintegra *for transition years 2001–2002 and 2002–2003 in dry sites. Note that stasis in vegetative and reproductive adults have the highest elasticities. (Maschinski et al. 2006)*

2001–2002 $\lambda = 0.961$

	Seedbank	Seedling	Juvenile	Vegetative Adult	Reproductive Adult
Seedbank	0	0	0	0	0
Seedling	0	0	0	0	0
Juvenile	0	0	0	0	0
Vegetative	0	0	0	0.998	0.0011
Reproductive	0	0	0	0.001	0

2002–2003 $\lambda = 0.779$

	Seedbank	Seedling	Juvenile	Vegetative Adult	Reproductive Adult
Seedbank	0	0	0	0	0
Seedling	0	0	0	0	0.0028
Juvenile	0	0.0028	0.0008	0	0
Vegetative	0	0	0.0028	0.188	0.1845
Reproductive	0	0	0	0.187	0.4313

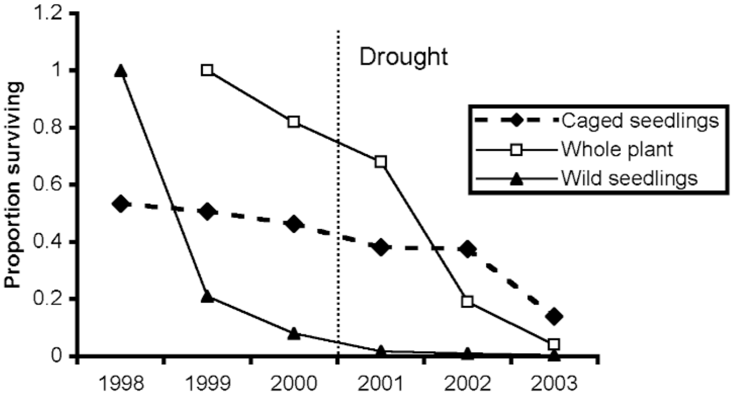

Figure 7-2. Proportion of surviving cohorts in *Purshia subintegra* reintroduction trials and in the natural population in Verde Valley, Arizona, measured from 1998–2003 (adapted from Maschinski et al. 2004). Reintroduced whole plants were propagated from cuttings taken from the Verde Valley population and watered for five months after transplanting to the site. Caged seedlings arose from seeds introduced into cages; the survival of seedlings is reported. No supplemental water was given to seeds or seedlings. The survival of naturally occurring wild seedlings was assessed in thirty demographic plots.

al. 2004; Maschinski et al. 2006). Several factors probably improved survival of the experimental versus natural seedlings, including the loosening of the soil during sowing that may have allowed better root development and the caging that provided protection from predation and desiccation. Using 4,800 *P. subintegra* seeds was also less expensive than propagating, growing, planting, and maintaining 450 whole plants. Thus elasticity analyses provided insight to current natural population behavior, but field testing and sound practice benefited the restoration (Maschinski, Albrecht et al. 2012).

Probability of Quasi-Extinction

One attribute of population health is measured as the probability of quasi-extinction within a given timeframe. The quasi-extinction threshold is a number set by the modeler as the minimum number of individuals below which a population is unlikely to recover from demographic and genetic stochasticity. Morris and Doak (2002) suggest that the most useful depiction of extinction risk is the cumulative distribution function (CDF), which gives the probability that a population will have fallen below a quasi-extinction threshold at or before a given future time. Extinction risk predictions can be incorporated into Population Viability Management (PVM) models, directly integrating them with population dynamics, monitoring practice, and management decisions (Bakker and Doak 2009). For example, using a PVM framework, land managers and modelers developed recovery standards directly linked to extinction risk of the endangered island fox (*Urocyon littoralis*), endemic to the Channel Islands of California, US. Previous PVA models, island fox ecology, and the needs and constraints of managers informed the recovery criteria. Because golden eagle (*Aquila chrysaetos*) predation posed great threats to the island fox, the PVM included simulations of the influence of changing eagle numbers on the fox population. These predicted that doubling efforts to control eagles would be necessary to reduce extinction risk of the island fox population (Bakker and Doak 2009).

Challenges of Population Modeling

Population models require long-term data sets and a good understanding of the species' biology. Ideally, long-term and well-designed data sets capture the spatial and temporal range of variation in vital rates of the species. Population model predictions are most accurate for short-time intervals (ten to twenty years), because models become increasingly imprecise as time from field data collection increases (Ellner et al. 2002). Long-lived species present a special problem in that they have very slow responses, low mortality, low turnover, and extremely episodic recruitment (Schwartz 2003; Nicole et al. 2005). These become especially problematic for measuring population growth of restored populations, because the time required to see population recruitment may exceed a funding cycle or even a principal investigator's lifetime (Albrecht et al. 2011).

Just as population behavior is controlled by the "weakest" links in time (Menges 1998), the models we are able to construct are limited by the weakest link(s) in our data. Notoriously large information gaps for many species are dormancy, seed or egg banks, survival of dispersed young, and the effects of stochasticity on all model parameters. Data required to estimate dormancy may be no faster or easier to collect than actual vital rates for seeds and seedlings (Doak et al. 2002). Further, vital rate measurements obtained in a greenhouse or laboratory setting, such as percent germination or percent survival, may not translate to field conditions (Dudash 1990). Even small changes in estimates of these parameters can result in dramatically different estimates of population extinction risk especially under conditions of highly variable environments (Doak et al. 2002).

For example, a twenty-one-year data set demonstrated that two co-occurring *Daphnia* species had dramatically different rates of dormancy and hatching (Caceres 1997; fig. 7-3). *Daphnia galeata mendotae* failed to reproduce in eight out of twenty-one years sampled in Oneida Lake, New York. Multiyear dormancy allowed this weak competitor to persist at this location. In contrast, the co-occurring *Daphnia pulicaria* did not rely on egg storage for persistence and had consistently

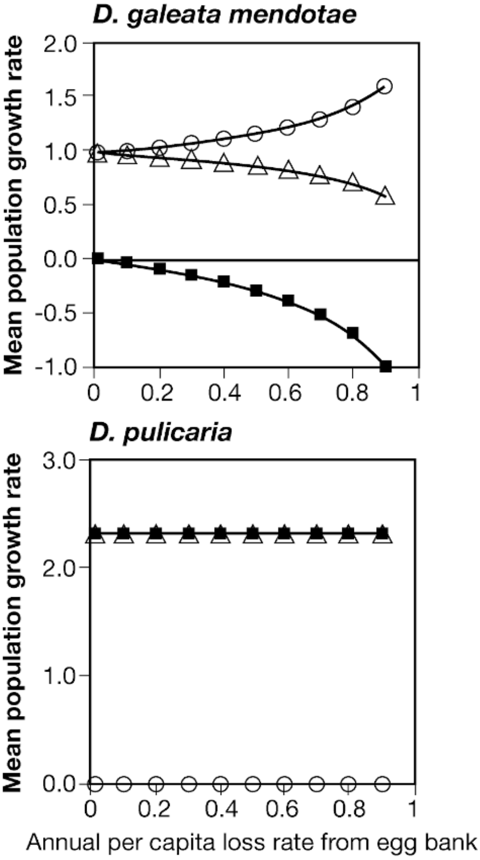

Figure 7-3. Mean population growth rates of two co-occurring *Daphnia* species with dramatically different egg dormancies in a homogeneous egg bank. The portion of the population growth rate that does not include recruitment variation is represented by black squares; the portion of the population growth rate that is due to annual variation in recruitment is represented by open circles; the boundary growth rate, represented by open triangles, is the sum of each circle/square pair. For *D. galeata mendotae*, all squares fall below the zero line, indicating that this species could not persist without variable recruitment and re-establishment from the egg bank. In contrast, *D. pulicaria* persistence did not depend upon egg bank storage. Redrawn from Caceres (1997).

high recruitment. Thus, the importance of the dormant stage had markedly different influences on population growth rates depending upon species-specific responses to environmental variation. Similarly, co-occurring plant species may germinate from seedbanks at different rates under varying environmental conditions thereby enabling coexistence of species (Baskin and Baskin 1998; Pake and Venable 1996; Stephens et al. 2014) and maintaining variation in population genetic structure (McCue and Holtsford 1998). Variable rates of germination from dormant stages reduce the ability to generalize seed or egg bank parameters across co-occurring species or across years (Clauss and Venable 2000).

Quantifying the survival or mortality of individuals that disperse from a study site is also problematic for building population models. Dispersal distances and densities are notoriously difficult to measure in the field, and may also have high year-to-year variation (Clark et al 2001; Muller-Landau et al. 2008). This is especially true for pelagic or wind-dispersed organisms whose young may settle far from the parent (Crowder et al. 1994). Assessment of juvenile dispersal and survival may be limited by sampling techniques (Szacki 1999) and the variable patterns of movement across season and location (Szacki 1999; Ball et al. 2003). Genetic techniques (paternity analysis and a two-generation pollen pool structure approach, TwoGener) are making it possible to identify parentage and dispersal distances (Sork and Smouse 2006). For example, using a six-locus microsatellite battery, Streiff et al. (1999) genotyped 13 maternal trees and 986 of their offspring and found that 310 progeny were compatible with a single pollen donor, while others were derivations of selfed, multiple donors, or were interspecific hybrids. With enough offspring, researchers can estimate the “spectrum” of paternity, even if each and every father cannot be designated exactly. Assuming a given dispersal function, TwoGener can estimate the average effective number of pollen donors and the effective neighborhood size for a site and derive the effective pollen dispersal curve (Sork and Smouse 2006).

Metapopulation Analysis

Spatial and temporal variation in demography is critical to the long-term dynamics and persistence of a species across its range (Pulliam 1988; Lande 1993; references in Kauffman et al. 2003). Metapopulation models link population ecology (local abundance) with biogeography (regional occurrence) and provide a useful framework for understanding correlative and experimental data on population distribution and abundance (Gotelli 1991; Hanski and Gaggiotti 2004). A metapopulation approach (see also chap. 4) is likely to provide useful tools for developing restoration strategies for optimizing among-population processes critical for the persistence of many natural systems (Thrall et al. 2000).

Hanski and Gyllenberg (1993) considered two theoretical models for metapopulation analysis as extremes of a continuum (fig. 7-4). The mainland-island model, based on equilibrium theory of island biogeography (MacArthur and Wilson 1967), assumes a large and invulnerable source population on the “mainland,” from which individuals migrate to smaller habitat patches (“islands”) with more transient populations. Levins’ model (1969, 1970) assumes a set of equally large habitat patches, or islands, with local populations frequently going extinct,

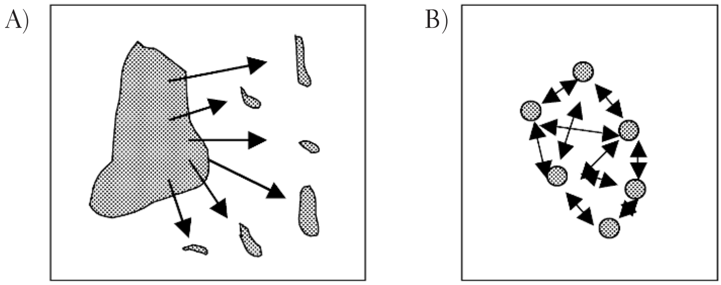

Figure 7-4. (A) Mainland-Island Model (from Hanski and Gyllenberg 1993) and (B) Levins Model (Levins 1969, 1970). In the Mainland-Island model, individuals migrate from the large, invulnerable source population to the smaller habitat patches. The smaller patches are vulnerable to extinction and can be recolonized. The Levins Model assumes equal-sized patches with multidirectional dispersal, and all patches capable of extinction and recolonization.

and vacated patches recolonized from the currently occupied set of patches. Most species occur intermediate to these extremes, where there is significant spatial variation in habitat patch sizes, even if there is no true mainland invulnerable to extinction (Harrison 1991).

Kareiva (1990) reviewed models that describe spatial organization in heterogeneous environments: island models, where populations are subdivided; stepping stone models, where patches have explicit spatial dimensions; and reaction-diffusion models, which assume a homogeneous environment and provide a null model describing spatial patterns that arise from random motion and population growth alone (fig. 7-5). All require good information about dispersal over given spatial scales, whether or not dispersal depends upon density and whether direction of movement is influenced by the quality of habitats.

Several generalities arise from metapopulation theory (see box 7-1). The theory predicts that a threshold number of suitable patches is required for large-scale metapopulation persistence; immigration and colonization must be greater than extinction. Nonequilibrium metapopulations are destined for ultimate extinction, with the time to extinction of the metapopulations being the same as the time to extinction of the largest populations (Hanski 1999). Spatially explicit models allow for inclusion of the areas and spatial locations of patches (Hanski 1994, 1999) and can be used for conservation and restoration applications to help determine the value of patches or preserves for species' persistence (e.g., Hanski and Ovaskainen 2003; Ovaskainen and Hanski 2003; Pelletier and Mahévas 2005), the spatial spread of undesirable species (Prasad et al. 2010), and can be used to support management decisions needed to preserve species threatened by climate change (Peterson et al. 2013).

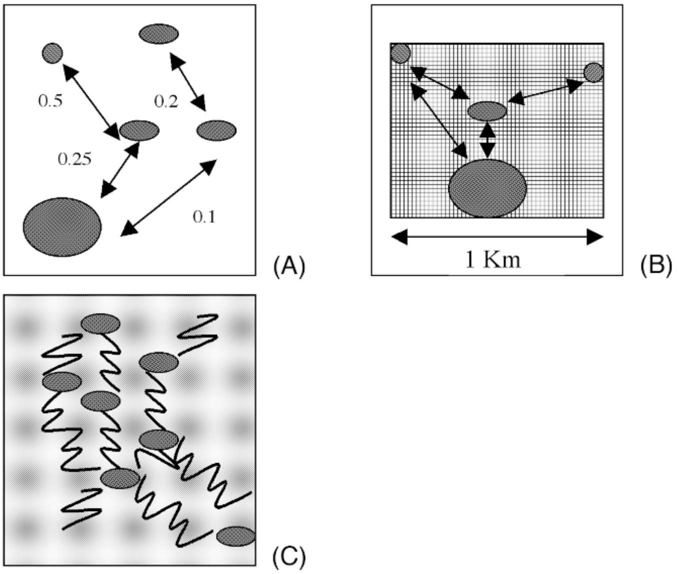

Figure 7-5. Types of spatial metapopulation models (adapted from Kareiva 1990); (A) *island models* have a collection of patches coupled by one common pool of dispersers; all patches are equally accessible; there is no explicit spatial dimension; and dispersal rates are fractions of individuals that move without regard to distance moved. Island models can be used to investigate how spatial subdivision (or fragmentation) alters the metapopulation behavior. (B) *stepping-stone models* have the same qualities as island models except that patches have fixed spatial coordinates. These can be used to examine consequences of long-range vs. short-range dispersal. (C) *reaction-diffusion models* assume a homogeneous environment, use standard continuous-time Lotka-Volterra representations of local dynamics, and a constant random rate of dispersal. These models can examine the consequences of population density and habitat quality on metapopulation structure.

As emphasized in chapter 4, spatial structure at local to landscape scales exerts a tremendous influence on the dynamics of ecological systems and their potential for recovery. Habitat fragmentation and/or disturbance influence metapopulation persistence (Collingham and Huntley 2000; Bélisle and Desrochers 2002; Hanski and Ovaskainen 2003; Johansson et al. 2013). Using a site occupancy and recruitment model of eighteen plant species growing in grasslands of Scandinavia, Eriksson and Kiviniemi (1999) found a significant relationship between species diversity, availability of suitable habitat, and ability to colonize roadsides. Generalist grassland species with good dispersal ability were predicted to increase or remain stable, while species with limited seed dispersal, low seed set and/or low disturbance tolerance had higher risk of extinction. Where habitats are fragmented, networks of small habitat patches can serve as stepping stones connect-

Box 7-1: Key Principles of Metapopulation Theory

1 The probability of extinction decreases as average population or patch size increases, as the fraction of large patches increases, and as the total number of patches increase. The largest patches have the lowest extinction risk, and these determine estimates of time to extinction of the metapopulation.

2 Persistence of a metapopulation is possible only if recolonization exceeds extinction. Preserving a metapopulation requires either increasing colonization or reducing extinction.

3 As maximum reproductive rate increases within a patch, the probability of extinction decreases.

4 The *rescue effect* occurs when increasing the number of immigrants increases patch occupancy and decreases the risk of extinction.

5 The *establishment effect* occurs when increasing the proportion of suitable habitats occupied by a species increases the rate of successful colonization through dispersal and augmentation.

6 Heavy emigration will make local populations smaller and hence more vulnerable to extinction.

7 The closer the proximity of patches, the higher the migration between the patches and the greater the likelihood of recolonization of vacant patches.

8 Larger patches have a greater probability of contributing migrants to a metapopulation; therefore the genetic composition of the largest population influences that of the entire metapopulation.

9 Patch arrangement and corridor quality can influence metapopulation size. Landscapes with greater interior patches will support larger metapopulations than those with more peripheral patches. Increasing the number of high-quality heterogeneous corridors (those that allow for greater survival after dispersal) will increase the metapopulation size and biodiversity.

References: Brown and Kodric-Brown 1977; Hanski 1991; Hanski and Gyllenberg 1993; Hess 1996a; Anderson and Danielson 1997; Earn et al. 2000; Lande 2002; Ovaskainen and Hanski 2003; Menges et al. 2004; Piessens et al. 2004; Chisolm et al. 2011; Eaton et al. 2014.

ing and facilitating migration between landscape patches (Huntley 1991), and larger patches are better. Models indicate that corridors are important for migrating species, but not necessarily sessile organisms (Collingham and Huntley 2000; chap. 4).

Hanski et al. (1996) defined minimum viable metapopulation (MVM) size as the minimum number of interacting local populations necessary for long-term persistence of a metapopulation. The minimum amount of suitable habitat (MASH) was defined as the minimum density (or number) of suitable habitat patches necessary for metapopulation persistence. A metapopulation can persist only if there is a balance between local extinctions and recolonizations of empty but suitable habitat patches.

Metapopulations with high turnover rates and habitat destruction are not at equilibrium and are headed for extinction. Metapopulations consisting of a small number of local populations, each with a high risk of extinction, are not likely to persist long. Hanski et al. (1996) concluded that many rare and endangered species fall below their minimum viable metapopulation size and may already be headed toward extinction, unless the fragmentation of their habitat is reversed. In the face of rising human populations and intensive land use, protecting and restoring habitat in clusters rather than randomly scattered fragments will minimize the effects of fragmentation and offers the best chance for preserving biodiversity (Rybicki and Hanski 2013).

Data collected over broad enough spatial and temporal scales with sufficient detail to test metapopulation theory are rare (Doak and Mills 1994). One exception originated with an extensive survey in 1989 at Archbold Biological Station, Lake Placid, Florida, US, which identified eighty-six plant species in eighty-eight patches of rosemary scrub habitat totaling thirty-nine hectares. Using an incidence-function model developed by Hanski (1994), Quintana-Ascencio and Menges (1996) estimated the extinction and colonization probabilities of twenty-five species thought to have metapopulation dynamics within the habitat. They calculated maximum-likelihood estimates of two model variables: e', a composite parameter representing turnover rate (extinction probability × colonization ability), and x, a parameter that describes the sensitivity of extinction probability to changes in patch size. Because estimates of colonization and extinction necessitate data on turnover in occupancy over time, they could not validate these estimates from the 1989 data alone. However, they resurveyed the sites in 2004–2005 and assessed if e' was associated positively with observed species extinction probabilities and whether x was associated with the average area and number of patches occupied by the target species at the end of the sixteen-year interval (Miller et al. 2012). The 1989 metapopulation model robustly predicted metacommunity dynamics. Values of e' were positively associated with variation in observed extinction rates ($r^2 = 0.41$, $p < 0.001$) and those of x, after adjusted by patch area, predicted the relative number of occupied patches (adjusted $r^2 = 0.84$, $p < 0.001$; fig. 7-6).

Sources, Sinks, and Population Regulation/Habitat Selection

In complex habitat mosaics, individuals may be distributed among habitat types and have variable or habitat-specific demographic rates, that is, different life spans, developmental rates, birth and death rates (Pulliam 1988; Pulliam and Danielson 1991). Surplus individuals from highly productive “source” habitats may immi-

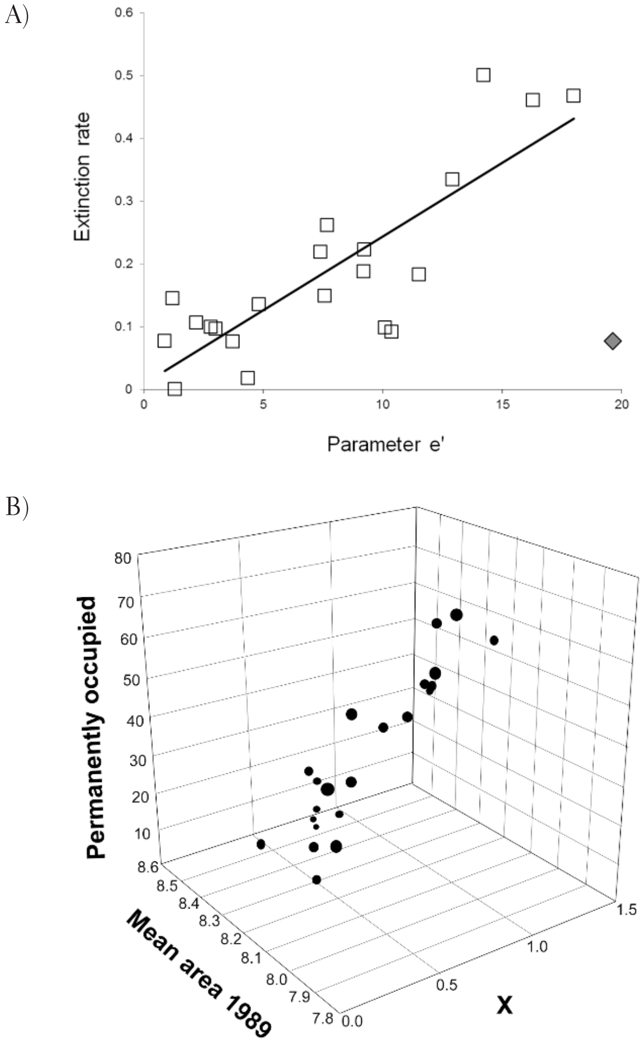

Figure 7-6. (A) Relationship between parameter *e'*, calculated from a patch occupancy model, and extinction rate, where *e'* is a composite parameter representing turnover rate (extinction probability × colonization ability). An outlier is indicated with a different symbol (Regression line, $r^2 = 0.43$). (B) Relationship of *x*, a parameter that describes the sensitivity of extinction probability, and patch size to observed occupancy. Relationship between parameter *x* and average patch size in 1989, compared with actual number of occupied patches in 2005 (adjusted $r^2 = 0.84$; Quintana-Ascencio and Menges 1996). Redrawn from Miller et al. (2012)

grate to less productive "sink" habitats, where within-habitat reproduction fails to keep pace with within-habitat mortality (Pulliam 1988). If good breeding sites in the source habitat are rare and poor sites in the sink are relatively common, a large population may occur in the sink and may be sustained by immigration from more-productive source habitats.

Because species may occur commonly (and breed successfully) in sink habitats, populations need to be studied in a landscape context to understand how habitat heterogeneity influences population dynamics (Pulliam 1988). Several studies have shown that population dynamics are affected by disturbance, spatial variation, and environmental heterogeneity (references in Menges and Quintana-Ascencio 2003; Rybicki and Hanski 2013). In large restoration sites, population size and growth rate may be a function of the relative proportion of the habitat types provided.

Although source-sink models apply to highly mobile species, the models offer insights to restoration planners, who are the "habitat selectors." Increasing the number of reintroduction attempts may ultimately stabilize populations. Because not all utilized habitats are necessarily valuable to the species, restoration using multiple habitats may help to determine where the species' demographic vital rates will be highest and which habitats are the most valuable to the species. Source-sink models allow us to determine the effect that a given change in the availability of high- and low-quality habitats will have on the global population (Pulliam and Danielson 1991).

Challenges of Metapopulation Theory

Metapopulation models have inherent limitations that present challenges to practitioners. As is true of population models, metapopulation models need all of the data required for a simple demographic model, including means and variances of all vital rates, but also require good estimates of migration, dispersal, or colonization, for which accurate and relevant data can be difficult to obtain (Freckleton and Watkinson 2002). Empirical estimates of the model parameters will significantly influence the results and their interpretation; these will be magnified by increasingly complex models (Doak and Mills 1994). Therefore, comparative simulations (for example, relative changes in population size or probability of persistence) rather than absolute risk assessments are recommended (Melbourne et al. 2004). Restoration experiments provide opportunities for testing population and metapopulation theory through long-term data sets that will aid our refinement of the theory and our understanding of biological patterns in species with varying life histories (case study box 7-1).

Addressing Restoration Questions Using Population and Metapopulation Theory

In this section, we illustrate how theory has been applied to restoration planning and implementation. In some cases, empirical tests have given insight into

Case Study Box 7-1

Jacquemontia reclinata

Southeastern coast of Florida: The federally endangered coastal perennial vine, beach jacquemontia, *Jacquemontia reclinata*, is endemic to the southeastern coast of Florida. Once populations were contiguous along the coast, however surveys completed in 2001 revealed that few populations ranging from 1 to 250 plants remained in isolated habitat fragments (fig. 7-10). Although all *J. reclinata* populations were small, the smallest northern populations had the highest extinction risk according to theory. Our fourteen years of monitoring unfortunately confirmed the precarious trajectory of the small northern populations. Four populations have suffered serious declines and/or extirpation (figs. 7-10 and 7-11A).

Supporting theory: The rescue effect

Theory predicts that increased immigration and gene flow can increase the probability of metapopulation persistence.

Expected outcome: Restoration can be the artificial "rescue effect" that moves migrants and the artificial "establishment effect" that increases colonization until the metapopulation stabilizes.

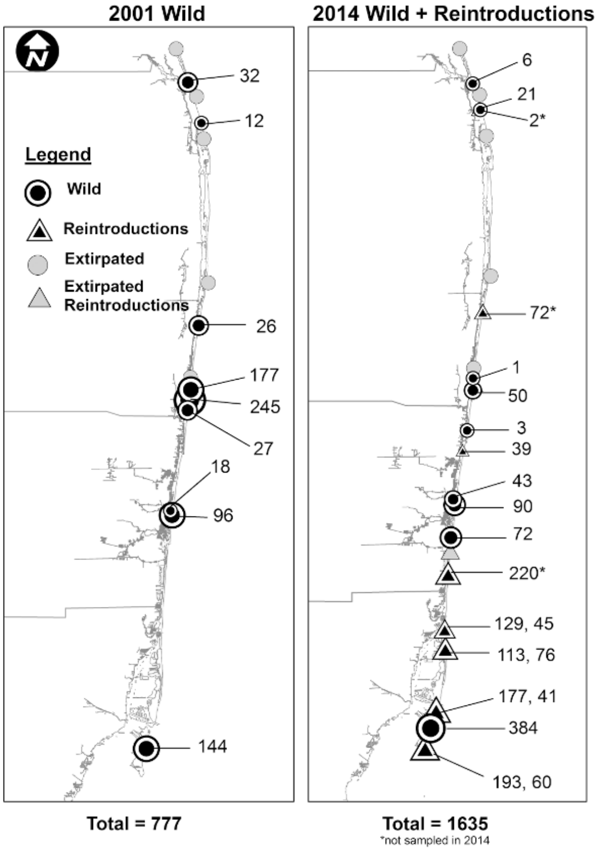

Figure 7-10. Map of extirpated, extant and reintroduced populations of *Jacquemontia reclinata* documented in 2001 and 2014 along the eastern coast of South Florida. Known population sizes are indicated.

Progress: Since 2002, Wright and colleagues created new patches or populations of various size into suitable habitat (ranging in size from 422 m^2 to 4800 m^2) within the species' range (fig. 7-10). Significantly, reintroductions conducted between 2001 and 2011 have increased the total plants in the wild 1.4-fold and have more than doubled the total populations. As was true for wild populations our experimental reintroductions confirmed that founding population sizes below 50 individuals had greater probability of extirpation than large founding populations (fig. 7-11B). Unfortunately, suitable habitat is limited, but wherever possible our future efforts will strive to introduce founding populations >50 individuals.

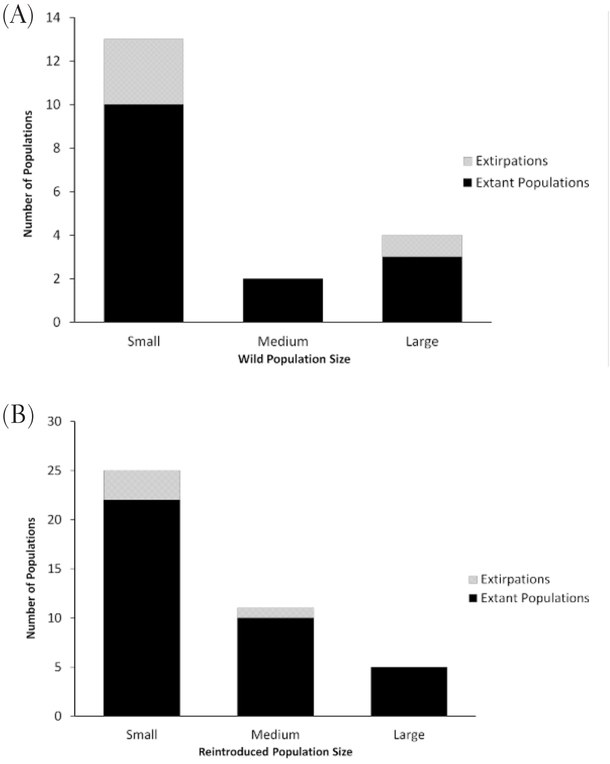

Figure 7-11. Number of extant versus extirpated populations or patches in three size categories for (A) wild and (B) reintroduced populations of endangered *Jacquemontia reclinata*.

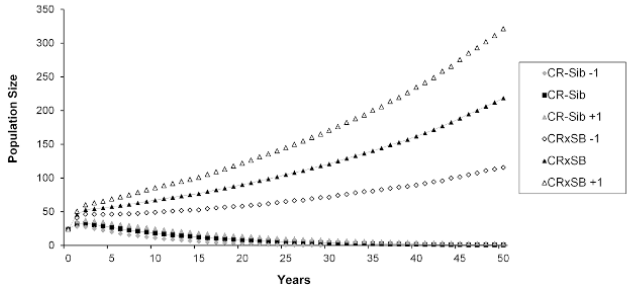

Figure 7-12. Population trajectories generated from models of two reintroduced *Jacquemontia reclinata* populations created with founders bred to siblings versus interpopulation crosses. Confidence intervals ± 1 SD are indicated for each trajectory.

References: Maschinski and Wright 2006; Thornton et al. 2008; Maschinski et al. 2012a; Maschinski et al. 2013**.**

limitations of theory or have not been done, while others show support for the generalizations of theory (see box 7-1). Incorporating experimentation in restorations offers opportunities to test and refine theory.

How Many Individuals Should Be Reintroduced?

Theory indicates that the smaller the population, the larger the influence of stochastic factors and the larger the extinction risk. Using as large a founding population as is practical should thus increase chances of reestablishing viable populations of a species (Albrecht and Maschinski 2012; Maschinski, Albrecht et al. 2012). Bell et al. (2003) compared the number of different propagule types that would be required to create a viable population with less than 5% extinction probability in the next 100 years. They found that more than 400 transplants of one-year rosettes, or 1,600 seedlings, or 250,000 seeds would be required to create a viable restored population of *Cirsium pitcheri*. These numbers may not be reasonable to achieve with extremely rare populations, especially if removing substantial propagules from a wild population for restoration to another location may endanger the wild population (Menges et al. 2004).

How Large Should Patches Be?

Theory indicates that large patches have lower extinction risk than small patches, and that the largest patches within a metapopulation will determine its persistence. Even though restoration sites may be limited, practitioners can choose the largest patches in the best available habitat for reintroducing target species. In southern Scotland, sites selected for capercaillie (*Tetrao urogallus*) reintroduction were forest blocks with the largest area and most suitable annual precipitation (Marshall and Edwards-Jones 1998; see also case study box 7-1.).

The degree of isolation interacts with population size to determine population fate. In a metapopulation analysis of the federally endangered wireweed, *Polygonella basiramia*, Boyle et al. (2003) found that populations growing in small isolated open patches in Florida scrub were more likely to go extinct than those growing in larger and aggregated patches. Gaps created by fires form critical open patches that benefit the species' persistence.

Patch size and patch isolation influence reproductive success. Large outcrops of serpentine morning glory (*Calystegia collina*) had greater flower and fruit production and greater densities of flowering patches than small sparse patches (Wolf and Harrison 2001). Pollination was positively correlated with flower and patch density due to higher quality of pollen being transferred.

What Is Suitable Habitat?

What constitutes a site suitable for colonization is sometimes unclear and is a growing concern with climate change (Maschinski, Falk et al. 2012). Experimental tests have demonstrated the existence of suitable, yet unoccupied habitat for a Florida scrub endemic plant (Quintana-Ascencio et al. 1998). Simply knowing that a species historically occurred at a site may not be an indication that the site still represents suitable habitat, especially if the factor that caused extirpation from the site has not been removed. Metapopulation models generally assume that patches in which extinction occurs are available immediately for recolonization (Hess 1996a), when in reality extinction may have been caused by habitat destruction or some other alteration that permanently changes the suitability of the habitat. Removing the cause of local extinction will make the largest contribution toward reducing extinction risk (Hess 1996a; Knight 2012).

When selecting suitable sites for restoration, one must consider physical, biological, logistical, and historical criteria (Maschinski, Albrecht et al 2012). Theory suggests that the spatial arrangement of restored patches, their size, and distance from one another are equally important considerations.

Two major factors complicate the selection of areas of suitable habitat for restoration. First, habitats may change over time due to anthropogenic or natural factors, making the determination of “suitability” less certain. Second, it is often difficult to identify what factors make a site suitable. Evaluating the quality of habitat using fitness attributes of the population (such as λ) must be done over a long enough time scale to average over good and bad years. Local extirpation of a population may reflect the marginal suitability of the site, lack of recolonization or recruitment in the site, or some permanently altering disturbance (Maschinski, Falk et al. 2012).

In a restoration context it is possible to test potentially suitable habitat. One natural population of the Florida endemic *Dalea carthagenensis* var. *floridana* declined from thirty-one woody individuals to just one woody plant and three seedlings between 2004 and 2008. In an effort to rescue the population, Possley et al. (2015) introduced 6,000 seeds in a factorial design of two seed pretreatments (frozen and control) and two habitats (natural and novel), where the novel habitat was a restored area adjacent to the natural site. Significantly more seedlings emerged in the natural compared to the novel habitat and frozen seeds had nearly three-fold more germination than untreated seed plots (fig. 7-7). After three years, 40% of the original seedling cohort survived, 55% matured to become reproductive adults, and new seedlings emerged, but only in natural plots. Overall the seed augmentation increased the population twenty-four fold and revealed that novel habitat was unsuitable.

Suitability of habitat may also change temporally with the advent of distur-

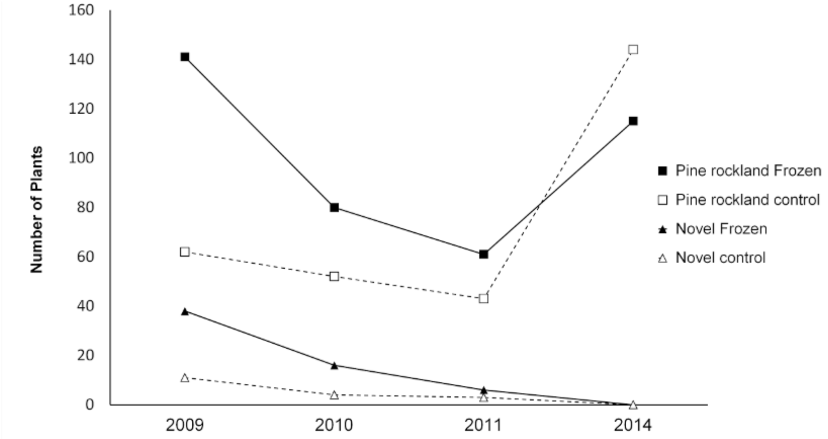

Figure 7-7. *Dalea carthagenensis* var. *floridana* plants that emerged and survived in experimental augmentation plots with frozen versus untreated control seeds in two habitats: natural pine rockland and a novel restored habitat (adapted from Possley et al. 2015).

bance events. A comparison of *Eucalyptus cladocalyx* in its native habitat in the Southern Flinders Ranges of South Australia and in southwestern Australia, where it is invasive, indicated that fire frequency is a primary force influencing the population dynamics of the species (Ruthrof et al. 2003). Following fire, the species has mass seedling recruitment. Because the introduced site has burned more frequently in the last fifteen years than the native site, *E. cladocalyx* has become invasive. Other studies have shown that time-since-fire affects the demography of plant species dramatically (e.g., Menges and Quintana-Ascencio 2004).

Can Increasing Dispersal and Colonization Improve Metapopulation Persistence?

Restoration practitioners can improve metapopulation persistence by repeatedly collecting and introducing new individuals (rescue effect and establishment effect) and by modifying the habitat to increase likelihood of survival (Maschinski et al. 2004). Kauffman et al. (2003) used population modeling to evaluate how past management activities influenced endangered peregrine falcons (*Falco peregrinus anatum*) in California. The authors used habitat-specific fecundity trends and estimated survival rates in a time-varying matrix model to estimate population growth rates of peregrine falcons in rural and urban habitats. In urban habitats, population growth rates were 29% per year, birds had higher fecundity, and survival rates of first-year birds were higher than in rural habitats, where $\lambda = 0.99$ and there was slower improvement in eggshell thickening through the 1980s. Population trajectories predicted that peregrine falcons would increase following the twofold conservation actions of organochlorine pesticide bans and captive release, and would continue to increase after population augmentation ceased (Wootton and Bell 1992). Christmas Bird Count abundance data calibrated to intensive population surveys showed that over the subsequent two decades that Peregrine falcons have indeed increased confirming the predictions of the PVA (Wootton and Bell 2014).

How Should Restoration Sites Be Spatially Arranged?

Selecting the spatial arrangement of restored patches can be critical to the long-term persistence of the metapopulation. Clustering of patches can benefit species retention due to increased dispersal and colonization opportunities (Kareiva and Wennergren 1995; Harrison et al. 2000; Rybicki and Hanski 2013) and pollinator visitation (Groom 2001). Because the interpatch matrix greatly influences dispersal between patches (Ricketts and Morris 2001), modifying the matrix could reduce patch isolation and extinction risk of populations in fragmented landscapes. The probability of occurrence in a fragment increased with proximity to source populations (fig. 7-8; Honnay et al. 2005) indicating that landscape connectivity is important. However increasing connectivity may also synchronize local population fluctuations and increase extinction risk (Earn et al. 2000), and it is possible to enhance the dispersal of undesirable organisms that may have adverse effects on target species (Hess 1996b).

For practitioners, these diametrically opposed views can make the decision about spatial arrangement of patches in the complex landscape matrix problematic. Knowledge of the species' biology is essential for assessing risks and benefits of spatial structure. This area has great potential for designing restoration experiments that can contribute to theory.

Clustering patches can either reduce or increase extinction risk, depending upon the species' ecology. In a review of twenty-five species of Sonoran Desert freshwater fishes, successful recolonization of empty habitat was related significantly to clustering and occasional long-distance dispersal during periods of high discharge (Fagan et al. 2002). Groom (2001) experimentally manipulated, (1) patch isolation while maintaining constant size, (2) patch spatial arrangement (whether clustered or single), and (3) pollen availability to examine whether levels of isolation influenced pollination, herbivory, population growth, and persistence. Small isolated patches of *Clarkia concinna* had lower population growth and more extinctions than connected patches. Although patch size interacted with isolation to influence pollinator behavior, Groom (2001) recommended clustering subpopulations of insect-pollinated plants to enhance long-term population growth.

In a comparison of fifty-seven species at eight-one sites, Dupre and Ehrlen (2002) found that habitat quality, especially pH, was more important for the inci-

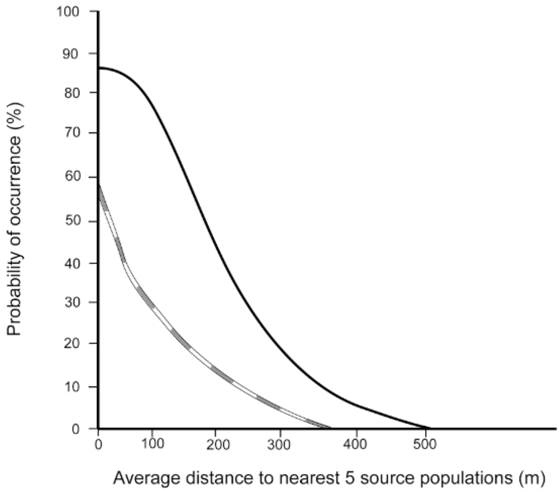

Figure 7-8. The influence of proximity to intact forest on colonization of forest herbaceous plants (redrawn from Honnay et al. 2005). The bold line indicates a highly connected forest matrix with 50% cover; the hatched line indicates a fragmented landscape with 5% cover.

dence of species than habitat configuration. Patch area and isolation significantly affected only eleven and four species, respectively. Species favored by larger area were also disadvantaged by greater isolation. The importance of habitat configuration varied with life history. Habitat specialists and clonal perennials that produced few seeds were more negatively affected by patch isolation, while animal-dispersed species were more negatively affected by small stand size.

Using decision analysis methods, Dreschsler et al. (2003) examined four hypothetical management scenarios where patches of larval host plants for the Glanville fritillary butterfly, *Melitaea cinxia*,in southwestern Finland were removed (fig. 7-9). The models indicated that the removal of the small, dispersed stepping stone patches would have the least detrimental effect on the butterfly metapopulation, while eliminating the largest, most closely clustered patches would have the greatest impact. This finding is in agreement with metapopulation theory, but does not take into account the risks associated with connectivity, nor the possible genetic cost of losing rare alleles from small isolated populations at the edge of the species' range.

Closing Remarks

Restoring new populations of common or rare species, or enhancing existing ones, will become more critical with changing climate and the growing human footprint on ecosystems. Several guidelines are available to assist efforts for plants

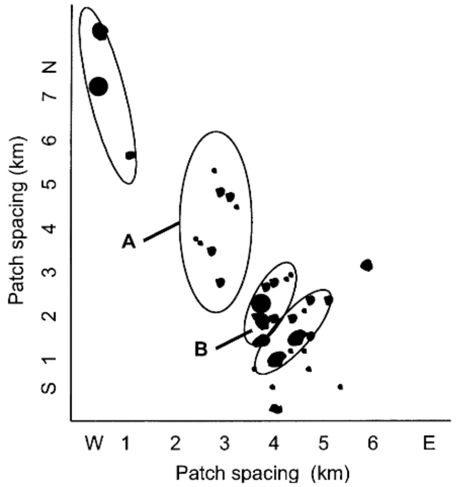

Figure 7-9. The network of habitat patches of the Glanville fritillary (*Melitaea cinxia*) in southwestern Finland used for a management decision exercise to determine which type of site (indicated by the numbered ellipses) could be removed with the least impact on the metapopulation. The coordinates on the axes give the east-west and north-south locations of the patches in the landscape, scaled in kilometers. The sizes of the dots indicate the sizes of the patches, with the largest patch (arrow A) having an area of 0.91 ha and the smallest one (arrow B) having an area of 0.01 ha. Adapted from Drechsler et al. (2003).

(Maschinski, Albrecht et al. 2012, and references therein) and animals (Ewen et al. 2012). Population and metapopulation theory underlie the tenets of the guidelines, but experimental evidence can help refine regulatory guidelines and restoration science.

Examining population and metapopulation structure is most helpful if it is integrated with population genetics (chap. 5) and ecological assessment of habitat heterogeneity (chap. 10) over the entire range of the species over many years. This is a tall order. However, new models provide opportunities to explore diverse factors underlying causes (and effects) of variation in demographic rates, and will be critical for guiding restoration decisions. By integrating connectivity of landscapes at a biogeographic scale with species' demography, it may become possible to examine potential demographic consequences of climate change and/or habitat destruction, and to develop conservation strategies across whole landscapes (chap. 4). Studies encompassing the entire range of a species may require cooperation across several land managing jurisdictions and incorporation of the social and cultural contexts in which they occur.

Many of the world's rare species have small populations lacking genetic diversity that have little habitat for expansion. Holsinger (2000) warned that populations with negative long-term growth rates will require constant management and frequent supplementation to prevent their extinction. Without long-term commitments and investments of time and human action, small populations have little chance of long-term persistence. It is encouraging that many restoration projects have improved species' persistence and sustainability (Maschinski and Haskins 2012), while simultaneously contributing to restoration science.

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Chapter 8

Invasive Species and Restoration Challenges

Carla M. D'Antonio, Elizabeth August-Schmidt, and
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Theory and Application

- An overarching goal of restoration is ecosystems that are resistant to invasive species and resilient to routine disturbance.
- Relevant theory begins with assessment of site conditions and includes alternative states theory and mechanisms of succession.
- Theory relevant to ecological resistance comes from research on community assembly, niche concepts, competition, and priority effects.
- Diversity of species, traits, and functional groups are predicted to play an important role in ecological resistance.
- Less is known about how local processes scale to the landscape where site heterogeneity and metapopulation dynamics influence invasion, ecological resistance, and resilience.

Established populations of nonnative plant species occur in most ecosystems. The ecological effects of these invaders can vary from benign to substantial, while management perspectives on them range from beneficial to harmful. In this chapter we focus on those nonnative plant species considered 'harmful', defined here as having an ecological and/or economic impact undesirable to management and they are typical targets of management and restoration actions. For information on animal invaders, see Simberloff and Rejmanek (2010). Harmful invaders have been variously referred to as "invasive" (Mack et al. 2000) or "transformer" plant species (Richardson et al. 2000). While there is some management concern over rapidly spreading native species (Carey et al. 2012), we use the term invasive in the sense of Richardson et al. (2000): nonnative (alien, nonindigenous or exotic)

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species with the potential for rapid population growth. In many cases ecological impacts of the species have not been measured. Within a restoration context, we assume invasive species would be a target when they (1) already dominate a restoration site or its seedbank and are difficult to remove, (2) may leave behind legacies after removal, or (3) could invade a restoration site and co-opt the direction of postdisturbance/restoration succession by interfering with desired species.

Ecological theories relevant to invader involvement in restoration will be discussed in the context of different phases in restoration planning and implementation. We begin with a short caveat on beneficial uses of nonnative species during ecological restoration and a summary of ideal restoration goals. We then discuss ecological theory relevant to evaluating constraints on restoration caused by the presence of invasive species and how these shape initial planning. Then we evaluate the application of theory to planning for disturbance, and post-disturbance community assembly (see chap. 9) over short and longer time scales, and over small versus larger spatial scales. Generally, restoration in the face of invasive species can be guided by theories relating to alternative stable states and assembly theory including priority effects, competition, niche preemption, and related diversity/invasibility hypotheses.

Changing Views on Nonindigenous Species in Restoration

Views of nonnative species are changing in both a general and a restoration context. Some introduced species can benefit land management or may be important for the achievement of specific restoration goals (D'Antonio and Meyerson 2002; Ewel and Putz 2004). This is particularly true in badly degraded ecosystems where restoration of basic ecosystem functions, such as soil protection against erosion, may depend on use of nonnative species (Whisenant 1999). In highly degraded sites needing *reclamation* or rehabilitation (Bradshaw 1987), nonnative species or genotypes may be some of the only species available, or are the most economically viable species to restore certain functions. When the substrate has lost most of its organic matter, has poor water-holding capacity and is extremely harsh for plant growth, the setting resembles *early primary succession*, rather than target ecosystem conditions (Walker and Chapin 1987; Walker and del Moral 2003). Classic succession theory *sensu* Clements (1916) proposes that early colonists are tolerant of harsh conditions and ameliorate the environment for later arriving species. More recent assessments of the importance of facilitation, like the stress-gradient hypothesis (Bertness and Callaway 1994), also posit that facilitation is important in harsh environments. In a restoration context, early colonists might be selected nonnative species or genotypes purposefully seeded or planted to facilitate establishment of less stress-tolerant species. Yet several recent studies have shown that nonnative species planted for facilitative purposes often interfere with, rather than facilitate, later arriving (or seeded) species, thus stalling achievement of restoration goals (e.g. Brown and Rice 2000; Hagen et al. 2014). So, while *facilitation* using nonindigenous species is an attractive concept in harsh settings, few studies show facilitation of the desired native species rather than interference by the planted nonnative species (but see Pec and Carlton 2014). Consistent with this, Maestre et al. (2009) and Holmgren and Scheffer (2010) suggest that the stress-gradient hypothesis needs refinement, because experimental work shows that species in stressful sites can be competitive rather than facilitative.

In other settings, nonnative species may purposefully be used in restoration to prevent invasion by transforming invaders (e.g., case study box 8-1). Several ecologists and practitioners stress that nonindigenous species are “here to stay” (Davis et al. 2011) and can be an important part of the palette of species available within a region to achieve particular management objectives. Hobbs et al. (2009) stress that “hybrid ecosystems” containing mixtures of native and nonnative species are often the most reasonable goal for degraded sites. Lugo (2004) emphasized that invasive nonindigenous species can be critical to the restoration of productivity and species richness, where past destructive land use has so altered soil structure that diverse native forests cannot reestablish. He suggests that targeted planting of nonnative species, even those shown to be invasive elsewhere but suited to the degraded site, can facilitate forest succession (Lugo 1997). In unmanaged sites, native species begin to colonize monotypic stands of invasive tree species by thirty to forty years (Lugo 2004). More work is needed identifying environmental contexts in which including exotic species in restoration would be beneficial.

Resistance and Resilience as Targets for a Restored System

The ultimate goal of restoration and management activities is self-sustaining ecosystems on a trajectory of desired composition and processes (chap. 1). A self-sustaining ecosystem is *resilient* to routine disturbances, returning to predisturbance conditions or a trajectory close to that within a reasonable timeframe following a disturbance (Holling 1973) and without human intervention. Ideally, these systems are also largely resistant to change following arrival of propagules of potentially damaging or unwanted species. *Ecological resistance* refers to the biotic and abiotic factors in a recipient ecosystem that limit the population of an invading species (Elton 1958; D’Antonio and Thomsen 2004). Accepting that ecological resistance is probabilistic (D’Antonio et al. 2001), the ecological processes in a self-sustaining system would at best greatly reduce the probability of invasion by strong competitors. Hence, promoting ecological resistance is a key element of restoration projects where invasive species are a threat.

Case Study Box 8-1

Using Plant Functional Traits to Improve Invasion Resistance

Lowland wet forest, HI: Lowland wet forests in the Hawaiian Islands are vulnerable to invasion by exotic species and few uninvaded forest patches remain. In the absence of restoration efforts, native species will likely be lost due to the high density of invasive species and the lack of canopy species regeneration.

Case Study 8-1. *Left* = control plot; *right* = newly planted along with relictual native individuls. Photos courtesy of E. August-Schmidt.

Relevant theories: Niche preemption, functional traits, priority effects:
Sixteen 30m x 30m forest plots were cleared of invasive species and replanted with mixes of ten species per plot. Species combinations were chosen to fill trait space and to compete with invasive species using desirable native and noninvasive exotic species (already present in Hawaii but not invasive). Many are culturally important. The resistance and carbon storage of these plots will be compared with nearby unrestored plots.

Expected outcome: Restored plots are expected to resist invasive species, to store more carbon, and to maintain populations of native species that might otherwise be excluded from the landscape.

Progress: Aboveground alien biomass was removed from treatment plots leaving native species. Cleared plots were then planted with one of four species mixes that targeted either slow or moderate carbon turnover with either redundant or complementary traits. After the first year, over 90% of outplants survived, and seedling recruitment by native species increased. Restored plots will continue to be weeded until the target canopy begins to close.

Long-term outcomes: Monitoring will determine which species combinations resist invasion, how they cycle carbon, and whether plant communities with complementary or redundant traits confer greater invasion resistance.

References: Cordell et al. 2009; Ostertag et al. 2009; Ostertag et al. 2015.

Resistance and resilience can potentially be enhanced by manipulation or maintenance of structural properties and ecosystem processes known to favor the persistence or recovery of desirable species. Knowledge of controls over resistance and resilience are therefore essential for restoration and management to achieve stated goals in most settings (chap. 2). Thus, they play a prominent role in this chapter.

Site Assessment

Before restorative actions are initiated, it is useful to assess the extent to which exotic species at the site will limit how the practitioner can direct succession. Does the presence of particular invaders indicate a fundamental shift in environmental parameters? Are the invaders present at the restoration site likely to affect which species can establish even after the invader is removed?

Alternative Stable States Theory Can Guide Early Decisions

As described in chapter 2, ecological systems can exhibit complex dynamics that can make restoration trajectories difficult to predict and lead to surprising outcomes. Recently a great deal of attention has been paid to the concept of alternative stable states (chap. 2) with reference to degraded ecosystems and invasive species (e.g., Beisner et al. 2003; Suding et al. 2004). The decision to initiate a restoration action that involves large-scale removal or control of an invasive species is based upon the belief or knowledge that the current, dominant invader (1) plays a role in keeping the site in its *degraded* state, thus perpetuating an alternative stable state (Suding et al. 2004), or (2) that the invader will return after the initial disturbances of restoration and then interfere with achievement of a desired ecosystem state, trajectory, or delivery of ecosystem services. Beisner et al. (2003) provide a useful framework for deciding the level of management required to restore a system dominated by invasive species. What matters for practitioners is an understanding of the forces keeping the system in its seemingly stable configuration of invader dominance. If these forces are not reversed by removal of the invaders, then further management will be required to restore conditions conducive to native dominance.

Beisner et al. (2003) suggest that alternative states come about when an invader (a) establishes priority effects, or (b) takes advantage of a shift in ecosystem conditions (fig. 8-1). Consideration of these alternatives helps to answer three important questions: (1) whether removing the invader is enough to restore the system to a desired condition, (2) whether the invader is generating a strong positive feedback that must be counteracted to achieve restoration, and (3) whether site conditions

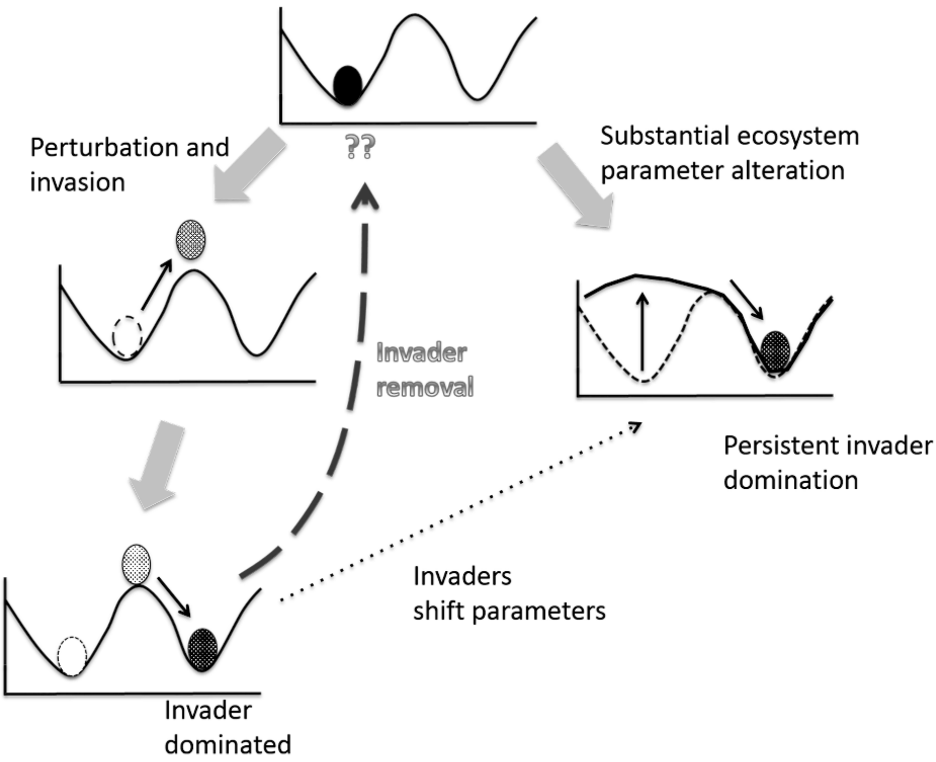

Figure 8-1. Figure adapted from Beisner et al. (2003). The ball represents a state variable, such as species composition, which may have been shifted due to invasion of the system by an invasive species. On the *left* side, removal of the invader could lead to restoration if system parameters have not been fundamentally altered. On the *right* pathway of the diagram, a shift in ecosystem parameters has occurred, and removal of the invader will not lead to restoration of the system.

have been so altered that the system cannot be readily restored. The latter two involve *hysteresis* (see chap. 2).

The alternative states framework is applicable to ongoing restoration of portions of western US river systems that are dominated by trees in the genus *Tamarix* (case study box 8-2). Where hydrological regimes have been altered by humans, *Tamarix*-dominated riparian forests are rarely restorable to native vegetation despite extensive manual *Tamarix* removal (e.g., Harms and Hiebert 2006) or biological control (Dudley and Bean 2012). Passive restoration after control is only likely in areas where hydrologic conditions are within the range for native species recruitment and persistence (Shafroth et al. 2008). Ongoing research seeks to evaluate the degree to which hydrological parameters must be improved and composition restored via outplanting of natives, in order to create persistent native riparian woodlands. Knowing where to target postcontrol restoration action saves time and money.

Similarly, in midwestern US wetlands, invasive genotypes of Reed canary grass (*Phalaris arundinacea*) now dominate wetlands within agricultural landscapes where both hydrology and nutrient inputs have been altered. Removal of *Phalaris* does not restore the ecosystem because nutrient enrichment via agricultural runoff, and *Phalaris*' phenology, and regrowth capability (dormant belowground buds) favor resprouting. Restoration is extremely difficult without addressing nutrient pollution and reversal of soil fertility (Adams and Galatowitsch 2006; Lavergne and Molofsky 2006; Healy and Zedler 2010).

While invaders may become abundant due to changing site conditions, they also can change conditions and create feedbacks that lock a system in an alternative state or create hysteresis so that restoration is difficult. To adequately restore an invaded site requires breaking the positive feedback cycle. The most widespread example is the invasion of western US deserts by fire-enhancing annual grasses of Eurasian origin at the expense of native species (Chambers et al. 2014). Because many native communities have limited resilience to frequent fire, breaking the grass/fire cycle is essential to direct the system toward desired communities. Researchers in the Great Basin desert are actively exploring restoration of fire tolerant native perennial grasses to suppress exotic annual grasses, reduce the continuity of fine fuels, and reduce the frequency and spread of desert fires (D'Antonio et al. 2009). Brooks et al. (2004) suggest a framework for controlling and restoring sites invaded by fire-altering plants. Overall, restoration in the face of invaders that create positive feedbacks, like fire-promoting grasses, is extremely challenging.

Legacy Effects of Invasive Species Can Shape Restoration Planning

Legacy effects, a type of *priority effect* (discussed below), are changes a species makes to the abiotic environment that persist after it is gone. Invasive species can alter soil conditions to the detriment of native species, and these changes can persist after the removal of the invader. Legacy effects can be anticipated prior to restoration by assessing who the invaders are and what is known about them. For example, such effects are pronounced with nitrogen-fixing invaders, such as scotch broom, *Cytisus scoparius*. The growth of Douglas fir was suppressed in soils collected from *Cytisus*-invaded sites compared to forest soils where *Cytisus* was absent (Grove et al. 2012). Although, *Cytisus* can elevate soil nitrogen, it also produces leaves with high concentrations of the toxic alkaloid, sparteine (Grove et al. 2012) which persists in the soil after it has been removed. Allelopathy has

Case Study Box 8-2
Alternative States—A Framework for *Tamarix* Control and Restoration

Western USA: *Tamarix* spp. are nonindigenous trees that have invaded riparian ecosystems throughout the western United States. *Tamarix* is the target of restoration because it transpires large amounts of water, reduces wildlife habitat, elevates soil salinity, and increases occurrence of fire.

Case Study 8-2. Widespread *Tamarix* in Virgin River (*left*). Restoration plantings survive if targeted to areas with suitable hydrology (*right*). Photos courtesy of Tom Dudley.

Relevant theory: Alternative stable states, priority effects.

Expected outcomes: If dominance of *Tamarix* is due to altered state variables, such as stochastic decline of cottonwood and willow and the stochastic recruitment of *Tamarix* post-disturbance, then removal of *Tamarix* should return a site to its previous dynamic equilibrium of willow/cottonwood domination. Alternatively, if *Tamarix* domination is due to altered ecosystem parameters such as altered hydrological regimes, then *Tamarix* removal (e.g., eliminating the priority effect of *Tamarix*) will not be enough to restore desired conditions.

Progress: Evidence supports both stochastic priority effects and ecosystem parameter shifts—specifically modification of river hydrology. Hydrological modification is considered to be more important. Removal of *Tamarix* through manual or biological means has generally not restored native riparian forests, suggesting both readjustment of ecosystem parameters and elimination of simple priority effects are necessary.

Long-term outcomes: New efforts include detailed hydrological assessments of the river terraces, outplanting native species where hydrology favors desired native species, and (proposed) carefully timed releases of water to mimic more natural flood regimes.

References: Shafroth et al. 2008; Harms and Heibert 2006; Dudley and Bean 2012.

also been suggested as a mechanism for native growth suppression in *Centaurea maculosa* (Ridenour and Callaway 2001) and *Alliaria petiolata* (Wolfe et al. 2008). Allelopathic effects may act directly on native species or indirectly via the microbial community (Kourtev et al. 2002). In some cases, the changes to the soil environment may establish positive feedbacks promoting the invader (e.g., Ehrenfeld et al. 2001).

Legacy effects may present a considerable challenge to restoration practitioners if they are strong or long lasting, leading to hysteresis (chap. 2). Yet, the strength and duration of legacies vary among systems (e.g., Eviner and Hawkes 2008). In deciduous forests researchers (Ehrenfeld et al. 2001) found that even two years after the removal of invasive *Berberis* spp. and native shrub planting, the structure and function of the microbial community reflected the past invader (Elgersma et al. 2011). Likewise, when nutrient pools are increased by invasive nitrogen-fixing shrubs and trees (e.g., Vitousek et al. 1987; Vitousek and Walker 1989; Stock et al 1995) or salts are concentrated by forbs (Vivrette and Muller 1977; Blank and Young 2002), removal of the invaders is unlikely to allow restoration of the vegetation without some creative way to restore the soil.

Succession Theory Can Help Prioritize Which Invasive Species to Control

Hypotheses to explain the role of species in succession can be used as a basis to prioritize use of limited resources for control when multiple invaders are present. Connell and Slatyer (1977) proposed three models to explain the potential influence of an early arriving species on subsequent compositional change: an invader could (1) facilitate, (2) inhibit, or (3) have no effect on subsequent species colonization. While they did not propose this as a framework for evaluating the impact of an invasive species, it nonetheless provides a baseline for ranking species of concern. An invader that can facilitate establishment of additional potentially undesirable invaders could lead to “invasional meltdown” (Simberloff and Von Holle 1999), a situation in which invaders facilitate other invaders until little of the original native system remains. For example, nitrogen-fixing invaders can facilitate establishment of undesirable species after their death or removal, potentially with dire consequences for native species (Maron and Connors 1996; Adler et al. 1998; Alexander and D’Antonio 2003). When desired ecosystem services depend on particular species, invaders that inhibit their establishment or facilitate other invaders should receive priority control. Such species can likely be predicted by careful evaluation of impacts elsewhere, species traits, and composition of the regional species pool.

Planning for Disturbance

The tight link between disturbance and invasion has been recognized for decades (Hobbs and Huenneke 1992; D'Antonio et al. 1999). Most restoration projects involve considerable site disturbance. Thus species with the capacity for rapid population growth, including invasive species, should be expected to benefit from restoration actions. Davis et al. (2000) provided an overarching model to explain community susceptibility to invasion, the *fluctuating resources hypothesis*. This framework predicts that invasibility (or resistance) is a function of the balance between community-level resource uptake and gross resource supply rates (fig. 8-2). When supply and uptake are equal, no invasion occurs, presumably because there are no extra resources for invaders to harvest. Disturbances, including those created by restoration, reduce resource uptake and alter supply rates, allowing for invasion. The duration of an invasion window is influenced by the type, size, and frequency of disturbance events, and tolerance and response of the resident species to those events. For example, severe disturbances can greatly depress resident populations and potentially destroy their seedbanks, increasing the length of time that the community is relatively open to invasion or conversely to rapid planting or seeding in a species-depauperate setting. If propagule sources of damaging invaders are limited, the community may eventually recover. Likewise, disturbance more frequent than resident species have experienced historically may select for undesirable short-lived species. The goal is to anticipate which species are likely to respond to different disturbances and to optimize disturbance in restoration. Identifying the regional pool of both native and invasive species and their disturbance-response-related traits would be helpful for achieving this aim.

The fluctuating resources hypothesis provides a dynamic framework for considering both the disturbance associated with restorative activities themselves, and for anticipating the trajectory of a site and its resilience after the initial years of restoration. In the short term, the hypothesis suggests that removal of invaders reduces resource uptake, thereby moving a site away from the uptake/supply rate isocline, which paradoxically can increase its further invasibility. Without rapid resumption of plant resource uptake, such as by planting or seeding native species, replacement species may perpetuate the impacts of the original invader or be worse than the original invader. For example, control efforts to remove *Hakea sericea* in South African fynbos sites can lead to invasion by *Acacia longiflora*, a species that is harder to control (Pieterse and Cairns 1986). Several studies have found that controlling one invader leads to colonization by other invasive species if no additional restoration actions are employed (e.g., Firn et al. 2010; Healy and Zedler 2010).

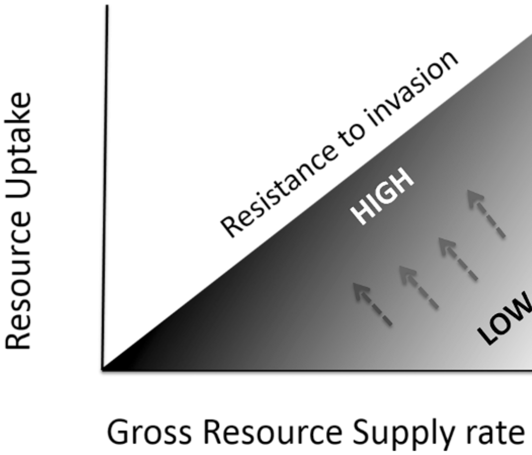

Figure 8-2. The theory of fluctuating resources suggests that factors like disturbance, that push a system away from the 1:1 line where resource uptake=gross resource supply rate and resistance to invasion is HIGH, enhance invasion susceptibility. Restoration actions initially usually involve disturbance and so will push a system towards lower resistance. These initial implementation actions must be followed by native species planting and other actions to push the system back towards the isocline. Arrows indicate restoration actions. Modified from Davis et al. (2000).

Because species evolve adaptations to disturbance regimes, restoration practitioners can manipulate disturbance to prevent invasion. For example, frequent prescribed burning in tallgrass prairie reduces invasion of prairie stands by Canada thistle, because the native flora is well adapted to fire whereas the thistle is not (Reever-Morghan et al. 2000). The role of disturbance in promoting versus preventing invasion is thus a function of the evolutionary history of both resident species and invaders (Hobbs and Huenneke 1992; D'Antonio et al. 1999; Pyke et al. 2010). Fires, for example, are essential for the maintenance of southeastern longleaf pine savannas. Yet poorly timed fires (outside the lightning season) can promote invasive species including exotic hardwoods in these species-rich systems. Additionally, decreasing fire frequency appears to favor invasive grasses and shrubs (e.g., DeCoster et al. 1999; Platt 1999; Platt and Gottschalk 2001; Drewa et al. 2002). The extensive work in pine savannas emphasizes the complications of manipulating disturbance regime to restore desired conditions.

Planning for Community Assembly

Early restoration ecology drew heavily from successional models, which assert that communities lie on a single trajectory toward a climax community. Because succession theory is largely deterministic, restoration founded on this model is straightforward and can rely on reference sites for standards to assess outcomes. However, there is a growing awareness of the importance of stochastic factors and invasive species in driving community assembly, and recent theory now attempts to incorporate random interannual variation in species arrival and establishment within communities (Young et al. 2001; chap. 9). Restoration founded on community assembly models is inherently less straightforward because it acknowledges both the existence of multiple stable states and the strong role that can be played by invasive species.

Priority Effects and Competition Theory

Multiple trajectories of community assembly exist because different species arrive at a site at different times by chance or by planning in restoration. *Priority effects* broadly refer to the influence of early-arriving species on community development because of inhibitory effects they have on later-arriving species (Diamond 1975). Priority effects make up the foundation of modern community assembly theory and operate via a number of different mechanisms that are relevant to restoration, including niche preemption, asymmetric competition, and soil legacy effects.

Niche preemption can occur when the existing community uses resources fully or to the extent that invasion probability is reduced, presumably because all niche space is occupied. This would be equivalent to a community being on the “resistant” line of the fluctuating resources hypothesis diagram (fig. 8-2). The importance of niche preemption in both time and space is already well understood by restoration practitioners who immediately seed or plant recently disturbed sites with native species.

The relationship between niche preemption and invasion resistance may depend heavily on the traits of the desired and undesirable species. Invasive species are often considered to be superior competitors to native species or to outperform them under a variety of circumstances (Daehler 2003). If all species arrive at a site at the same time, invaders may then be expected to win, although this has not been well studied. Some work has shown that invasive species or genotypes germinate earlier or more rapidly than their native counterparts, giving them a competitive advantage. For example, invasive genotypes of *Rhododendron ponticum* (Irish and Georgian strains) took fewer days to reach 50%–90% germination than a native genotype (Spanish) (Erfmeier and Bruelheide 2005). Because these researchers assessed differences among growth rates independently of germination ability, it remains unclear if the rapid germination of the invasive genotypes would lead to differences in biomass. In contrast, competition experiments with native and exotic grassland species show that, for at least some species combinations, native species can outcompete exotic annual grasses when started at the same time or when natives have a chance to establish first (Corbin and D'Antonio 2004; Abraham et al. 2009; Firn et al. 2010). Thus, much of invaders' perceived competitive dominance may result from earlier arrival and establishment.

In California grasslands, exotic annual grasses often germinate and establish within days after the first fall rains. Early emergence can lead to the suppression of native perennial grass seedlings, but it has little impact on exotic perennial grasses, suggesting that natives may be more susceptible to priority effects than nonnatives (Abraham et al. 2009). Exotic species removal or seed bank exhaustion combined with native seed addition is a viable restoration approach. Wainwright et al. (2012) showed that manipulating the start of the rainy season (by hand watering) forced the germination of annual exotic grasses but not native species in coastal sage scrub. The annual grasses died during the gap between watering and the onset of rains, depleting the exotic seedbank. However, priority effects may include legacy effects (discussed above) even after exotics are removed.

Historical contingency, including arrival history and growing conditions when a restoration project begins, can influence who becomes dominant at a site, yet effects of historical contingency can diminish over time. For example, in experimental plantings of restored vernal pools, Collinge and Ray (2009) demonstrated that early-arriving species had a strong influence on pool dominance, and as a result different pools appeared to be on different community composition trajectories. But by the end of the seven-year study, species composition of most pools had converged (Collinge and Ray 2009). In this instance, priority effects were strong initially, but short lived. Understanding whether effects of historical contingency persist is important for understanding when initial invaders should be controlled versus when they might decline, allowing succession toward a more desirable community.

Role of Species Diversity in Invasion Resistance

Classical ecological theory predicts that invasibility of an ecosystem will be negatively correlated with diversity (MacArthur 1955; Elton 1958; MacArthur 1972). The proposed mechanism by which species diversity confers resistance to invasion is through competition for resources. A positive correlation between species richness and resistance to invasion is supported by many studies that manipulate diversity at small spatial scales (Stachowicz et al. 1999; Levine 2000; Dukes 2002; Kennedy et al. 2002; Maron and Marler 2007). For example, using experimentally assembled plant communities in 1.3 by 1.3 m plots, Maron and Marler (2007) found a positive relationship between species diversity and resistance to *Centau-*

rea maculosa invasion. The assumption is that a more diverse species assemblage will use available resources more completely, making them inaccessible to new arrivals.

Another potential mechanism for the inverse relationship between invasibility and diversity is the increased likelihood of including a strong competitor to the would-be invader in a species-rich assemblage. Some work suggests that the establishment of key native species may be sufficient to reduce exotic invaders (Lulow 2006; Stevens and Fehmi 2009), although diversity may be desirable for other reasons. Lulow (2006) showed that invasion resistance did not increase with species diversity in an assemblage of grasses, suggesting that species identity may matter more than diversity. In this case, resistance to invaders is not a function of diversity per se, but an indirect result of its interactions with one or a few species. Knowing which native species best resist invaders and establishing them first may be a more effective strategy than planting a diverse suite of native species.

Are Functional Diversity and Trait Diversity More Important than Species Diversity?

There is increasing evidence that an informed trait-based approach can greatly improve the invasion resistance and stability of restored communities (Palmer et al. 1997; Funk et al. 2008). To establish and become abundant on a site, both native and exotic species must pass through a series of filters that select for a given suite of traits, moving from regional to local scales, where biotic interactions become more important (Theoharides and Dukes 2007; Funk et al. 2008; also chap. 9). At the broadest scales, factors such as climate and soils filter species from the regional pool, while factors such as competition and herbivory determine which species coexist within a local community. Understanding environmental constraints of the restoration site combined with collecting trait data associated with resource use and competitive ability of native and exotic species can greatly inform restoration and management strategies.

Restoration may begin by removing exotic species and adding native seed, particularly in degraded sites with a poor seedbank (Turnbull et al. 2000). However, the traits of the natives that are seeded can strongly influence the outcome. Ideally, seed mixes would include species with traits associated with rapid colonization and establishment, including rapid germination, rapid flowering, and high allocation to seed production (Grime 1979). For example, in an analysis of twenty-five case studies of grassland restoration in Britain, high seed viability, autumn germination, and high seedling growth rates were significantly correlated with colonization (Pywell et al. 2003). In another British grassland study, regenerative traits were the best predictors of who invaded sites after two years, but not after five, suggesting a decline in importance of colonization traits with time (Thompson et al. 2001). Understanding the dispersal and colonization traits of nonnative species in the regional species pool may allow managers to better ascertain which species are likely to arrive at a particular location.

To some extent, we can predict which native species will be good colonizers, but the ability to restore an invasion-resistant community will largely depend on matching traits to seasonal patterns of resource availability to fully utilize resources across the year. The *limiting similarity hypothesis* predicts that a species is less likely to invade if it is functionally similar to species well established in the community, or if the native community fills the full breadth of the available niche space (Funk et al. 2008; Moles et al. 2008). For example, in a California serpentine grassland, functional diversity decreased invader establishment and reproductive success, suggesting it not only decreased invasion susceptibility but also impacts (Hooper and Dukes 2010). Further, invaders were more strongly suppressed in plots containing the same functional group (e.g., both being early season annuals), and some effects were synergistic in that the invader was more strongly suppressed when all functional groups were present. Phylogenetic distance can sometimes serve as a proxy for functional similarity. Strauss et al. (2006) found that highly invasive species were significantly less phylogenetically related to native grassland species and that the least-related invaders had the largest ecological impacts. These results suggest that, at least for grasslands, invaders are occupying available niche space not used by native species.

Much of the support for the limiting similarity hypothesis comes from artificially constructed communities, rather than from experimental removals of species from more natural communities. A recent meta-analysis (Price and Pärtel 2013) found that functional similarity between invaders and native species reduced invasion and performance of forb invaders, but not grasses. However, the extent to which the limiting similarity hypothesis holds true remains unclear for natural communities or invaders defined by specific traits rather than broad functional categories. In any case, restoration of bare ground would likely benefit from introducing species across the functional group spectrum selecting complementary species from the pool of potential colonists.

Resource Enrichment Influences Dominance and Composition

Resource conditions have a strong influence on the outcome of management actions because they affect the interactions among desirable and undesirable species and influence the diversity of species that can be established. Site productivity can affect growth rates of invading species and influence the tendency for a single species to rise to dominance at the expense of others. This paradox, that diversity generally declines with increasing soil fertility and productivity (Cleland and Harpole 2010; Maskell et al. 2010; Isbell et al. 2013), is well recognized and could influence how practitioners control invasive species and promote desired diversity. Fertilization studies have demonstrated that invaders can increase with fertilization (e.g., Huenneke et al. 1990; Maron and Jeffries 2001; Woo and Zedler 2002). Likewise greenhouse competition studies show that invaders outperform co-occurring native species in fertile conditions (Daehler 2003). Thus, careful consideration of soil fertility is an essential first step to restoration in sites where invasive species could become dominant.

The application of sucrose or sawdust to soils during or prior to the planting of desirable species has been evaluated as a tool to reduce performance of fast-growing weeds (e.g., Blumenthal et al. 2003; Perry et al. 2004; James et al. 2011; chap. 12). This approach is based on the assumption that added carbon will stimulate microbial immobilization of nitrogen which in turn will reduce competitive suppression of the desired species by nitrophilous weeds. While studies generally confirm that carbon addition immobilizes available nitrogen, not all support the prediction that decreased N will alter the strength of competition, thereby favoring a more diverse assemblage of slower growing native species (e.g., Reever-Morghan and Seastedt 1999; Alpert and Maron 2000; Paschke et al. 2000; Perry et al. 2004). Still this has proven to be a useful tool in enough settings that it should be considered in resource-rich sites but with careful attention to contingencies influencing outcomes of this method (Eviner and Hawkes 2008; chaps. 12 and 13 further discuss the roles of nutrients in restoration).

Other practitioners trying to restore native species to N-enriched sites have experimented with mowing or cutting followed by biomass removal to reduce the growth of undesirable species. The ultimate goals include reduction of ecosystem N and reduction of competitive effects from invasive species. For example, prior to the last two decades, serpentine grasslands in California were refugia for native diversity, presumably because low soil nutrients limited the growth of fast-growing natives (McNaughton 1968; Harrison 1999). In recent decades nitrogen deposition from automobiles has resulted in fertilization of these grasslands, which has favored invasion by fast-growing European grasses to the detriment of native annual forbs (Weiss 1999). To ameliorate the effects of N deposition and promote native richness, Weiss (1999) instituted a mowing and biomass removal program that appears to be effective. Likewise, in a northern California prairie, Alpert and Maron (2000) repeatedly mowed N-enriched pasture soils and found that exotic plant cover declined with repeated mowing, although the mechanism of reduction of the exotics was not clearly identified. European wetland scientists consider topsoil removal an essential first step in restoring species-rich fens that have become eutrophic (Lamers et al. 2015).

Planning for Long-Term Resilience and Resistance

The long-term success of a given restoration project depends in large part on the broader landscape context the site fits into.

Landscape Considerations—Spatial Heterogeneity and Invasion Resistance

To date, much of the literature within restoration ecology has focused on relatively small spatial scales, ranging from meter-square plots to a single field. However, important considerations may only become apparent from a landscape perspective, including spatial heterogeneity, edge effects, and metapopulation dynamics (chap. 4). A clear example of where small-scale processes do not scale easily to landscape restoration concerns how species richness creates invasion resistance. High native species richness can limit invader establishment at small spatial scales as discussed above (e.g., Levine 2000; Naeem et al. 2000; Maron and Marler 2007; DiAllesandro et al. 2013,; see case study box 8-3). At these scales, roots interact for belowground nutrients and water, and leaves interact for light. However, at larger spatial scales, the same factors that drive overall diversity of the resident community, such as soil fertility, water availability, and habitat heterogeneity, also promote invasion (chap. 10), and a number of researchers have found a positive correlation between exotic and native species richness at landscape scales (Stohlgren et al. 1999; Davies et al. 2005). This apparent paradox is driven, in part, by spatial heterogeneity. Nevertheless, increasing species diversity at the scale of restoration sites has been shown to improve local and landscape invasion resistance in some ecosystems (see case study box 8-3).

In the selection of reference sites (chap. 1), there is often the implicit assumption that intact ecosystems are naturally stable and have few invaders, yet this is often not the case (e.g., Eriksson et al. 2006). Both native and exotic diversity have been positively correlated with spatial variation in abiotic variables (Deutschewitz et al. 2003; Davies et al. 2005) and such variation could be acting to promote invader diversity both in reference and in restoration sites. Within heterogeneous plantings sites, ideally assemblages of natives used to generate invasion resistance will vary across the abiotic heterogeneity. Additionally, diversely planted assemblages within restoration sites could benefit from reduced invader impacts compared to relatively species-poor plantings. Dukes (2002) for example found that while high species diversity was insufficient to repel invasion of *Centauria solstitialis*

Case Study Box 8-3
Species Richness and Invasion Resistance in Large Plots

Tallgrass prairie, Great Plains, US: About 90% of North America's largest vegetation province has been lost to agriculture and urbanization.

Case Study 8-3. (From *L* to *R*) A monoculture, low-diversity mixture, and high-diversity mixture from The Nature Conservancy experimental research plots. Photos TNC.

Relevant theories: Priority effects, species richness confers invasion resistance

Expected outcome: Theory predicts that increased species richness and increased planting density reduce invasion. This experiment compared cover of seeded versus unseeded and invasive species to compare the relative strength of species richness and seeding density.

Progress: For decades, large plots (3,025 m^2) had been cultivated and managed with conventional tillage and chemicals. In April 2006, twenty-four plots (55m x 55m) were seeded with either 97 or 15 species, sown at either high (336±8 seeds/m^2) or low density (168±4 seeds/m^2). Plots were burned and weeded in 2008; composition was assessed yearly in 2007–09.

Long term: Three years after seeding, there were twenty-two species in both density treatments of the high-richness plots versus nine species in low-richness, low-density plots and thirteen species in low-richness, high-density plots. High richness plots had ~5.5 cm basal cover of unseeded species compared to low richness plots with 13cm. Cover of unseeded species was not affected by density. Species-rich plots resisted invasion more than low-richness plots planted at the same density. These results from large plots are consistent with results of smaller scale studies (see text.)

References: Samson and Knopf 1994; Nemec et al. 2013.

in California grassland mesocosms, higher diversity limited the weed's impact on native species growth (Dukes 2002). Thus, while restoring patches for invasion resistance within a highly heterogeneous landscape is difficult, all else being equal, building robust, relatively diverse and higher-resistance assemblages may be one of the best methods available for reducing overall invader impacts.

Fragmentation and Metapopulation Dynamics

Habitat fragmentation increases habitat edge and a patch's exposure to outside influences, which may promote species invasions. Fragmentation can also increase the distance that native species, including those desired in restoration, must disperse to reach suitable habitat (Soons et al. 2005). Together these factors can decrease resilience of the restored site. In addition to the landscape context of a restoration site, the size of a habitat patch may influence invasion potential. Exotic species richness was significantly higher in small serpentine grassland patches than in large ones, suggesting that small patches are more easily invaded (Harrison 1999), perhaps because high propagule pressure eventually overwhelms local resistance (D'Antonio et al. 2001). However, a study from California riparian communities did not show any correlation between patch size and exotic or native species richness (Holl and Crone 2004), suggesting this relationship may depend on the system. In addition to patch size, distance between patches and connectivity are also important, with greater connectivity often supporting more native species (Soons et al. 2005; Minor et al. 2009; chap. 4), potentially via metapopulation dynamics.

Restored sites surrounded by a matrix with altered disturbance regimes are potentially vulnerable to invasion due to high propagule pressure. Adjacent habitat patches with altered disturbance regimes may also have depleted native seed sources, tipping the balance of colonizers reaching the restored site toward exotic rather than native species. Thus, restored patches may eventually degrade as native species within them are extirpated due to stochastic demographic variation, and invasive species from the surrounding landscape replace them.

Closing Remarks

Exotic and invasive species are a reality in most landscapes, and eradication during restoration is unlikely to be feasible. In some cases, invaders are superior competitors or more rapid colonizers than native species, and the historical disturbance regimes or environmental characteristics of restoration sites have been altered so that invaders are favored. However, there are steps restoration practitioners can take to improve resistance to invaders of greatest concern and to limit their impacts in restored areas:

- *Mediate legacy effects of previous invaders*. Some species have long-lasting effects that can push the system into an alternative state that persists after invader removal and may promote recolonization by exotic species. Addressing legacy effects may involve adjusting nutrient availability or soil pH, for example.
- *Reduce nutrient availability*. If nutrient-loving invaders are a threat, lowering overall nutrient availability can buy time for desirable species to establish. Tools include topsoil removal and addition of carbon-rich substrates.
- *Reduce potential for invasive species priority effects* in the post-disturbance environment. Depleting the seedbank or local colonizer pool of invasive species is often critical to ensuring they do not establish first after site preparation.
- *Promote diversity* by using species rich seeding or planting mixes. Maximizing resource use by desired species can limit resources for would-be invaders. High diversity plantings are more likely to include strong competitors and species that could preemptively fill shared niches.
- *Match plant traits and functional groups to those of the potential invaders*. Including desired species with traits similar to those of harmful exotics can limit their ability to invade. In the absence of trait data, phylogenetic distance has been used as a proxy for functional similarity. Plantings with broader functional group coverage should be positioned to resist invasion.

Although the study of invasive species has been an area of active research for decades, there is still much that remains unknown, particularly with reference to restoration.

- A large number of restoration studies are done in grasslands and herbaceous wetlands presumably because they are responsive systems that can be studied in the timeframe of a dissertation or grant. Herbaceous invaders in these systems are relatively small and easy to remove, and native species are easy to manipulate and reach reproductive maturity quickly. Yet many degraded and invaded ecosystems are not grasslands. It remains unclear if mechanisms and processes observed to operate within short-lived communities hold for communities dominated by long-lived species, such as forests. *More long-term research needs to be done on restoring invaded ecosystems other than grasslands and wetlands*.
- Most experiments that test ecological hypotheses, or theories relevant to restoration, are done at small spatial scales such as 1 × 1 m up to 10 × 10 m plots, which are appropriate for testing the importance of competition or priority

effects. Yet we know from landscape patterns that these experiments do not readily scale up for reasons discussed above. *More experiments are needed that include heterogeneous, larger plots ($\geq$1 ha).*

- The impact of restoration site landscape configuration on the seed supply of invasive species has not been well studied. Both modeling and regional analyses using GIS could shed light on how rapidly restoration sites could degrade given different configurations of invader source population patches in the landscape.
- The opportunities and challenges of restoration under rapid climate change have not been well explored with regard to invasive species. Climate change may offer restoration opportunities by decreasing the performance due to reduced resources (Sorte et al. 2013) or shifting invader range or competitiveness (Bradley et al. 2009). More research such as the modeling in Bradley et al. (2009) is needed in this area (chap. 17).
- Because the volume of transcontinental trade and number of trading partners continue to expand (e.g., Bradley et al. 2012), invaders will be an increasing part of most landscapes. More research is needed to identify conditions that foster coexistence of native and nonnative species versus situations where invaders proceed rapidly to dominance once present. Similarly, because ecological resistance is probabilistic over space and time, particularly at the landscape scale, ongoing invader control may be necessary to ensure that restoration projects meet their goals. Levels of invader abundance that are compatible with native species persistence could be identified if they exist. Even when they exist, thresholds are rarely identified (see Adams and Galatowitsch 2006; Healy and Zedler 2010 for examples). More research is needed on thresholds of invader abundance that result in impact to native species (plants or animals).

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Chapter 9

Assembly Theory for Restoring Ecosystem Structure and Functioning: Timing is Everything?

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Theory and Application

- Interactions between species can have important implications for community assembly.
- Priority effects, caused by first arrivals, occur in many habitats and can lead to different ecosystem trajectories and alternative states.
- There is potential for using priority effects during restoration to steer toward desired outcomes.
- The strength of priority effects seems to relate indirectly to inter-annual weather conditions.
- Consequently, we now need to start setting up multiple-initiation experiments and restoration projects to tease apart the relative role of stochastic versus directed assembly drivers.

The field of ecology focuses on interactions between organisms and between organisms and their environment. This includes an explicit focus on a large variety of different ways that species interact with one another. Such interactions form the basis of a key question in ecology, namely, what is found where and why? Species can have positive, neutral or negative effects on each other. The most famous ecological interactions are those of predation and competition. In plant ecology, we often invoke competition as the key driver of interactions between species that require the same essential resources.

However, we focus on, and know a lot less about, positive interactions in nature. *Mutualism* occurs when both partners benefit from the interaction in some way. During pollination, one organism (e.g., a bumble bee) indirectly improves the performance of another organism by pollinating a flower and enabling a plant

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to reproduce sexually, an important side effect of the bee's feeding activities. *Commensalism* occurs when one partner benefits but the other is neither harmed nor benefitted by the interaction. Anemone fishes live unharmed and protected from prey within the stinging tentacles of sea anemones, portraying a classic example of commensalism.

Because plants are dependent on a few critical resources to survive (sunlight, water, nutrients), it is often assumed that competition between plants is the key biotic driver of plant performance in communities (Harper 1977). The role of positive interactions between plants, known as *facilitation*, is often overlooked. In particular both negative and positive interactions can occur either at the same time or be of different strengths at different stages of the life cycles of the plants. Even more critically, what is measured as the outcome of interactions between plants in ecology is often named competition, but is actually the outcome of the interplay of both competition and facilitation (Brooker et al. 2008). In a continuum of positive interactions, mutualism would be on one end, with facilitation (possibly as a form of commensalism) on the other. Facilitation is a term often used in plant ecology, while commensalism is more common in animal ecology.

The Role of Positive Interactions

Under harsh abiotic conditions, facilitation is hypothesized to increase (Bertness and Callaway 1994), such that along environmental gradients of water or nutrient availability, one would expect the role of positive interactions between plants to increase as conditions become more harsh. The classic example is the *nurse plant* interaction that occurs in deserts, whereby an already established adult plant provides favorable microsites for the germination and establishment of another species. The creosote bush provides such microsites for young Saguaro cacti, enabling them to survive extremely harsh abiotic conditions during establishment. This type of facilitative interaction seems like a clear form of commensalism, since one partner benefits but the other neither gains nor is harmed. If one follows the interaction longer, however, the cactus gradually outgrows the bush and becomes a competitor for resources (Fowler 1986). Thus, the interplay of positive and negative interactions changes over time. Holmgren et al. (1997) modeled the interplay of competition and facilitation in arid conditions and concluded that, "positive and negative effects of plant canopies always occur simultaneously. In the presented light–water model, facilitation only occurs when the improvement of plant-water relations under the canopy exceeds the costs caused by lower light levels." Morzaria-Luna and Zedler (2014) demonstrated a related point that two plant species can change behavior across stress gradients. They found that an N accumulator facilitated N availability to another species when N was in short supply, but that the two salt marsh species were otherwise competitors.

Such nurse plant interactions can also facilitate the flow of nutrients between different individuals and species. Nitrogen facilitation can occur, for example, when N_2-fixing species grow in the vicinity of nonfixing species and the latter benefit from the extra N imported into the soil via fixation of atmospheric nitrogen (Temperton et al. 2007), either via root exudation, N transfer through mycorrhizae, or during decomposition of N-fixing legumes. Such effects of higher availability of nitrogen are usually neglected during the study of nurse-plant interactions. Intriguingly, we know that such nurse-plant interactions enabled species to survive the climatic changes that occurred from the Tertiary to the Quaternary (65 to 2 mya) when the climate became cooler and drier. Valiente-Banuet et al. (2006) indicated that the recently evolved species provided a nurse plant role for the older Tertiary species, enabling them to survive the climatic changes. A number of the suggested nurse plants were N_2-fixing species.

We also know that facilitative interactions of this kind often explain the positive effects of grassland diversity on ecosystem functioning (Spehn et al. 2002; Temperton et al. 2007). Here, nutrients in the system are lost during hay removal, but are partly compensated for by extra nitrogen inputs into the system via N_2-fixing plants which nonfixers then subsequently benefit from. N_2-fixing legume species are often coined *keystone species* or a key functional group in such grasslands, as their effect on the system is larger than that of other species.

When populations of different plant species interact, the identity and number of species interacting can have strong spinoff effects on ecosystem productivity (Marquard et al. 2009), decomposition, nutrient cycling (Temperton et al. 2007), water cycling (Leimer et al. 2014), and provision of food for higher trophic levels (Scherber et al. 2010). Many biodiversity ecosystem functioning experiments (hereafter *BEF*; see also chap. 3) that manipulate species number and functional group composition, as well as species identity, have found positive effects of diverse plantings (both species number and functional diversity) on several terrestrial ecosystem functions (mostly grasslands, but also in tree experiments). This outcome contrasts with results from a salt marsh where planting more species did not lead to higher productivity or more nitrogen accumulation beyond the early years of weeding plots (Doherty et al. 2011; Zedler et al. 2012). The issue of why diversity can increase functioning in some habitats but less so in others is beyond the scope of this chapter, but effects of diverse plantings are of great interest and relevance to restoration (Temperton et al. 2014).

As a concrete example, in one of the world's largest BEF experiments, the Jena Experiment in Germany (Roscher et al. 2004) included a gradient of grassland plant species and functional richness treatments to assess the effects of plant diversity on ecosystem processes and functions. The diversity gradient was initiated in 2002 by sowing the desired number of species and functional group combinations (grasses, small and tall non-N_2-fixing forbs and legumes), then weeding to maintain the desired species in each plot. The main outcome of this long-term experiment is that assemblages with more species (particularly those with species from different functional groups interacting) function better than assemblages with fewer and more similar species. Functional group identity and specific combinations of functional groups (particularly grasses combined with legumes) also often drive biogeochemical cycles, as well as affecting other trophic levels (Scherber et al. 2010).

Critics of these mechanistic and academic BEF experiments have often argued that we do not know how relevant such experiments are for real communities and their interactions in nature, where one does not weed out undesired species (but see Doherty et al. 2011). The question arises, do positive diversity effects, as found in terrestrial grassland experiments, play an important role in more natural communities experiencing assembly (Srivastava 2002)? This has important implications for restoration: if sowing a specific combination of seeds of a certain diversity can lead to strong positive effects on ecosystem functioning, even after natural assembly is allowed to take place, this could be a powerful tool for achieving restoration goals (see also chap. 3).

The Role of Diversity during Natural Assembly of Communities

The most powerful way to assess the true importance of specific processes and ecological theories is to test them in the field. Stein et al. (2008) asked whether one can increase the diversity of naturally assembling, species-rich montane grasslands in Germany, postulating that seed dispersal would be limiting. They sowed seeds of sixty species (at a high sowing density) into twenty grassland sites ranging in diversity at time zero from ten to thirty-four species. Prior to sowing, there was no relationship between species richness and aboveground productivity. One year after sowing extra species, however, species richness averaged six species per m^2 higher, especially in intermediately productive sites (based on soil nutrient content). This study suggests that such grasslands are indeed dispersal-limited, and that germination niches (microsites) are freely available. This outcome is relevant to restoration since species-rich grasslands that are degraded are often assumed to lack free-niche space/germination microsites. The increase in species richness following seed addition may be maximal at intermediate levels of productivity, because, at higher soil productivity, seedling recruitment is inhibited by competition from established plants and by plant litter (Foster and Gross 1998), while at lower soil productivity, nutrients are more likely limiting.

Species-rich grasslands are extremely threatened in Europe by both land use intensification and abandonment. Bullock et al. (2001) were curious to see whether one could transfer outcomes from BEF experiments to aid restoration of calcareous grassland restoration on ex-arable land in southern England. Their main question was this: Would sowing a diverse species mix increase both diversity and productivity? Productivity is not a trivial issue, since a land manager who can maintain both a high hay yield and species diversity would have a major incentive to keep grazing or mowing while sustaining culturally diverse landscapes. Bullock et al. (2001, 2007) sowed high- (25–41 species) and low-diversity (6–17 species) mixtures typically used in calcareous grassland restoration and followed the species richness and hay yield over eight years on seventeen sites in England. Natural assembly was allowed after the initial sowing event. They found that the one sowing event created a clear signal in the vegetation that was still detectable after eight years. Sowing more species created more diverse and more productive vegetation, a win-win situation for land managers and restoration practitioners.

In a large succession experiment, Bezemer and van der Putten (2007) sowed either none, four, or fifteen species on old-fields in the Netherlands and followed their development. They found that the fields sown with more species were more diverse, more productive and more stable (defined as having lower species turnover) than those sown with four species or those with free succession (defined as unsown plots). This signal was still detectable many years after the one sowing event. Thus a form of priority effect occurred during assembly (see below).

Different Approaches to Community Assembly

Jared Diamond (1975) coined the term "*assembly rule*." He gathered data on the distribution of dove species on the islands of Papua New Guinea and found that species were nonrandomly distributed on the islands. He concluded that the presence of one particular species may hamper the establishment of another species (otherwise known as *competitive exclusion*). He called this an assembly rule. Today, such rules focus on environmental filters (both abiotic and biotic) and on priority effects, e.g., species that arrive first define who can establish after that (*sensu* Drake 1991; Fukami 2015).

Filter Theory in Assembly

The metaphor of environmental filters is often used to describe establishment and invasion of species in community ecology during assembly. The idea is that abiotic conditions at a site constrain the species that might occur at a particular site. Only those that can survive and establish reproducing populations under the extant abiotic conditions will be able to pass through the "filter mesh" (Kelt et al. 1995). At regional scales, speciation, migration, and dispersal control the total available species pool, whereas at smaller scales only species that can pass through the environmental filters will subsist (Fattorini and Halle 2004). Mueller-Dombois and Ellenberg (1974) and many others considered the filter to be driven only by abiotic environmental characteristics.

Currently, however, biotic interactions are considered critical filtering effects during assembly (Fattorini and Halle 2004; Temperton and Hobbs 2004). Species without the necessary traits to survive will not form part of the local species pool. Thus, if strong abiotic filtering effects are occurring, one would expect the traits of plant species at a site to converge and become more similar under more extreme environmental conditions. For example, a limited number of plant species thrive in the bogs and moors of Great Britain, and this is clearly related to extreme abiotic conditions. Kirmer et al. (2008) studied species recolonization following large-scale mining destruction and found that the large-scale, nutrient-deficient open sites acted as huge seed traps in the landscape. Key traits related to plant species establishment included high light and low nutrient availability (as well as the capacity for long-distance dispersal by wind or via birds).

At sites with more benign nutrient, water and weather conditions, one would expect abiotic filtering to be less strong, and biotic filtering to play a more influential role. If competition between species is very strong (as is often the case in nutrient-rich sites, but see Brooker et al. (2008) for a discussion on competition and site productivity), then one would expect a variety of traits to allow survival of species. Under these conditions, the biotic interactions may be selecting for differential species traits, thus ensuring complementary uptake of resources and reducing the threat of competitive exclusion. Viewed from a restoration perspective, one can also include a socioeconomic filter (Hobbs and Norton 2004; see fig. 9-1).

The filter concept is useful for investigating how abiotic and biotic factors drive community composition. Just as with the concepts of facilitation and competition, the species that are extant at a site are the outcome of abiotic and biotic filters acting simultaneously. Because the visible community is the outcome of both processes, it is difficult to separate the individual role of either factor in structuring the community. This reality is increasingly recognized in other research arenas, for example, the now popular term *ecohydrology* indicates the inability to separate the abiotic from the biotic effects at the ecosystem level.

> Although filter models can provide insight into what is limiting membership of the species pool and so point to specific interventions, they tell us little about how the community is structured or how the ecosystem functions. Even if we are interested only in restoring a particular list of species to a site, is it sufficient simply to have all the species present? (Belyea 2004)

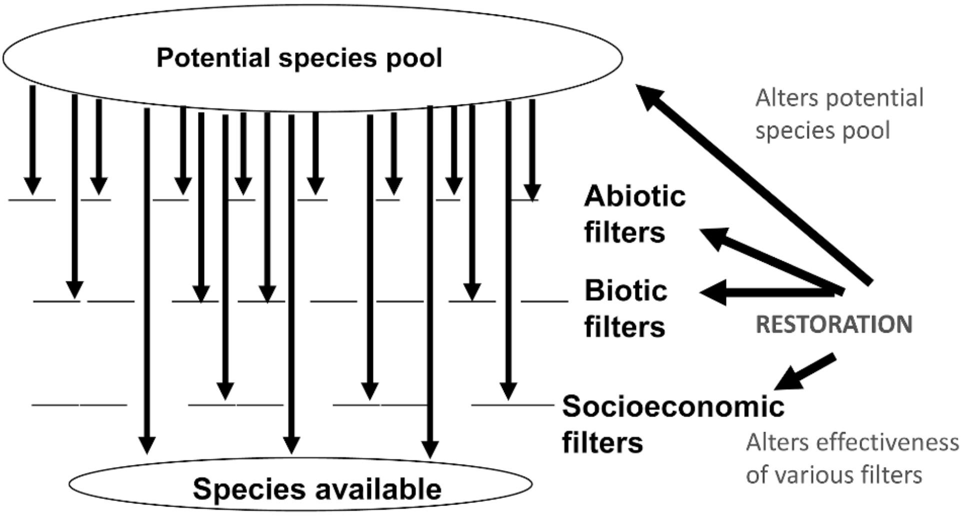

Figure 9-1. A conceptual diagram of filter theory in assembly and how it relates to ecological restoration. Note that issues of costs and preferences (socioeconomic filters) also have a filtering effect as well as the abiotic and biotic filters discussed in this chapter. Figure from Hobbs and Norton (2004).

Species pools are often treated as rather static entities by community ecologists interested in interactions between species and their effects on assembly, but a recent review (Mittelbach and Schemske 2015) emphasizes how dynamic species pools are, including the importance of understanding the connection between local and regional processes.

Filter theory can help answer this important restoration question: How do I attempt to exclude certain species from a site? Funk et al. (2008) use the filter model to plant species with traits that are similar to those of undesired invasive species, hoping to exclude the unwanted invader. Bear in mind, however, that in some regions (e.g., Europe and parts of Asia) invasive species are less threatening to biodiversity than habitat loss and eutrophication. Of course, eutrophication can facilitate species invasions and vice versa; examples are phosphorus pumping, also known as internal eutrophication, by Eurasian milfoil in Lake Wingra and by cattails in Wisconsin wetlands in the United States (Loucks 1985; Boers and Zedler 2008).

Priority Effects during Assembly: Why History Matters

The species that arrive at a site first can drive subsequent assembly; this is known as a *priority* or *founder effect* (Samuels and Drake 1997; Fukami 2015). We use the more popular term *priority effect* from here on to avoid confusion with founder effect, which also denotes the role of genetic variability and its transfer to future generations. Priority effects occur at different frequencies in both aquatic and terrestrial ecosystems, and priority effects can lead to *alternative states* (see chap. 2) that can persist for long periods of time. This chapter focuses on assembly and priority effects in terrestrial plants, not aquatic communities (but see Harvey and MacDougall 2014; Stier et al. 2014; Zhou et al. 2014). If the species that arrive first can drive a system toward trajectories that depend on those species' traits *and* if the trajectory taken is strongly affected by stochastic drivers such as weather conditions, then there are profound implications for when and how a restoration experiment is initiated.

To compare effects of the species that arrive first at a site, one can either sow different species mixtures at the same time (and see how these initial mixes affect assembly) or manipulate the timing of arrival of specific species or functional groups (and follow how this affects further assembly). In essence, if natural assembly were allowed during BEF experiments, the initial introduction of particular species could create a priority effect, but only if the particular diversity and composition of mixture introduced has long-term effects on further assembly (as in Bullock et al. 2007). While it is difficult to test such a hypothesis, for example, in weeded grassland or tree BEF experiments, one can test the effects of kick-starting assembly by introducing specific species at time zero.

At intermediate time scales (years to decades) priority effects can lead to different stable states in communities. Lewontin (1969) and Sutherland (1974) introduced the important concept of *alternative stable states* to community ecology. Since then, ecologists tend to agree that perhaps the most useful concept would be alternative states, since their level of stability varies greatly between ecosystems and case studies (see Fukami and Nagajima 2011 for discussion).

To understand this in relation to classical successional theory (as posed by Clements 1916 or Gleason 1926), it is important to know that there are two general frameworks applied to the study of community dynamics during succession and assembly. Continuous linear dynamics are contrasted with the different paradigm of nonlinear threshold dynamics (see chap. 2 for more details). Continuous linear dynamics involve the idea of a system moving gradually from one state to the other (e.g., from white, bare sand dune to gray and brown dune, to grassland and forest), as embedded in classical succession theory. Threshold dynamics, in contrast, involve the idea that certain interactions and driving forces can create a number of alternative states depending on the initial conditions. Such dynamics are often called state-transition models of assembly, which are increasingly popular now that ecologists realize that succession is often cyclical and nonlinear, and that interactions and random stochastic effects (e.g., disturbance) play important roles in creating a range of alternative stable (or not so stable) states. Walker and del Moral (2008) comment wisely that, "in the context of restoration, stability may be of less conceptual value than the idea of transitions because each organism is constantly responding to ever-present fluctuations in the environment." What one defines as stable depends on the parameter of focus and the overall timescales that one is using to understand an ecosystem.

Priority effects are expected to occur at local scales on abiotically similar sites, such that the history of immigration on one site may lead to a different community than on a site with a different history. This means that even priority effects that create lower alpha diversity (small scale) may create higher beta diversity if the state of the ecosystem remains relatively stable for a number of years. As Martin and Wilsey (2012) point out:

> Variation in community assembly history (historical order of species arrival) is hypothesized to generate beta diversity by producing alternate states, but restorations are hindered because there have been few tests using long-term field experiments.

In a prairie restoration experiment, Martin and Wilsey (2012) were able to show that alternative native or exotic-dominated states could be created on environmentally uniform sites just by altering assembly history. If priority effects do lead to alternative states then this can have important effects on diversity as one moves from the local to the multipatch or regional scale.

Fukami and Nakajima (2011) advocate not focusing on alternative stable states but on *alternative transient states* as a productive way forward in assembly research. They define alternative transient states as those where sites differ in either structure (species composition and diversity) or function (e.g., total biomass or carbon flux) due to different assembly history, despite assembling under the same environmental conditions. They propose this idea of transience because disturbance and stochastic weather events rarely allow communities to remain in the same stable state for a very long time. Strong disturbance events can remove priority effects and end alternative states, creating what is increasingly considered cyclical succession. We propose to avoid the issue of how stable a particular state is and use the term alternative states for the rest of this chapter.

What are the implications of priority effects and alternative states for restoration? Restoration is inherently dynamic and includes trajectories of ecological communities over time. Succession and assembly are increasingly seen as both structured (niche-driven: Hutchinson 1957) as well as stochastic (neutral theory of biodiversity and biogeography: Hubbell 2001) with overall cyclical patterns occurring (Walker and DelMoral 2008). The concept of priority effects (Samuels and Drake 1997) leading to alternative states fits this current conceptual model well, in that they portray both a level of niche-driven as well as random components of ecosystem trajectories. Thus priority effects and alternative states may be the most useful concepts for understanding community assembly within a restoration context.

Priority effects can have either desired (positive) or undesired (negative) effects on the further trajectory of assembly over time, and are thus of prime importance for restoration where a specific species composition or at least the establishment of keystone or dominant species is a restoration goal. Classic examples of priority effects causing a specific and persistent unwanted state, is the invasion of exotic N-fixing trees to the islands of Hawaii leading to changes in the biogeochemistry of the soils that allow the invader to grow well (Vitousek and Walker 1989). The invasion of exotic species into restoration sites is a major problem in many parts of the world (Pyšek and Richardson 2010; chap. 8), and a strong body of ecological theory has developed in response to this problem (Jeschke et al. 2012). In restoration, invasions link priority and filter effects.

Funk et al. (2008) proposed using filter theory of assembly to help resist invasion of unwanted exotic species during restoration. Species with similar traits are predicted to compete more strongly than those with more complementary traits. Thus invasive species will be unlikely to establish if native species with similar traits are already present in a community. Biotic competition between the extant species and the newcomers will increase resistance to invasion. Restoration could therefore select species with similar traits to those of expected invaders to reduce unwanted invasion. The key question is this: Which traits should one focus on? Would one trait in common suffice, or should there be a suite of traits, preferably including the three main trait axes of reproduction, growth, and resource-use efficiency?

In a similar way, the issue of what parameter one focuses on when trying to understand whether a priority effect has occurred is critical here. In a field experiment, Plückers et al. (2013) sowed either a highly diverse or low diversity seed mixture typical of dry acidic grassland restoration and found that priority effects occurred over the first four years, but only if one focused on the aboveground biomass of the community and the proportions of plant functional groups found in the sites. In contrast, species identity and richness had a very high turnover from year to year with no clear priority effects using those parameters. According to the definition of Fukami and Nakajima (2011), however, either differences in structure or function between sites/patches can denote an alternative state, thus allowing one to talk of priority effects and alternative states in the dry acidic grassland example (Plückers et al. 2013).

If a priority effect only lasts for one year, it can barely be called a priority effect. Beta diversity will only be increased in a region if the priority effects occurring create relatively stable states at local scales, thus increasing the differences in diversity between sites. This is possible, however, as has partly been shown by previous succession and assembly studies (e.g., see Bullock et al. 2007; Bezemer and van der Putten 2007; and Martin and Wilsey 2012). Fukami and Nakajima (2011) modeled plant community assembly and found that transient states can last for a long time in relation to immigration rate and generation times of the organisms involved, confirming what is being found in field experiments and observations.

Mechanisms of Priority Effects

What are the possible mechanisms behind priority effects? The classical answers to this question include (a) asymmetric competition, and (b) plant-soil feedback (Grman and Suding 2010). Fukami (2015) describes these different mechanisms as *niche preemption* and *niche modification*. During asymmetric competition (or niche preemption), newly establishing plants are usually seedlings, and they have to compete with much larger plants that are already present and have a major competitive advantage. Plant-soil feedback is a rapidly expanding area of ecological research, and traditionally includes feedback effects of plant species on microbial species in the soil (van der Putten et al. 2013). If a specific plant species grows at a site for a long time, specific microbial communities that accumulate over time may have a net detrimental effect on the plant in question. This is similar to the Janzen-Connell effect: "Janzen (1970) and Connell (1971) suggested that adults, by harboring host-specific predators and herbivores, could locally reduce the recruitment success of conspecific juveniles" (Petermann et al. 2008). The Janzen-Connell effect promotes diversity and coexistence by reducing the vigor of plants that exist on the same site for long periods of time. However, the importance of the Janzen-Connell effect for promoting species coexistence has been debated, and current discussions concern the relative importance of plant-soil feedback found under controlled conditions for structuring plant communities and influencing assembly under natural conditions where a multitude of factors and species exist next to one another.

We consider it important to distinguish between negative and positive plant-soil feedbacks as possible mechanisms of priority effects (van de Voorde et al. 2011). Nitrogen facilitation between legumes and neighbors provides extra nutrients for the non-conspecific neighbors. This can change the abiotic filter of a community, thus providing an example of positive plant-soil feedback in relation to priority effects. Species that require more N in the soil than others may be able to colonize once N_2-fixing plants have established, creating a form of priority effect. Equally, if some plant species require low nutrient soil (as do many rare grassland species in Europe) to survive, then the early arrival of N_2-fixing legumes could preclude their establishment.

Using Priority Effects to Steer the Restoration of Ecosystems

There is now evidence that priority effects play an important role in the assembly of many communities and can lead to alternative states, and that this can affect the *beta* diversity of a larger site. This means the time is ripe to test the potential of using priority effects to aid restoration. To do this we need a suite of different priority-effect experiments in a range of habitats across the world. An example is that of Young et al. (2014), who tested the effects of arrival time of native Californian species in relation to interactions with exotic annual grasses as well as the effect of watering on the outcome. They found multiple levels of contingency (i.e., the outcome depended on the specific sequence of events occurring during assembly history)—Negative effects of exotics on natives were significantly reduced if the natives were planted two weeks earlier than the exotics, and in a drought year watering significantly reduced the benefit of earlier planting. The three sites investigated all showed significant differences in overall native cover, responses of natives to interactions with exotics, and the strength of priority effects.

Knowing that nitrogen facilitation by legumes species plays a key role in positive diversity effects in grassland BEF experiments, Körner et al. (2007) tested the effect of altering the timing of arrival of different plant functional groups in a microcosm experiment. They sowed grasses, nonlegume forbs (hereafter called forbs) or legumes first and measured how above- and belowground biomass were affected. Intriguingly, they found that sowing the N_2-fixing legumes first created a higher aboveground biomass of the community of nine species, but reduced overall root biomass, and this effect was still visible in the second year of the experiment. They hypothesized that legumes (when they actively gain most of their N_2 from the atmosphere) do not need large root systems, so when the grasses and forbs arrive six weeks later, they could forage more freely for space and nutrients within the soil, and the overall belowground productivity of the community would be lower. It is possible that extra N fixed by the legumes in the legume-first treatments provided extra N for the later arriving neighbors, but this did not occur as much in the other treatments.

As an incentive to European land managers to continue managing extensive grasslands, we decided to test whether we could increase aboveground biomass, while not reducing diversity of grassland communities. To do this we set up greenhouse, mesocosm, and field experiments (see results in case study boxes 9-1 and 9-2 plus fig. 9-2, 9-3, and 9-4). In addition to the experiments in the case studies, we set up a large field experiment in Jülich in 2012 (The Jülich Priority Effect Experiment) and again sowed legumes, grasses, or forbs earlier (five weeks) than the other two functional groups. At this site we only tested the mechanistic approach (see the Bernburg Priority Effect Experiment in case study box 9.1 comparing a restoration versus a more mechanistic design), but we included two soil

Case Study Box 9-1
The Bernburg Priority Effect Experiment (2011–2012)

By Annett Baasch, Vicky Temperton, and Anita Kirmer

Supporting theory: Priority effects during community assembly

Species that arrive first at a disturbed site can significantly affect the further assembly for many years to come. Since Körner et al. (2007) and von Gillhaussen et al. (2014) found that sowing legumes before grasses and nonlegume forbs created more aboveground biomass in controlled experiments, we wanted to test whether this effect also occurs in the field, since an economic use of hay from meadows depends on adequate hay yields. We hypothesized that sowing legumes before the other functional groups would lead to both higher aboveground biomass and higher diversity of the ensuing communities. In addition, we expected that a longer sowing interval between sowing one group and the next seed mixture would stimulate the priority effect. We also tested a more restoration-focused approach versus a more mechanistic experimental design.

Experimental setup:

In the Bernburg field experiment on the Campus of the Anhalt University of Applied Sciences, Germany, we used a *mechanistic* approach (sowing legumes before grasses and forbs), and a *restoration* approach (sowing legumes first before the whole seed mixture, including legumes), both with different sowing intervals between the sowing of legumes and the second seed mixture. The site has a relatively nutrient-rich chernozem soil with a seed bank of both ruderal and grassland species. The overall seed mixtures contained twenty-eight typical mesic grassland species, of which half were forbs, seven legumes, and seven grasses (typical proportions of central European grasslands). Each priority treatment (mechanistic versus restoration versus control/untreated control) and sowing interval (0-, 4-, 8-, and 12-week sowing interval) was replicated five times on plots of 1m² in a Latin square, giving a total of forty plots. Sowing started the end of March 2011. The grassland was mown twice a year in July and September.

Case Study Box 9-1.

***Left* Panel:** Site beginning of July 2011, before mowing

***Right* Panel**: Site in June 2012, after mowing

Case Study Box 9-1 continued

Vegetation development

We followed the community and functional composition over two years, including measuring aboveground biomass in 2011. In spring 2011, central Europe experienced a strong drought, such that establishment of sown target species was slower than normal. Overall, we found that variants with a sowing interval of eight weeks after sowing legumes had the highest aboveground biomass, which confirms findings from von Gillhaussen et al. (2014), and the restoration treatment did not create more biomass than the mechanistic treatment (see fig. 9-2). In general there was no significant effect of either priority treatments (mechanistic versus restoration versus control) or sowing interval ($p > 0.05$). The restoration treatment however, had a higher proportion of legume species (as expected, since more were sown), and a lower invasion of nonsown species than the mechanistic or control treatments, even though the resulting total species numbers were similar. Since a number of the species sown were also in the seed bank, we could not always distinguish between sown and nonsown species. The lack of a clear priority effect may have derived from the relatively nutrient-rich soils, as well as the particularly dry weather conditions during establishment.

References: Körner et al. 2007; von Gillhaussen et al. 2014.

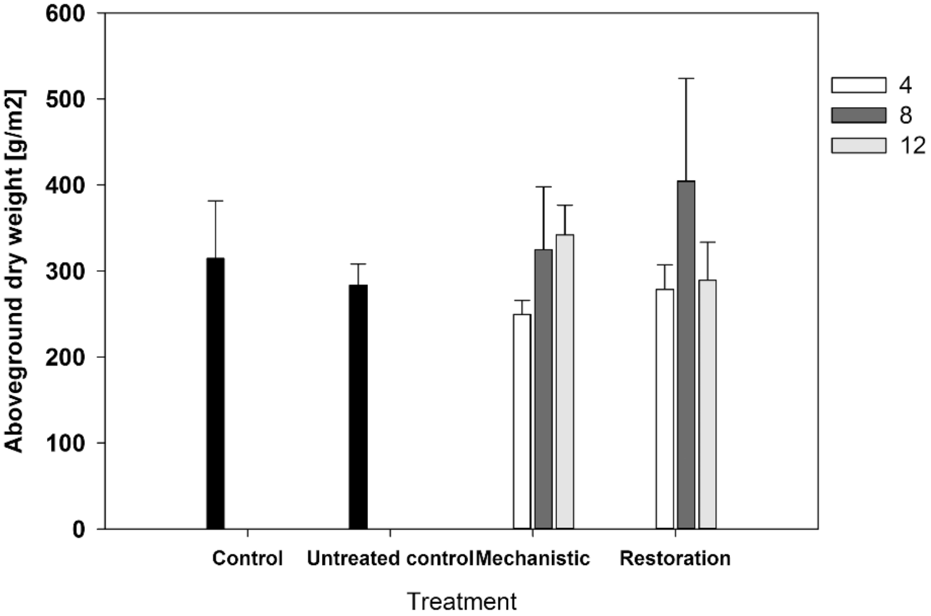

Figure 9-2. Aboveground biomass production in different treatments of the Bernburg Priority Effect Field Experiment in the first year (harvest, end of September 2011). For description of treatments see experimental setup above.

Case Study Box 9-2

Testing Priority Effects for Grassland Restoration under Controlled and Outdoor Conditions

By Vicky Temperton, Christina Küppers, Simone Gröbel, and Philipp von Gillhaussen

Jülich, Germany: Species that arrive first at a disturbed site can significantly affect the further assembly for many years to come. Such priority effects can lead to alternative states in vegetation. Körner et al. (2007) found that sowing legumes before grasses and nonlegume forbs created more aboveground biomass in controlled experiments. We wanted to test whether we could replicate this effect under both controlled greenhouse and mesocosm experimental conditions outdoors.

The overall aim is to improve productivity as well as maintaining or increasing diversity of restored grasslands since an economic use of hay from meadows depends on adequate hay yields. Here we showcase a selection of experiments addressing priority effects.

Top-left: Priority experiment under controlled conditions in the greenhouse.

Top-right: Harvesting of mesocosms in July 2012.

Bottom-left: Priority experiment under near-natural conditions in large mesocosms outdoors.

Priority effect experiment in greenhouse—legumes-first

Here we sowed either legumes, forbs or grasses prior to the other two functional groups; we also tested the effect of sowing density and sowing interval (three or six weeks between sowing events) compared to a control sown at the same time. We chose common species of mesic grasslands of central and northern Europe. As in Körner et al. (2007), we found a clear positive effect of sowing the legumes before the other functional groups (see fig. 9-3A), especially when the sowing interval was quite long (six weeks). The sowing density and sowing interval modulated the result, but the main driver was the priority effect caused by the first arriving group.

Case Study Box 9-2 continued

Delayed sowing experiment in greenhouse—legumes last

We hypothesized that sowing legumes later than other functional groups would reduce asymmetric competition as a mechanism of priority effect formation. In 2009 we tested the effect of sowing grasses and forbs three weeks before legume species (or at the same time). We assessed aboveground cover and biomass and found that all factors had significant effects on aboveground biomass of the communities: the identity of the seed mixture, the presence of legumes and the delayed sowing of legumes ($p < 0.05$ see fig. 9-3B). Contrary to our hypothesis, community biomass was higher when the legumes were sown at the same time as the other functional groups and lower when legumes were sown after grasses and forbs, indicating a strong role of asymmetric competition during legume establishment.

Mesocosm priority effect experiment—outdoors

In 2011 we initiated a mesocosm experiment (1m x 1m x 1m tubs filled with topsoil form an old field in western Germany) and tested the order of arrival of three different plant functional groups (legumes, grasses and nonlegume forbs) and sowing intervals (two, four, or six weeks) between the first and subsequent functional groups. Additionally, we tested the effect of sowing low versus high diversity seed mixtures (eight versus twenty-eight species). Priority effects were found in the first year when forbs (not legumes) were sown before the other groups ($p = 0.036$ in 2011), but in 2012 and 2013 any effects of the first-sown functional group disappeared ($p > 0.05$; see fig. 9-4).

Possible Implications: see the main text section, "What do the results of our experiments imply for the potential of priority effects for restoration?"

References: Körner et al. 2007; von Gillhaussen et al. 2014.

types, as well as a diversity treatment of high versus low species mixtures (as in the Mesocosm Priority Effect Experiment in case study box 9-2, and as in Bullock et al. 2001). Overall, we found that plots were more productive when legumes were sown before the other groups, but intriguingly this priority effect disappeared in the second year and reappeared only on one soil type in the third and fourth year (Weidlich et al., forthcoming).

What Do the Results of Our Experiments Imply for the Potential Application of Priority Effects in Restoration?

The results of the mesocosm, field, and greenhouse experiments often differed, even though the main factors in these experiments were similar (see figs. 9-2, 9-3 and 9-4). A series of factors may have influenced the outcomes. Most striking was the difference in weather conditions during the initial establishment of the experiments. In the greenhouse, we found strong effects on productivity and diversity of

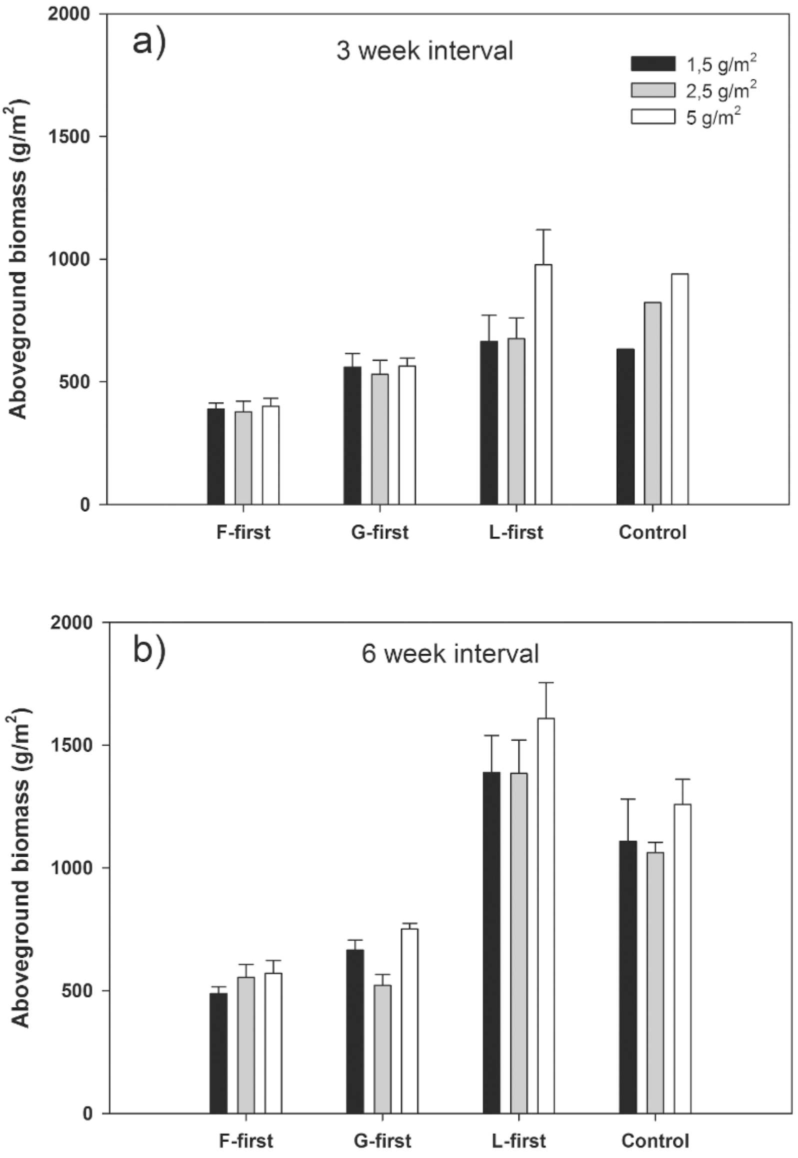

Figure 9-3A. Results of the Greenhouse Priority Effect Experiment with legumes, forbs, or grasses sown before the other two groups. Sowing legumes first (L-first) produced the highest aboveground biomass, especially in the six-week interval treatment. Density (1.5, 2.5, and 5 gm^{-2} of seeds sown) had weaker effects on biomass than the priority effect treatment or sowing interval. Data show mean aboveground biomass (plus one standard error of the mean) per priority effect treatment separated into the three density levels. This is shown per sowing interval treatment with panel (a) describing the three-week sowing interval and panel (b) the six-week sowing interval treatment. Reprinted with permission from PLoS ONE von Gillhaussen et al. (2014): doi:10.1371/journal.pone.0086906.g002.

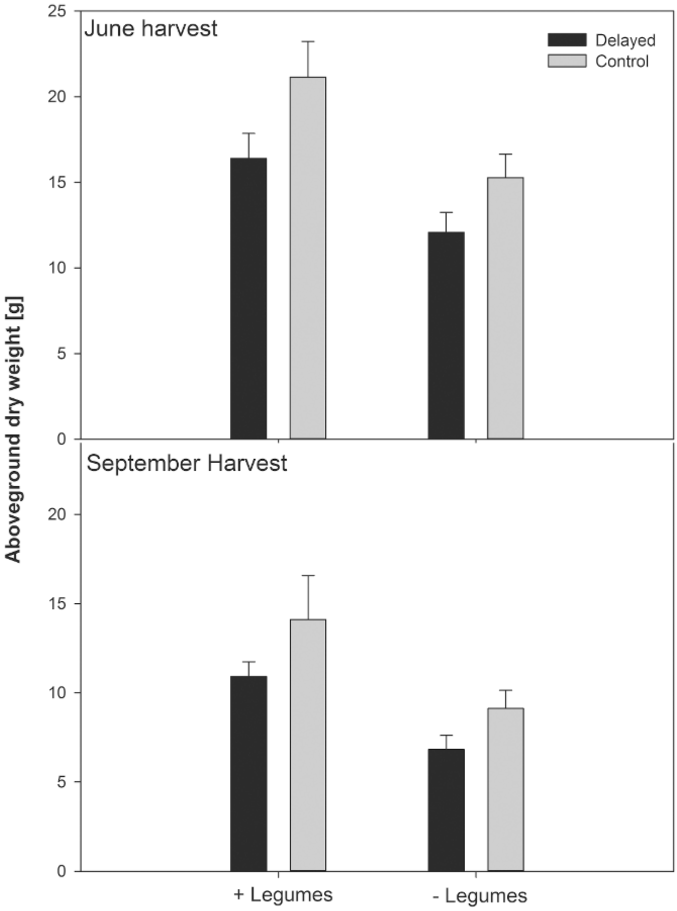

Figure 9-3B. Results of the Delayed Sowing Greenhouse Priority Effect Experiment. Here, instead of sowing legumes before the other functional groups, we sowed them later, to see how this affected the creation of priority effects. In this case delayed sowing of legumes reduced aboveground biomass significantly at both harvests. Mixtures that included legumes were more productive than those that did not ($p < 0.05$). The species composition of the four-species mixtures also had a significant effect on biomass (data not shown here). Data are means plus one SEM (N=4).

sowing legumes earlier (or later) than other functional groups, whereas in outdoor mesocosms and in the field, the outcome was different in each experiment.

In the Jülich Priority Effect Experiment, we found similar results to the greenhouse experiment (von Gillhaussen et al. 2014) even though the effect sizes (the amount of variability in the data explained by a particular treatment factor) in the field were somewhat smaller than in the greenhouse. The weather conditions during 2011 (Mesocosm and Bernburg Experiment in field) and 2012 (start of large Priority Effect Experiment Jülich) were very different, with central Europe experiencing a strong drought in spring 2011. We found no clear sign of a legume-

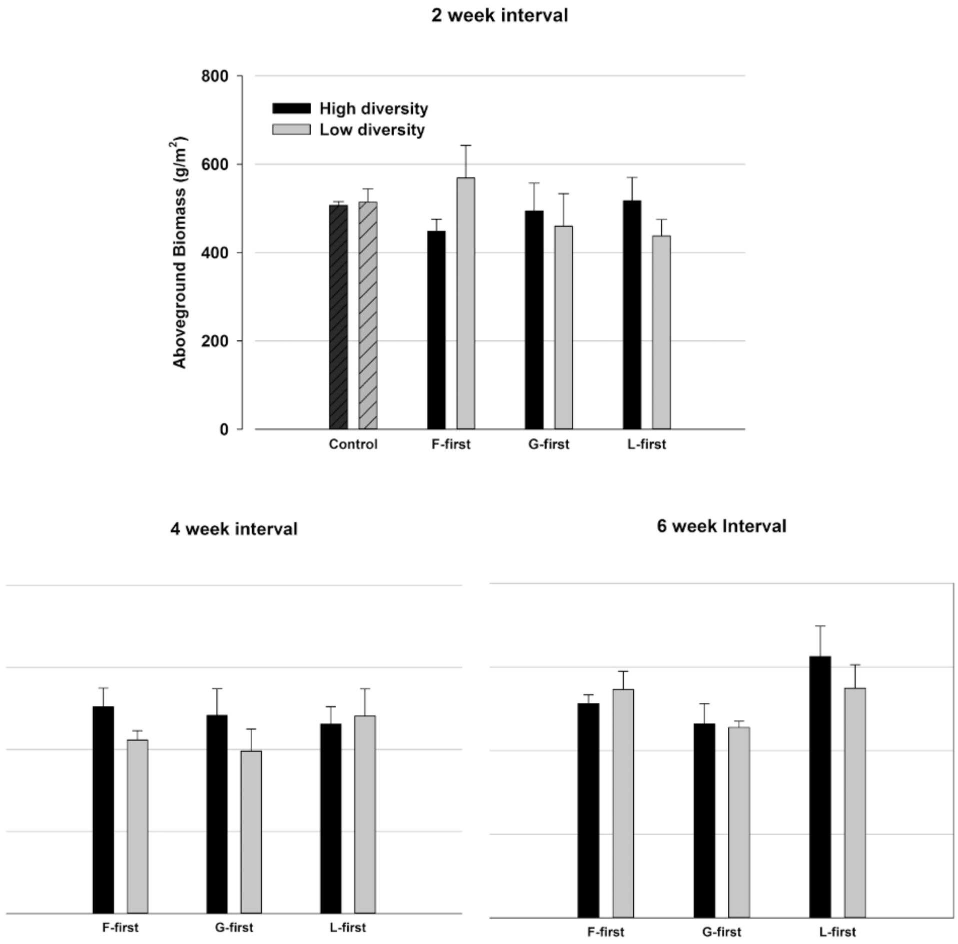

Figure 9-4. Results of the Mesocosm Priority Effect Experiment. As in the greenhouse experiment (fig. 9-3A) we sowed either legumes, grasses, or forbs before the other two functional groups, as well as a control sown at the same time. We also tested the effect of sowing a high- or a low diversity seed mix. We additionally tested the effect of the sowing interval on the possible creation of priority effects. Data are means plus one SEM. This dataset is from 2013 in the third summer after the establishment of the experiment, in spring 2011. There were no significant effects of any of the treatments on aboveground biomass in these communities except in the forb-first treatment during the first year ($p = 0.031$ in 2011). The functional groups that dominated the vegetation changed over time, with differences between years in terms of which group was most dominant.

first priority effect in the experiments set up in 2011, but strong effects in the field experiment set up in 2012 during more clement conditions. We know from centuries of agriculture and gardening that the weather influences plant performance significantly, especially during the establishment phase of the life cycle. It seems that weather conditions during initiation of the experiments played a crucial role in whether a priority effect occurred or not, and how long it lasted. The water treatment of Young et al. (2014) shows clearly how (in their case) watering reduced a priority effect in California. Since legumes are known to shed their N_2-fixing nodules during severe droughts, it may be that providing more water in central Europe may sustain priority effects of sowing legumes before other groups, contrary to the results from California.

In addition, the soil seedbank probably influenced outcomes. Competition from typical agricultural old-field "weeds" (mainly forbs) in the seedbank probably also caused results to deviate from those of similar experiments (e.g., the greenhouse experiments where potting soil lacked seedbanks). There was, however, a strong soil seedbank present in the large field Priority Effect Experiment in Jülich (set up in 2012), but this did not prevent strong priority effects of sowing legumes first. It is intriguing that the legume-first priority effect disappeared and then reappeared in the Jülich field experiment, and we plan now to see whether microbial community composition and activity was different between treatments and years.

Soil fertility and soil structure clearly also modulate how strong and for how long priority effects can be found in grasslands. Chase (2010) found that randomness increased in productive environments during assembly of pond communities. The soil fertility in our Jülich Priority Effect Experiment was higher than that of the calcareous soils in Bullock et al. (2001), and our priority effect appeared, disappeared, and then reappeared on the more fertile soil type (Weidlich et al., forthcoming). This more dynamic and less stable priority effect of sowing legumes first concurs with the findings of Chase (2010), yet the fact that the priority effect reappeared on the more fertile soil type does not (here we would expect more randomness and hence less stable priority effects).

In general, the outcomes of our priority effect experiments do indicate that sowing legumes, either earlier or at the same time as other plant functional groups, can lead to strong priority effects on productivity as well as diversity provided the weather conditions during establishment are not extreme. This is in agreement with extensive grassland management experience in central and northern Europe, where fast growing legumes can establish and compete well during early years until grasses become more dominant (Baasch et al. 2012). Legumes do not do well when sown later than other groups, however, as our experiments also underline (see delayed sowing experiment, case study box 9-2). During years of drought, therefore, it may be advisable not to expect legume-first priority effects to steer a community toward higher productivity while staying diverse.

Most of all, we learned from our range of priority effect experiments that it is time to explicitly test exactly the same priority effect treatments in different years; for example, reinitiate the same experiment again and again to test how robust effects are to weather conditions.

Closing Remarks

What is the role of time and year in community assembly? Although field ecologists and restoration ecologists strive to generalize across space and time, any field ecologist will confirm that field sites often vary dramatically from year to year. This is often driven by changes in the plant species that dominate, with further effects on trophic interactions among soil fauna, herbivores, pathogens, and carnivores (Montoya et al. 2012). Bakker et al. (2003) initiated the same seeding method and herbicide treatments over three consecutive years in two different rangeland settings and found very large differences in outcomes. Establishment of native grass species varied fourfold between years and threefold between sites (Bakker et al. 2003). Doherty and Zedler (2015) set up topographic treatments for sedge meadow restoration in 2012 and again in 2013; the most effective microsites differed by year, depending on whether June was unusually wet or dry (see chap. 10). As underlined by Vaughn and Young (2010) the effect size of experimental treatments and therefore the conclusions drawn can differ significantly between years. As such, the conclusions drawn about ecological assembly processes may be quite different depending on when an experiment was initiated, even if the treatments applied were the same.

Based on multisite meta-analyses over the past decade, it is surprising that the issue of temporal scale has received much less attention than that of spatial/geographic effects. Vaughn and Young (2010) addressed the question of temporal effects by comparing field studies in seven journals: five in ecology, one in agronomy, and one in restoration ecology. Only 5% of the ecological field studies initiated experiments more than once (e.g., repeated a very similar experiment in another year, to investigate so-called treatment by initiation year interactions), and this occurred even more rarely in the field of restoration ecology. In agronomic settings, however, 48% of studies were repeated over multiple years. This difference is understandable, given that agronomic studies generally include annual plant species grown in monoculture with a short growing season until harvest.

Vaughn and Young (2010) conclude that “this gap in long-term multiple-initiation ecological experimentation is likely to have profound implications if systems with long-lasting effects of establishment are sensitive to the year of experimental initiation.” During ecological restoration, where plant species are usually sown or planted, the role of weather and soil conditions (both fertility and competition from the seedbank) during the establishment phase may be critical for the outcome of restoration if priority effects are occurring. After sowing or planting and other treatments (e.g., herbicide) the system is allowed to assemble further, with little intervention. For this reason, if we are to be able to use priority effects to set communities of plants on desired trajectories during restoration, we need to understand better what the main drivers are, including the interaction between weather effects and priority effects treatments. Our goal now is to study the role of year of initiation effects by setting up the same priority effect experiments each year, allowing us to elucidate to what extent useful priority effects (such as those found by sowing legumes before other functional groups) are modulated by the weather during establishment as well as by soil conditions. A useful outcome of such *year of initiation priority effect* experiments could be that one could predict that clear priority effects can be achieved by sowing legumes before other groups as long as the weather conditions were wet enough. In drier years, other management may be necessary.

Recent research on priority effects during assembly underlines that outcomes can be contingent on the interactions between first arrivals, plant-soil feedbacks, and weather conditions. This means that we need to understand more about how starting conditions may affect restoration trajectories and hence project goals.

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Chapter 10

Heterogeneity Theory and Ecological Restoration

Daniel J. Larkin, Gregory L. Bruland, and Joy B. Zedler

Theory and Application

- Theory relevant to habitat heterogeneity in restoration comes from work on ecological niches, fractal dynamics, and mechanisms of species coexistence.
- Habitat heterogeneity is a key factor in landscape, ecosystem, and community processes across aquatic and terrestrial systems.
- Heterogeneity encompasses not only visible structural aspects of heterogeneity, but also spatial variation in soil properties, chemistry, and other features.
- Heterogeneity is predicted to be an important influence on biodiversity and ecosystem function in restored systems. Further research is needed to understand fundamental cause-effect relationships and to improve methods for incorporating appropriate heterogeneity into restoration.

Natural ecosystems are heterogeneous; their physical, chemical, and biological characteristics display variability in space and time. In trying to understand vegetation heterogeneity, early ecologists found that species sorted among habitats according to environmental conditions, such as along lakeshore dunes of different size and age (Cowles 1899; Gleason 1926). Later, ecologists recognized that some species act as "engineers," creating heterogeneity and affecting other species and ecosystem processes (Jones et al. 1994). Examples are sedge tussocks (Watt 1947), ant mounds (Vestergaard 1998; Nkem et al. 2000), and bison and alligator wallows (Collins and Barber 1985; Gunderson 1997). With the emergence of landscape ecology, spatial heterogeneity drew interest across spatial scales—no longer a "troublesome source of error," but a key variable for explaining ecosystem structure and function (Pickett and Cadenasso 1995).

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In contrast to heterogeneous natural systems, humans tend to homogenize landscapes, as is apparent in agriculture, forestry, and engineered waterways (Krummel et al. 1987; Koebel 1995; Paz González et al. 2000). Evident landscape features in the United States are orderly patterns—square fields, straight lines—that emerge from human activity (Cardille and Lambois 2009). This tendency for neatness is reflected in restoration efforts with smoothly graded soil surfaces or unnaturally linear stream channels. However, there is growing interest among restoration practitioners in incorporating forms of heterogeneity observed in reference systems, such as soil patchiness and microtopographic variability (Barry et al. 1996; Bruland and Richardson 2005; Moser et al. 2009; Palmer 2009; Jarzemsky et al. 2013). Several apply heterogeneity (both vertical and horizontal patchiness) as a key element of reserve design (Dobkin et al. 1987; Miller et al. 1987), species conservation (Fleishman et al. 1997), and provisioning of ecosystem functions (Ludwig and Tongway 1996).

Increasing interest in the role of heterogeneity in shaping ecological processes is reflected in a rapidly growing body of ecological literature that includes genetic, population, biogeochemical, and physiological processes (e.g., Fleishman et al. 1997; Clegg et al. 1998; Li et al. 2001; Stoeckel and Miller-Goodman 2001) (fig. 10-1). This interest is coupled with widespread concern that anthropogenic global change is homogenizing the planet's ecosystems (McKinney and Lockwood 1999). However, there are still key questions about when and how to provide heterogeneity in a restoration context. Achieving a better understanding of the influence of habitat heterogeneity on ecological structure and function remains a major challenge (Cardinale et al. 2002). As Palmer (2009) argued, there are cases where adopting heterogeneity as a management principle—and the sometimes massive financial investments associated with this goal—has outpaced the scientific evidence of its effectiveness for meeting restoration objectives.

Here, we review the theory of heterogeneity and its applications to ecological restoration. Our discussion spans micro to macro spatial scales, that is, from molehills to mountains. Restoration projects typically fall in the middle of that range. After highlighting key findings from the literature, we identify questions in need of further study within an ecological restoration context.

Roots of Heterogeneity Theory

To understand how heterogeneity might influence the structure and performance of restored systems, we draw upon a large body of theory describing how environmental variability influences diversity patterns, availability of multidimensional niche space, room for species in fractal systems, maintenance of coexistence

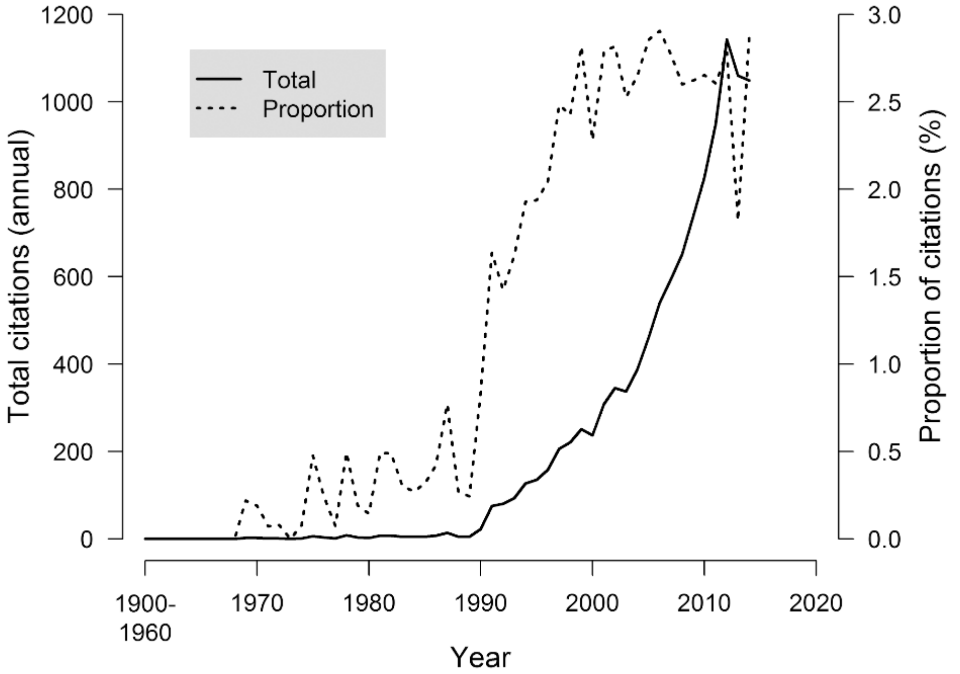


Figure 10-1. The scientific literature addressing heterogeneity in ecology has risen rapidly in recent decades. The solid line depicts annual citations (from 1900–2014) in *Web of Science* (Thomson Reuters 2015) matching the search terms "heterogene* and ecolog*" To correct for growth in the ecological literature in general, the dashed line depicts papers referencing "heterogene*" as a proportion of all "ecolog*" papers.

among species, and concentrations of hot spots and hot moments driving key ecosystem processes.

Spatial heterogeneity promotes diversity by maintaining habitats in nonequilibrial states (Tessier et al. 2002). For example, in wetlands, Brose (2001) posited that area was simply a "surrogate variable for habitat heterogeneity, which directly enhances vascular plant species diversity." Earlier, Pickett and Cadenasso (1995) argued that spatial heterogeneity across scales—and interactions among scales—is a powerful causal factor in ecology; Wu and Loucks (1995) showed that heterogeneity contributes to the persistence of entire ecological systems; and Levin (1976) predicted that spatial heterogeneity gives rise to mosaics of locally stable communities.

Supporting diverse species is arguably the most common goal of ecological restoration (Ruiz-Jaen and Aide 2005). In classical community ecology, heterogeneity provides a variety of ecological niches, where a niche is the "N-dimensional hypervolume" that characterizes the spatial distribution and function of a species (Hutchinson 1957). Each dimension indicates the range of an important environmental condition that governs a species' population growth rate. With more spatial heterogeneity, one expects greater diversity of niche spaces, thus facilitating species coexistence (Jeltsch et al. 1998).

Features that lend a fractal dimension (Mandelbrot 1983) to habitat may have important ramifications for species diversity (Williamson and Lawton 1991). Fractals describe self-similarity at multiple scales; for example, large rivers that fan out into deltas display geometry similar to tidal marsh creek networks, and tiny rivulets mimic this geometry at a still-smaller scale. Palmer's (1992) simulations showed that increasing the fractal dimension of a habitat allows more species to coexist. Fractal surfaces increase disproportionately as measurement units decrease, so that smaller animals experience more space (absolute and relative) than larger animals (Williamson and Lawton 1991). This can facilitate "packing" of species, leading to diversity that is higher than expected based on area alone (Ritchie and Olff 1999). For example, incorporating complex creek networks into tidal marsh restoration (Larkin et al. 2008; Bostrom et al. 2011) imparts fractal habitat heterogeneity and enhances diversity.

Habitat heterogeneity is also an important component of coexistence theory (Chesson 2000; HilleRisLambers et al. 2012). Community diversity results from the balance between (a) "relative fitness differences" that predict outcomes of interspecific competition and lead to displacement of weaker competitors (Chesson 2000; Adler et al. 2007) and (b) "stabilizing niche differences" that promote coexistence by causing species to limit themselves more strongly than they do other species, via mechanisms such as resource partitioning, accumulation of pathogens, and responses to environmental heterogeneity (Whittaker et al. 1973; Chesson and Warner 1981; Chu and Adler 2015). Building heterogeneity into restoration sites could facilitate persistence of weaker competitors by increasing availability of spatial refugia (chap. 9).

Ecosystem theory focuses on processes and functions, which also respond to and amplify heterogeneity. McClain et al. (2003) proposed that biogeochemical processes are driven largely by spatial hot spots and temporal hot moments with high reaction rates. Pockets of elevated biogeochemical activity often occur in boundaries between landscape features, such as converging water flows. Thus, spatial heterogeneity can create hot spots, which in turn confer heterogeneity, for example, patchiness in soil nutrient availability (McClain et al. 2003; Bruland et al. 2006). Hot spots for denitrification to improve water quality could be factored into riparian restoration efforts (Bruland et al. 2006; Orr et al. 2007; Orr et al. 2014).

Heterogeneity is both a cause and consequence of biogeochemical hotspots, and some positive feedbacks increase spatial structuring. Sharitz and McCormick (1973) describe how slight wind-sheltered depressions in barren, granite outcroppings accumulate sediments. This allows cushion plants to establish, which generates biotic patchiness. In rangeland restoration, roughened soil surfaces capture water and other resources in pockets that accelerate vegetation recovery (Whisenant 1999). In marine systems, coral reefs create zones of hydrodynamic convergence that sieve debris and concentrate organisms (Netto et al. 1999), and seagrass beds transform monotonous sediment bottoms by decreasing water velocity, which increases sedimentation, allowing more plants to establish (Duffy 2006) (fig. 10-2). The influence of heterogeneity is not just a static habitat feature but also a mediator of key processes in community assembly and ecosystem development.

We propose that building environmental heterogeneity into restoration sites will facilitate biodiversity and key ecosystem functions, with the caveat that levels of heterogeneity that exceed those of reference systems may be ineffective or harmful. Thus, we call for site and system specificity and more research on the effects of heterogeneity on restoration outcomes, particularly in an adaptive context, that is, testing the influence of heterogeneity in actual restoration projects (Zedler 2000).

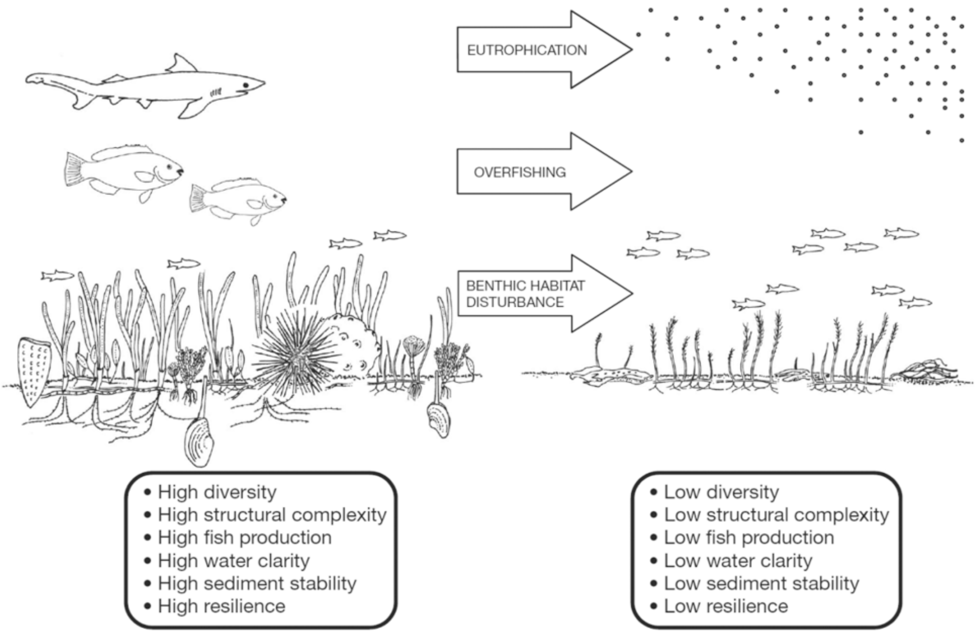


Figure 10-2. Habitat heterogeneity imparted by seagrass beds in a tropical marine system is associated with benefits to biodiversity and ecosystem functioning. Reprinted with permission from Duffy (2006).

Hypotheses and Tests of Heterogeneity

Next, we pose hypotheses and then summarize how restoration ecologists have tested effects of experimentally manipulated heterogeneity.

Landscape Heterogeneity Is an Important Contributor to Regional Diversity

Large-scale spatial heterogeneity is a driver of ecological structure and function (chap. 3). Variations in topography and energy availability are two of the best predictors of mammalian diversity over much of North America (Kerr and Packer 1997). Similarly, regional topographic heterogeneity is second only to potential evapotranspiration in predicting richness of North American *Papilionidae* (swallowtail butterflies) (Kerr et al. 1998). In Pampa grasslands of Argentina, heterogeneity in elevation and salinity had stronger effects on regional species composition than did latitude (Perelman et al. 2001).

Spatial heterogeneity often reflects the imprint of past disturbance. In Yellowstone National Park, vegetation recovery following the 1988 fires was influenced strongly by complex mosaics of unburned, moderately burned, and severely burned areas (Turner et al. 2003). Large fires, volcanic eruptions, and floods all leave behind heterogeneous patterns of surviving biota, which influence successional pathways and colonization dynamics (Turner et al. 1998). At smaller scales, disturbance is both a barrier to overcome in meeting conservation targets and a management tool (Hobbs and Huenneke 1992).

Whisenant (1999) alerted restorationists to pay attention to the landscape, arguing that a landscape approach can help reduce causes of degradation, initiate soil-improving processes, and aid vegetation establishment. He also argued that landscape components should be arranged strategically in order to limit potentially detrimental interactions while facilitating synergies among landscape components. In wetland restoration, a landscape or watershed perspective is vital. A wetland positioned downstream from agriculture may not support high plant diversity due to hydrologic disruption and eutrophication, but it could provide water-quality and flood-retention services (Zedler 2003; Zedler and Kercher 2004).

Spatial Variability Strongly Influences Species Distributions

In aquatic communities, patterns in hydrodynamic processes led Guichard and Bourget (1998) to link biomass and diversity of rocky-shore intertidal macrobenthos to interactions between topographic heterogeneity and hydrodynamics. Likewise, Netto et al. (1999) related the diversity and distribution of South Atlantic reef invertebrates to hydrodynamic sorting of substrate texture and organic-matter content.

In terrestrial and wetland communities, topographic variability can create “safe sites” with elevated germination and establishment rates (Smith and Capelle 1992). Both mounds and hollows can influence recruitment, for example, wallows created by bison and mounds engineered by prairie dogs interacted with fire and grazing to maximize community diversity (Collins and Barber 1985). In a mangrove forest, seedling establishment and sapling density were higher on mounds created by burrowing crabs (Minchinton 2001). In coastal meadows, anthills and hillocks had high plant species richness (Vestergaard 1998). Experimentation with microtopography promoted establishment of rare woody species and wetland plant diversity (Vivian-Smith 1997). In Wisconsin sedge meadows, tussocks created by *Carex stricta* increased diversity by adding surface area, providing diverse microhabitats, and supporting a seasonal progression of plant species (Peach and Zedler 2006). In a North Carolina wetland, diversity was enhanced by reestablishing microtopography, with little overlap of species between hummocks, flats, and hollows (Bruland and Richardson 2006).

In tidal marshes worldwide, one or a few “low-marsh” species typically occur next to the water’s edge, while a richer mixture occurs further inland (Adam 1990). Within a meter’s rise in elevation, tides lead to frequent inundation and buffered variability at the low end to intermittently wet and variable moisture and salinity at the high end. In a little-disturbed marsh in Baja California, Mexico, *Spartina foliosa* (Pacific cordgrass) showed both vertical and horizontal pattern: it occupied only the bayward margin despite similar elevations farther inland; similarly, four marsh-plain species occupied slightly lower elevations only next to tidal creeks, perhaps due to better drainage (Zedler et al. 1999). In Gulf of Mexico coastal marshes, *Spartina patens* also responds to both vertical and horizontal dimensions. Plants in better drained dune-and-swale habitats generally respire aerobically, while anaerobic metabolism is more common in lower, more poorly drained habitat (Burdick and Mendelssohn 1987).

Effects of small-scale heterogeneity were not easily identified in field experiments that varied heterogeneity. Holl et al. (2013) planted trees in “islands” to create heterogeneous habitat, then compared results with tree plantations and unplanted controls, all aimed at restoring forest vegetation to former Costa Rican farmlands. Although plant diversity was not greater in the tree-island treatment after five to seven years, the tree canopy was more variable, causing variation in light reaching the forest floor. Patchy light helped explain why the arthropod community was more diverse in species and functional groups after seven to eight years (Cole et al. unpub. data). Farmland being restored to tallgrass prairie in Kansas was initially more diverse and more variable in productivity and canopy cover in treatments with greater heterogeneity of soil depth and nitrogen, but over time, the differences yielded to the homogenizing effect of the local dominant grass, *Panicum virginicum* (Baer et al. 2005). Effects of heterogeneity treatments can differ with ecosystem components, and effects can diminish over time.

Disturbance Mediates the Ecological Effects of Heterogeneity

In coastal Alaska, sites subjected to intermediate flooding frequency, with high spatial variation in flooding, had higher plant diversity than sites with rare, frequent, or permanent flooding and lower spatial variation in flood frequency (Pollock et al. 1998). In coastal Queensland, Australia, spatial heterogeneity defined seedbank structure in seagrass (*Halodule uninervis*) meadows. Water turbulence and foraging by dugongs (*Dugong dugon*) removed vegetation from depressions, resulting in dense patches of *Halodule* seeds (Inglis 2000).

In forest systems, strong winds alter forest structure, remove trees or canopy, and alter plant recruitment. In a southern Appalachian forest, hurricane Opal (1995) uprooted trees, creating pit and mound heterogeneity that increased species richness and mixing of shade-tolerant and light-demanding species in the post-disturbance community (Elliott et al. 2002). Carlton and Bazzaz (1998) simulated a hurricane by pulling down trees in a New England woodland; seeds accumulated in pits, seedlings established on scarified flats, and trees grew best on tip-up mounds. In Puerto Rico, Lenart et al. (2010) found that soil mounds and pits from trees uprooted by hurricanes accounted for a soil turnover rate of 1,600–4,800 years, faster than with landslides or background rates of treefall.

Heterogeneity Influences Animal Behavior, Interactions, and Habitat Selection

In a saltwater lake, Aronson and Harms (1985) experimentally manipulated topographic complexity and found that suspension-feeding ophiuroids (*Ophiothrix oerstedii*) remained in plots with greater heterogeneity but emigrated from homogeneous control plots, apparently a predator-avoidance behavior. In a shallow reef, all juvenile fish died in low-complexity treatments compared to only 13% mortality in high-complexity treatments (Connell and Jones 1991). Prey mortality was also high in a rocky intertidal area with low substrate complexity but mitigated where holes and crevices were abundant (Menge et al. 1985).

In wetlands, interspersed cover types impart heterogeneity important for wildlife and trophic support. In New York wetlands, secretive marsh birds (American bittern, *Botaurus lentiginosus*; least bittern, *Ixobrychus exilis*; sora rail, *Porzana* *carolina*; and Virginia rail, *Rallus limicola*) were more abundant where there was greater interspersion of water and vegetation; thus, managing for spatial patterning should benefit wetland-dependent wildlife (Rehm and Baldassarre 2007). In coastal wetlands, marsh plains are dotted with small pools that benefit wetland food webs. In contrast, non-native *Phragmites australis* (common reed), an aggressive invader, eliminates pool-flat heterogeneity, causing lower macroinvertebrate diversity (Angradi et al. 2001) and reduced nursery, reproduction, and feeding support functions for fishes (Able et al. 2003).

Environmental Heterogeneity Influences Ecosystem Functions

Across diverse plant communities, horizontal and vertical heterogeneity induces differential moisture stress, waterlogging, redox conditions, root mass, and productivity (Pinay et al. 1989; Roy and Singh 1994; Ehrenfeld 1995; Werner and Zedler 2002). In a dune grassland, Gibson (1988) found that soil under hummocks was moister, more acidic, and higher in conductivity than that under hollows, with higher levels of root biomass, organic carbon, and key nutrients. In a deciduous woodlot, microtopographic depressions had greater litter accumulation and moisture retention, less temperature variation, and many more bacteria than flat or high sites (Dwyer and Merriam 1981). Cantelmo and Ehrenfeld (1999) found differences in the intensity of mycorrhizal infection on tops, sides, and bottoms of hummocks in Atlantic white cedar swamps. Specific ecosystem services can be targeted by including heterogeneity in predictive models (McClain et al. 2003; Wolf et al. 2011).

Cardinale et al. (2002) tested the effects of fine-scale vertical and horizontal heterogeneity on benthic algal and biofilm activity by manipulating streambed sediments. Benthic respiration rates were 65% higher in high-heterogeneity than low-heterogeneity riffles, and benthic biofilms had 39% higher gross productivity. The authors attributed differences to near-bed flow velocity and turbulence resulting from increased substrate heterogeneity.

Spatial heterogeneity also affects greenhouse gas fluxes. In boreal wetlands, Bubier et al. (1993) explained most of the variability in methane (CH_4) emissions ($R^2 = 0.74$) based on interactions of water levels and hummock-hollow heterogeneity on soil temperature and moisture. In a Minnesota peatland, carbon dioxide (CO_2) emissions were higher from hummocks than from hollows, apparently due to temperature and water-depth covariates (Kim and Verma 1992). In fertilized grassland, nitrous oxide (N_2O) emissions differed by plot elevation, along with differences in air permeability and nitrate, ammonium, and soil water content (Ball et al. 1997). In North Carolina wetlands, hotspots of soil nitrate and ammonium led to hotspots in denitrification potential (case study box 10-1; Bruland et al.

2006). The effects of heterogeneity on nutrient cycling and greenhouse-gas emissions highlight the need for ecosystem models to account for small-scale variations (Bubier et al. 1993).

Applying Heterogeneity Theory in Restoration Sites

Compelling evidence reviewed above indicates that many variables could be manipulated in restoration projects to incorporate the influence of heterogeneity at multiple vertical and spatial scales. At the large scale, landscape structure has been restored by breaching levees and rewetting fields, for example, along the Illinois River and in San Francisco Bay salt ponds. There are many unexploited opportunities to establish large field experiments to test the effects of heterogeneity on restoration outcomes (Wagner et al. 2008). Heterogeneity is best incorporated during the initial construction phase of a project to avoid damaging biota and functions that might be in place at a later stage.

An appropriate menu of actions depends on natural heterogeneity in reference systems. Within individual sites, heterogeneity can be imparted through contouring, roughening soil surfaces, or planting (Barry et al. 1996; Tweedy and Evans 2001). Manipulations need to be tailored to the surrounding landscape, as well as the site's size, history, and specific project goals. In moderately degraded sites, there may be little need to engineer heterogeneity. In recently drained prairie-pothole wetlands, spatial features like pothole shape, area, depth, and slope are likely to persist. Restoration might require only removing drainage structures and reestablishing wetland species. However, in heavily degraded sites, there is a stronger rationale for manipulating heterogeneity actively. For example, dredge spoils can be excavated to mimic the spatial complexity of natural marshes, rather than the simplistic designs of some mitigation projects (Zedler and Callaway 1999) (fig. 10-3).

Here we consider ramifications of heterogeneity on the restoration of ecological processes at landscape, habitat, and finer scales.

Enhance Landscape Functions

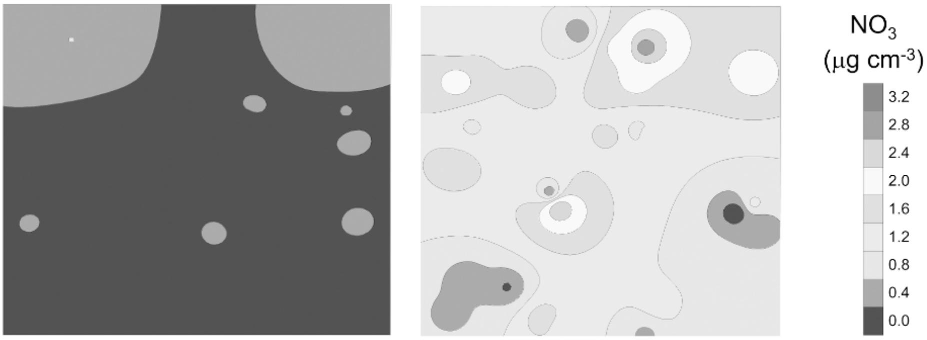
Processes such as movements of organisms, trophic interactions, and fluxes of materials are influenced by aspects of large-scale heterogeneity that include variation in the size, shape, edge characteristics, distribution, and connectivity of patches (Turner 1989). Various strategies aim to restore landscape-level structure and function by mimicking natural heterogeneity. Mladenoff et al. (1993) recommended using patterns of spatial complexity in old-growth forests as a model for restoring forest functioning in managed landscapes. For tallgrass prairie restoration, Howe

Case Study Box 10-1
Adding Spatial Heterogeneity to Restore Soil Processes

By Greg Bruland, Principia College

North Carolina Coastal Plain: Riverine and nonriverine wetlands

Test of theory: Spatially heterogeneous soil supports natural soil processes
We compared soil cores from flat terrain (mean ± 0.5 m) within created or restored (left panel) and paired natural wetlands (right panel). Sampling sites had relatively homogeneous topography, yet soil nitrate (shown below), moisture, ammonium, and denitrification activity (estimated with the denitrification enzyme assay) were all more variable in natural wetlands than in paired created or restored wetlands.



Spatial variability in soil nitrate concentrations in a created or restored wetland (*left*) and natural wetland (*right*).

Progress: Created/restored wetlands generally had much more homogeneous soil properties than found in paired natural sites. Homogeneous distributions of nitrate and ammonium limit the range of soil chemical conditions and biogeochemical transformations that can be expected to occur in these sites. In contrast, soluble organic carbon (SOC) exhibited more heterogeneous distributions in both created/restored than in natural wetlands across multiple hydrogeomorphic subclasses.

Expected outcome: Created and restored wetlands will develop greater soil heterogeneity if local patterns are first described and then used as restoration targets. SOC may be less influenced by factors such as historical land use, restoration versus creation, and hydrogeomorphic setting (riverine or not).

Long-term outcomes: Prior agricultural land use as well as grading and earth moving during restoration homogenize wetland soils. Future restoration projects should include spatial heterogeneity of soils as targets. This could be accomplished by reestablishing microtopography or amending certain areas with compost.

References: Bruland et al. 2006.

Figure 10-3. A consequence of smooth mounding of islands in a tidal marsh restoration site (San Diego Bay, California) was that salts that wicked to the surface could not be flushed away by the tidal creeks typical of reference sites. This led to substrates too saline for plant establishment. Even though this site was made tidal in 1984, and the islands' elevations are within tidal range, they remained largely unvegetated thirty years later (photo by J. Zedler 2014).

(1994) suggested using a variety of management actions to create spatial complexity similar to that under which prairie species evolved.

While benefits from large-scale manipulations of topographic heterogeneity might be inferred from the literature, examples are few. Relevant examples come from river restoration, where management actions reconnect and reconfigure channels, alter floodplain habitats, and restore meanders (Kern 1992; Toth et al. 1993; Gore and Shields 1995; Stanford et al. 1996). Reestablishing tidal flushing and complex creek networks also occurs over large scales, thereby enhancing connectivity, animal movement, and trophic transfer between habitats (Peterson and Turner 1994; West and Zedler 2000).

The landscape position of restoration projects is critical to understanding large-scale processes like succession, water movement, fire, and surrounding land use (Whisenant 1999; chap. 4). Landscape heterogeneity is a key component of forest restoration plans for Oregon and Washington, where mosaics of tree size/age are called for at multiple spatial scales across thousands of acres (Franklin and Johnson 2012). Spatial heterogeneity at the watershed scale is particularly important for wetland restoration, because water-flow patterns dictate wetland condition and restoration potential. A recent planning process in Wisconsin created strategies for prioritizing wetland restoration in a subwatershed with substantial loss of a target ecosystem service (e.g., flood abatement, water quality, water delivery, and/or carbon storage), and then choosing among potentially restorable sites that will best restore that service (Miller et al. 2012).

Shape Community Assembly

Species diversity can be low in restoration sites that lack suitable microhabitats and propagules (Ash et al. 1994). Fine-scale heterogeneity can enable species coexistence by providing more germination niches (Grubb 1977). Manipulating microsites can facilitate plant establishment and diversity (case study box 10-2). In early successional pastures, Reader and Buck (1991) found more species where they created small mounds, simulating natural disturbance by burrowing animals. In prairie restoration, mounding had a positive effect on growth and survival of three species and negatively affected just one species (Ewing 2002). In west Texas oak vegetation, rabbit mounds led to increased survival, shoot and root biomass, root length, tiller density, mycorrhizal infection, and nutrient uptake by *Schizachyrium scoparium* (little bluestem) (Dhillion 1999). Artificial mounds created to mimic rabbit mounds facilitated vegetation restoration. Mounding has also shown promise as a restoration technique in deep-sea benthic communities, deciduous forest, and desert (examples in Ewing 2002).

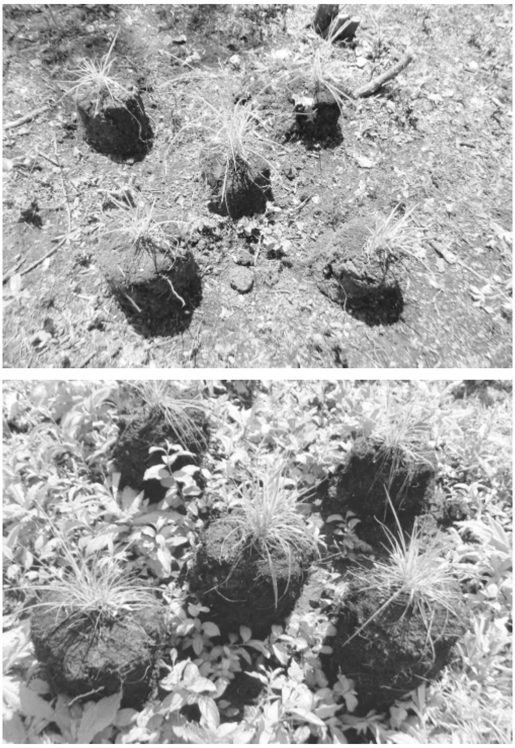
In wetlands, restoring microtopography influences plant establishment through interactions with hydrological dynamics (Middleton 2000). Created wetlands tend to have narrower bands of emergent vegetation than natural wetlands (Confer and Niering 1992), so the gradient structure of natural reference marshes should be mimicked for created marshes (Kentula et al. 1992). Barry et al. (1996) proposed that mound and pool heterogeneity is vital to restoring forested wetlands. Tweedy and Evans (2001) found that, relative to smooth treatments, rough contours in two restored agricultural wetlands led to higher water tables, reduced outflow and peak outflow rates, and increased duration of outflow events. Numerous researchers recommend reestablishing microtopography, especially for restoring wetlands in former agricultural (flat, smooth) land (Cantelmo and Ehrenfeld 1999; Tweedy and Evans 2001; Bruland and Richardson 2005).

Wetland plants respond to subtle changes in topography. Tire ruts were loci of elevated plant diversity in a New Jersey freshwater wetland mitigation site (G. Vivian-Smith, pers. comm.), presumably due to fine scale patterns of inundation and soil compaction. In a related mesocosm experiment, varying microtopography by only 1–3 cm increased species richness, evenness and abundances compared to homogeneous treatments (Vivian-Smith 1997). Diversity-support functions should be

Case Study Box 10-2
Increasing Topographic Heterogeneity to Assist Sedge Meadow Restoration

By Joy Zedler, University of Wisconsin–Madison

UW Arboretum: A wooded wetland (~5 hectares) was "forest-mowed" by grinding shrubs and trees (up to 4" diameter) and spreading the debris over the soil. The restoration target is tussock sedge (*Carex stricta*), to be followed with more diverse sedge meadow plantings, once tussock topography develops.



Establishing microtopographic heterogeneity within a wetland.

Test of theory: Heterogeneous topography supports diverse vegetation

Native *Carex stricta* meadows have diverse vegetation, with larger tussocks supporting more species. Tussocks are organic structures that develop within a decade. *Carex stricta* is a "matrix dominant" that supports other species, including preferential species.

Doherty and Zedler (2015) tested the ability of mounded topography to accelerate sedge meadow restoration in a large field experiment within a restoration site. The experiment began with small, medium, and large artificial mounds, constructed in 2012 and again in 2013.

Expected outcome: *C. stricta* would establish and support other species differentially across the vertical range of microtopography.

Case Study Box 10-2 continued

Progress: In year one, a severe June drought restricted survival of plugs to shorter mounds and peat pots that held moisture better than soil mounds. In year two, extreme June rainfall facilitated survival on tall mounds but not in shallow depressions. A broad range of microsites for sedge plug plantings increased chances that some plants would establish even under extreme early-spring conditions. Topographic heterogeneity hedged bets against stresses of both drought and local flooding.

Midterm outcomes: In 2014, *C. stricta* was widespread within the planting area, and native vegetation had developed with and without seed sowing.

References: Peach and Zedler 2006; Frieswyk et al. 2007; Lawrence and Zedler 2011; Johnston and Zedler 2012; Doherty and Zedler 2015.

restorable by providing rough surfaces, and irregular boundaries between vegetation types. Note, however, that ridges created perpendicular to water flows can be flattened rapidly—a costly lesson (J. Zedler, pers. obs.).

An 8 ha restoration experiment at Tijuana Estuary, CA, tested the effects of tidal creek heterogeneity on trophic development. Replicate areas with and without tidal creek networks showed that creeks were "conduits" for longjaw mudsuckers (*Gillichthys mirabilis*) to access the marsh surface (Larkin et al. 2008). Meanwhile, California killifish (*Fundulus parvipinnis*) responded to finer-scale heterogeneity (shallow marsh-surface pools), which functioned as "oases" of abundant invertebrate prey, verified by constructing artificial pools that jumpstarted algal production and supported higher numbers and diversity of invertebrates (Larkin et al. 2009) (fig. 10-4). At the same site, geomorphological development and plant establishment benefited from creek and pool heterogeneity (Wallace et al. 2005; Varty and Zedler 2008). These are key variables along the California coast, where sedimentation and hypersalinity can constrain restoration effectiveness (Zedler et al. 2003) (fig. 10-3).

In stream and river restoration, restoring small-scale heterogeneity is a common target (Gore and Shields 1995; Stanford et al. 1996). Woody debris, rock weirs, and gravel are used to improve streambed morphology and increase local heterogeneity, with benefits for plants, benthic invertebrates, and fish (Gore and Shields 1995; Jungwirth et al. 1995; Muhar 1996; Hilderbrand et al. 1998). However, further work is needed to determine when, where, and how heterogeneity is beneficial (or not; Palmer 2009). Expected benefits of restoring in-stream heterogeneity were not found for fish and invertebrate diversity in northern Sweden (Lepori et al. 2005). There is need to improve understanding of how heterogeneity influences the biota and functions targeted in restoration in specific ecological systems.

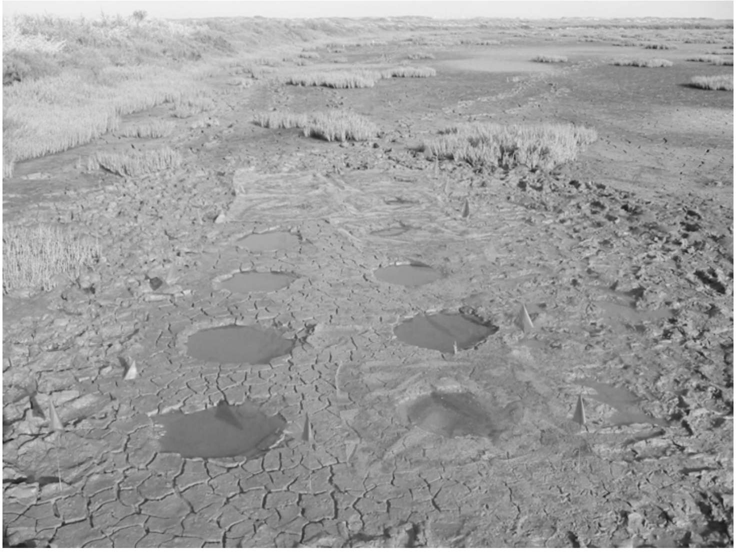


Figure 10-4. Experimental tests of the influence of fine-scale horizontal and vertical heterogeneity in wetland restoration. *Top*: Artificial tussocks added to a sedge meadow restoration (Madison, Wisconsin) widened the range of moisture microenvironments available, which helped plantings withstand interannual variability in rainfall (Doherty and Zedler 2015). *Bottom*: Created pools in a southern California salt marsh restoration site (San Diego, California) increased availability of invertebrate prey items for fishes (Larkin et al. 2009).

Support Ecosystem Services

Heterogeneity influences ecosystem functions and services that are restoration targets. In Delaware, experimental manipulations affected ecosystem services of constructed wetlands (Alsfeld et al. 2009): insect richness and the biomass of insects, *Ephemeroptera* and *Odonata*, increased with coarse, woody debris volume and obligate wetland plants became more abundant with greater microtopographic variation. Further research is needed to assess effects of organic-matter amendments and microtopography on ecosystem services (Alsfeld et al. 2009).

Soil organic matter (SOM) amendments have enhanced ecosystem function and services in restored and created wetlands. In Virginia, Bruland and Richardson (2004) showed that SOM improved soil microbial biomass, water-holding capacity, and phosphorus sorption in created wetlands. In another created wetland, pH, microbial biomass carbon, and P sorption responded strongly to compost amendment (Bruland et al. 2009). Microbial and geochemical responses to compost amendments were complex—such that optimal amendments for one ecosystem service might trade off with another. This suggests that patchy, variable compost additions would be a good bet-hedging strategy.

In the Sacramento-San Joaquin Delta, researchers found that drained agricultural fields were net sources of greenhouse gases, while restored wetlands were net sinks for CO_2 (Knox et al. 2015). This benefit of restoration was countered by restored wetlands that emitted CH_4, which has ~25 times the warming effect as CO_2. However, in a parallel study, Matthes et al. (2014) found that elevated CH_4 emissions could be tempered by managing for heterogeneous vegetation: vegetation patches with complex, fractal structure (convoluted edges) had lower CH_4 emissions. The authors suggested that higher edge-to-area ratios enhance canopy light-uptake and efficiency of roots in scavenging soil CH_4.

A recent study of termite-driven heterogeneity demonstrates what indigenous people have long known, that termite mounds have rich soil (Pennisi 2015). Mounds that are 2–3 m tall increase the types and levels of ecosystem functioning (fig. 10-5), providing perches and lookouts for wildlife, increasing water infiltration (via macropores), and creating "islands of fertility," plant refugia, and revegetation nuclei. But it took a new model of spatial dynamics to show that termite mounds can also reduce negative impacts of climate change. Rather than indicating impending desertification, termite mounds buffer dryland ecosystems against future climates with lower rainfall (Bonachela et al. 2015).

Even small differences in heterogeneity can cause large differences in ecosystem functioning. At the UW–Madison Arboretum, unintended heterogeneity in subsurface clay layers caused three wetlands (otherwise identical) to have slightly different hydroperiods and to develop along unique trajectories (Doherty et al.

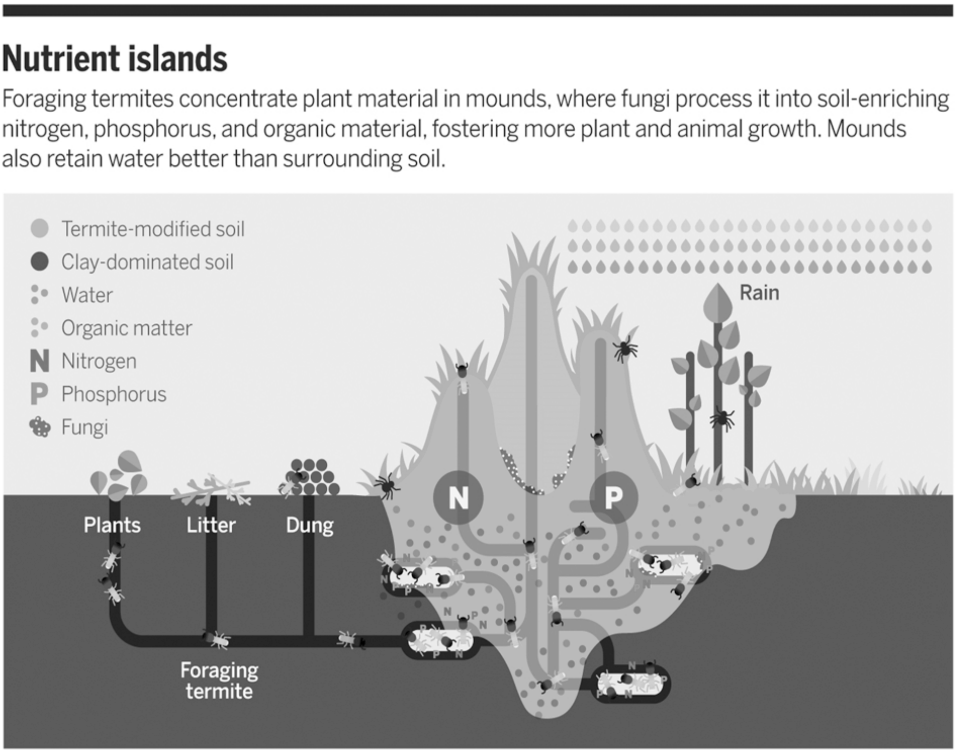


Figure 10-5. Vertical and horizontal heterogeneity created by termite mounds has important ecological consequences, and can confer resilience to climate change in arid ecosystems. Reprinted with permission from Pennisi (2015), credit: G. Grullón/*Science*.

2014). A continuous clay layer impounded water, promoted invasive cattail dominance, and produced the most biomass. The two wetlands with patchier underlying clay allowed infiltration, so that hydroperiods were intermittent; more plant species established, biomass was low, flood peaks were attenuated, and soil erosion was minimal. Those five ecosystem services were bundled, with high productivity being a trade-off.

Constrain Species Invasions

A heterogeneous restoration site can support diverse vegetation by limiting strong dominant species that displace weaker competitors (Chesson and Warner 1981; Chesson 2000). Alternatively, fugitive species might persist better in heterogeneous sites (Hanski 1995), because invasive plants are often good colonizers, highly plastic in their habitat requirements, and able to exploit patchiness (Birch and Hutchings 1994). The task for restorationists is to judge the level of heterogeneity that will support native species without attracting invaders. Researchers have not yet met that challenge for aggressive wetland invaders (chap. 8).

Sedge meadows with tussock-forming species offer opportunities to test the roles of heterogeneity in accelerating the establishment of a native matrix species (*sensu* Frieswyk et al. 2007) while also providing high cover that deters weed colonization. Evidence suggests that *Phalaris arundinacea* (reed canarygrass) might invade less aggressively if *C. stricta* tussocks were jump-started to enhance species richness (Werner and Zedler 2002; Peach and Zedler 2006). Recent studies offer encouragement: in mesocosms, *C. stricta* began forming tussocks within two years in standing water. In a restoration site this sedge produced 15 cm tussocks within a decade, while storing carbon aboveground and creating heterogeneous topography (Lawrence and Zedler 2011; Lawrence et al. 2013). Further research is needed to link three restoration challenges: (1) controlling weeds, (2) reestablishing native plants, and (3) reestablishing or sustaining hummock/tussock topography.

Accelerate Restoration of Highly Degraded Habitats

Reintroducing spatial heterogeneity has been a key to restoring productivity and diversity in arid regions. In degraded rangelands, constructing pits or depressions increased primary productivity and vegetation recovery by slowing runoff and increasing infiltration (Slayback and Cable 1970; Hessary and Gifford 1979; Garner and Steinberger 1989; Whisenant 1999). In semiarid Australian woodland, patches of branches were arranged to simulate natural patchiness (Ludwig and Tongway 1996). After three years, more soil had accumulated under branches and conditions were more hospitable, with greater nutrient concentrations, more rapid water infiltration, and buffered temperature extremes. These changes promoted establishment of perennial grasses and ant populations.

In a desertified area in Israel, excavated pits and adjacent mounds helped to restore natural patch dynamics (Boeken and Shachak 1994), with more species and higher biomass and plant density than untreated areas. Similar restoration strategies have been used in other arid and semiarid habitats to trap seeds and enhance germination and establishment.

In other climates, conditions range from too dry to too wet, making bet-hedging an important strategy. For example, when hydrologic conditions are altered with climate change, there is a greater chance that a site with reestablished microtopography will continue to provide suitable hydrologic conditions than a site with uniform topography (Barry et al. 1996). This was demonstrated by Doherty and Zedler (2015; case study box 10-2).

Promising Approaches and Research Needs

Modeling can illustrate various components of heterogeneity theory. Gardner and Engelhardt (2008) used a spatially explicit multispecies model to predict community diversity in relation to landscape factors (limits to immigration and community size), neighborhood interactions (colonization and extinction rates), and disturbances. Although rare long-distance dispersal events were critical for population establishment, richness always declined in the absence of disturbances. The authors' recommendation that more attention be paid to disturbance regimes is critical for restoration sites, which are, by definition, disturbed—not only prior to but also during restoration.

More recently, Rodhouse et al. (2011) modeled variation in a recovering plant population in Idaho (camas, *Camassia quamash*) in relation to landscape heterogeneity. Camas density in zones with the highest topographic relief responded most strongly to land-use history. Their results suggest that restorationists transplant camas bulbs into unoccupied swales where low dispersal capacity limits patch formation, and that they plug ditches that alter surface flow patterns where subpopulations perform below average. Because restoration sites have complex, spatially variable disturbance histories, spatially explicit hierarchical modeling can provide guidance on where to plant or not to plant.

The examples from natural and restored systems reviewed above support the value of restoring habitat heterogeneity where it has been lost and where its return is likely to advance achievement of restoration aims. But to ensure that the added effort and cost of building-in heterogeneity are worthwhile, researchers and practitioners need to further explore cause-and-effect relationships, understand how system- and goal-specific contingencies mediate the role of heterogeneity, and develop improved methods for adding appropriate variability to restored sites.

Issues that merit further investigation include the following:

- Untangling effects of habitat heterogeneity from related variables like habitat area or regional rarity of specific habitats (Palmer 2009). Many experiments that we reviewed tested treatments with and without heterogeneity, but others were observational and potentially confounded by covarying factors.
- Better understanding how the scale of heterogeneity influences restoration outcomes, enabling matching of restoration goals with specific forms of heterogeneity at microhabitat, site, or landscape scales and interactions across scales (Pickett and Cadenasso 1995).
- Learning how heterogeneity affects restoration trajectories. Most studies in this chapter were short-term, but heterogeneity interacts with processes operating

over decades to centuries, such as soil development (Matthes et al. 2014) and environmental extremes (Doherty and Zedler 2015). Longer horizons and more studies across ecosystem types and climatic zones should address how heterogeneity affects complex, emergent properties of restored systems, especially resilience.
- Improving methodology for adding heterogeneity to restoration sites. Features should be sustainable and/or adaptable despite sedimentation, erosion, and other leveling forces.
- Addressing challenges inherent to resource management over large areas. As always, cost-effective approaches are needed to overcome barriers to adoption.

Answering these and other challenging questions will be of great potential benefit for restoration theory and practice.

Closing Remarks

A review of the ecological literature shows that heterogeneity acts as a key driver of landscape-, community-, and ecosystem-level processes across Earth's diverse ecological systems. Fundamental ecology, including theory on landscapes, niches, fractals, and species coexistence, offers mechanisms to explain these effects. Responses to environmental heterogeneity have been identified in organisms as diverse as microbes, cushion plants, and kangaroos and in functions ranging from methane flux to trophic support of fish. Findings from restoration experiments echo effects observed in natural settings, and spatially explicit models inform understanding of how form influences function. We advocate continued research in reference systems to understand better how heterogeneity influences community assembly and ecosystem function. We urge more rigorous and quantitative tests of experimentally manipulated heterogeneity in restoration sites, and we applaud efforts to build appropriate heterogeneity into restoration planning and implementation.

Acknowledgments

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Chapter 11

Food Web Theory and Ecological Restoration

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Theory and Application

- A food web can convey many different types of information: the number of trophic levels, the pathways of energy flow, the biomass of organisms, or the most dynamically important linkages. Specifying what is meant is an essential first step.
- Simple food chain models have been useful in restoration, for example, the use of biomanipulation to improve lake water quality via trophic cascades.
- Systems often exhibit complex interactions such as apparent competition, which has deeply influenced restoration of island ecosystems affected by invasive species.
- Our intent is to highlight the potential value of ‘food web thinking’—recognizing the role of predator-prey relationships—in ecological restoration.

No species exists in a vacuum. Rather, species are embedded within a network of predator-prey interactions in what Charles Darwin referred to as an “entangled bank” (Darwin 1859) and is now known more generally as a *food web*. In its most fundamental form, a food web provides insight into the feeding relationships in a system. More broadly, food webs represent a way of envisioning ecological systems that considers trophic (consumer-resource) interactions among species or groups of similar species (trophic guilds or trophic levels). Food web ecology is a constantly evolving subdiscipline of ecology, and it is important to appreciate the diversity of approaches to the study of food webs (Schoener 1989; Polis and Winemiller 1996; Montoya et al. 2006).

The term *food web structure* can have several meanings to ecologists. Food web structure can refer simply to the number of trophic levels in a food chain (fig. 11-1a), or can represent the linkages within a complex food web network (fig. 11-1b).

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Food web diagrams may be used to represent the pathways of energy flow through a system (energetic webs; fig. 11-1c), or alternatively, the dynamically important linkages for regulating the abundance of other organisms (functional webs; Figure 11-1d). Additionally, food web structure sometimes refers to the distribution of biomass across different trophic levels, and ultimately how bottom-up and top-down factors regulate biomass across multiple trophic levels (fig. 11-2a,b). These diverse food web concepts serve as the basis for our discussion of food web theory and applications to ecological restoration.

Despite the intuitive importance of explicitly considering trophic connections, food web approaches are not often used in applied endeavors such as fisheries and wildlife management, conservation biology, and ecological restoration (Dobson et al. 2009; Memmott 2009). We argue that food web ecology has the potential to contribute to ecological restoration by encouraging a dynamic, interaction-driven view of ecosystems and can alert practitioners to the types of trophic interactions that have bearing on restoration outcomes (Zavaleta et al. 2001; DeCesare et al. 2010; Naiman et al. 2012). In many situations, a food web perspective will provide valuable insights into ecological restoration that would not otherwise be attained from a more static, community-based approach. For example, the reintroduction of gray wolves (*Canis lupus*) into Yellowstone Park, Wyoming, US, in the 1990s has precipitated a cascade of food web changes that has allowed the recovery of riparian vegetation from damaging effects of overgrazing by elk (*Cervus elaphus*). This has led to subsequent increases in populations of beaver (*Castor canadensis*) and bison (*Bison bison*) (Ripple and Beschta 2012), as well as implications for grizzly bear (*Ursus arctos*) foraging (Ripple et al. 2014a). Such changes only make sense by considering the cascading effects of predator-prey interactions across trophic levels.

Many of the world's ecosystems are highly degraded, and natural recovery processes are often inadequate to achieve desired goals for ecosystem recovery (Dobson et al. 2009; Hobbs et al. 2011). Ecological restoration is undertaken to hasten the recovery of damaged ecosystems, restore ecosystem function, and slow the declines of biodiversity. Ecological restoration in North America is historically rooted in plant community ecology: a perusal of the leading journals in the field such as *Ecological Restoration* and *Restoration Ecology* reveals the botanical slant of the discipline. As such, succession and community assembly theory have provided the theoretical underpinnings for restoration ecology (Weiher and Keddy 1999; Young 2000). Yet ecological restoration and species recovery may be hampered by focusing on plant communities rather than the broader suite of direct and indirect food web interactions in natural ecosystems (Aschehoug et al. 2015).

An important aspect of ecological restoration is the establishment of well-defined restoration targets, which may be structural, functional, or both (Hobbs

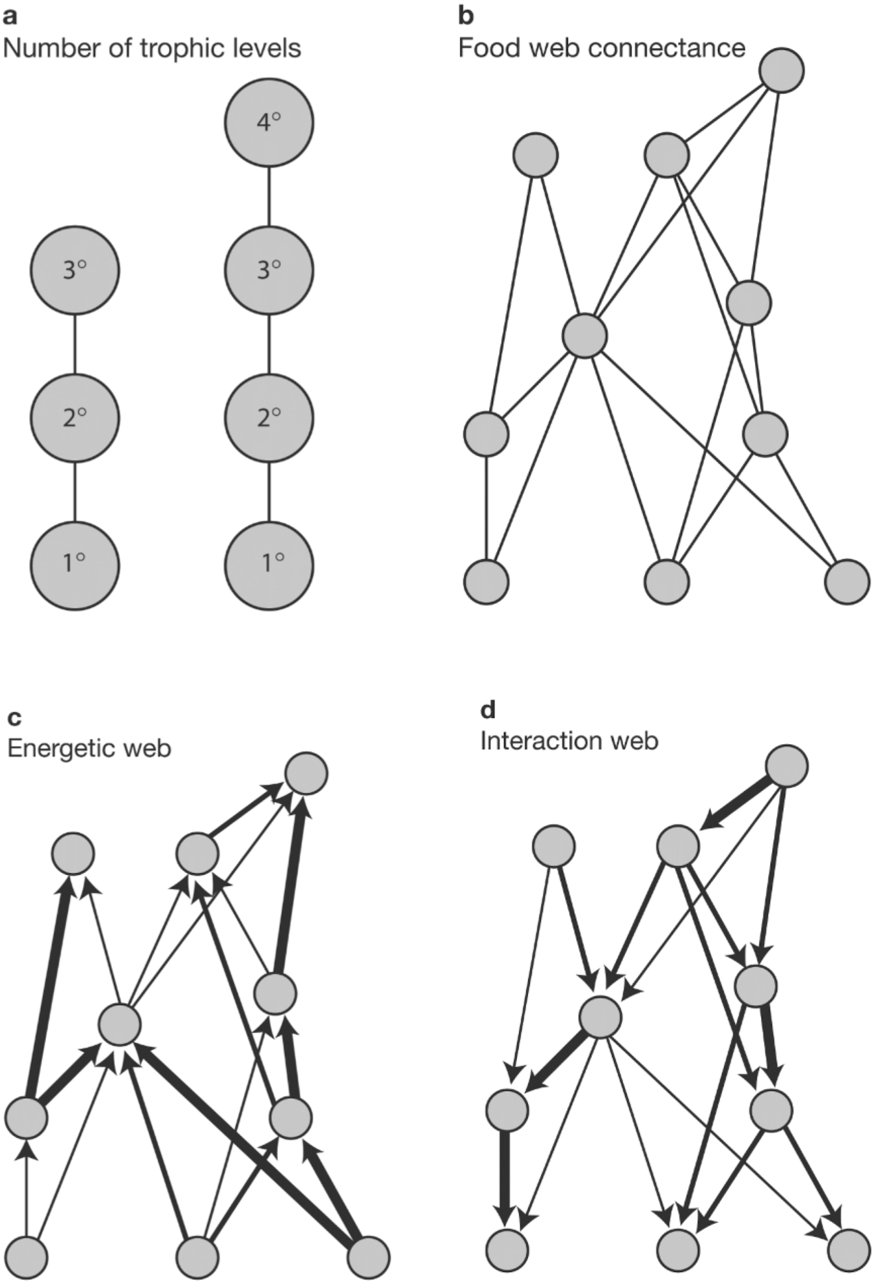

Figure 11-1. Different meaning of "trophic structure" used by food web ecologists: (a) number of trophic levels (3 versus 4 levels); (b) food web connectance, the pattern of trophic linkages among species in a complex web; (c) energetic web, depicting the pathways of energy flow; and (d) interaction web, showing the dynamically important food web linkages.

and Harris 2001). Structural and functional approaches are not mutually exclusive, and food web-based targets may incorporate both components. This chapter examines how food web theory and food web concepts more generally contribute to the planning, implementation, and evaluation of ecological restoration.

Relevant Theory—A Historical Overview

This section provides a brief overview of food web ecology from a historical perspective. For more in-depth background reading, we refer the reader to Montoya (2006); Polis and Winemiller (1996); Polis et al. (2004); McCann (2012); Schoener (1989); and De Ruiter (2005).

Published food web diagrams date back to at least 1880 and the work of Lorenzo Camerano (Cohen 1994). Early food web diagrams based feeding relationships on a diverse range of sources, including scientist intuition. Nevertheless, these abstractions were invaluable for the development of ideas about the direct and indirect interdependence of organisms (Elton 1927). In his classic book *Animal Ecology*, Elton (1927) presented food webs ("food-cycles") as collections of vertically size-structured food chains, whereby links represented feeding interactions. Elton also stressed the idea that abundance in food webs is a pyramid of numbers in which animals at the base of the food chain are more abundant than those at the top.

Lindeman's study (1942) of a small Minnesota lake marked a next major advance in food web ecology. Lindeman viewed the lake biota as a chain of energy transformations—energy was "produced" via photosynthesis, a portion was converted to herbivore biomass, and transfers continued on up the food chain (Lindeman 1942). Production decreased at successive trophic levels due to metabolic inefficiencies at each trophic link. In this view, primary production limited higher trophic level production, suggesting 'bottom-up control of the distribution of biomass in food webs (fig. 11-2a). This work provided the operational structure for modern food web research by introducing the concept of trophic levels and the use of energy as a currency. One implication of this work was that available energy could limit the number of trophic levels (Pimm 1982; Power 1992), an idea that can serve as a basis for assessing whether the energetic needs of higher consumers are likely to be met within a restored ecosystem. Lindeman's ideas also raise the issue of whether variables such as food chain length provide meaningful restoration endpoints.

Two decades later, Hairston et al. (1960) argued that terrestrial food chains have three functional trophic levels—predators keep herbivores in check, thus allowing plant biomass to accumulate. The top-down perspective offered by Hairston et al. (1960) was predicated on the idea that predators control the abundance of

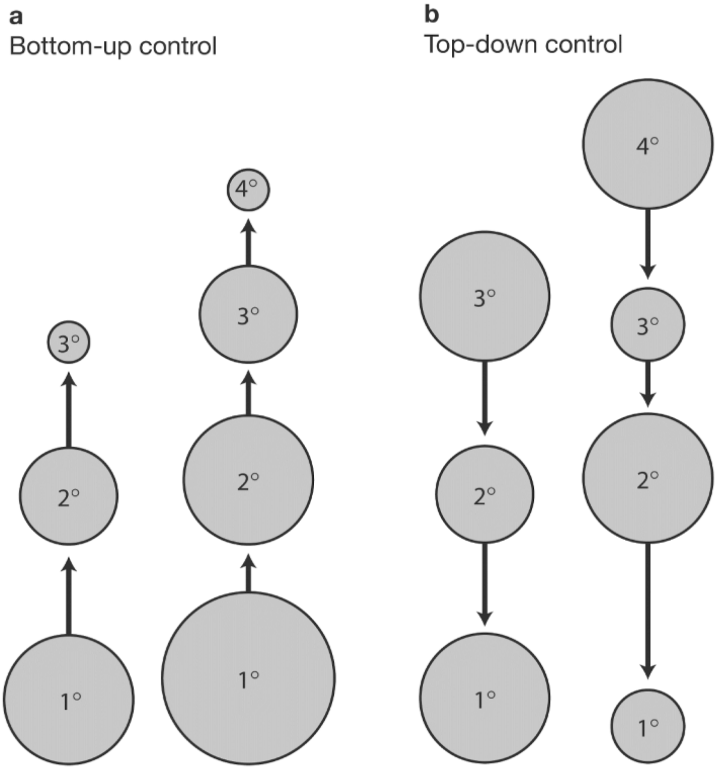

Figure 11-2. Bottom-up versus top-down control of the distribution of biomass at different trophic levels. Note that compartment size indicates trophic level biomass: (a) In the case of bottom-up control, primary production is the basis for higher trophic levels. Increasing primary production allows higher biomass at subsequent trophic levels, and possibly the support of additional trophic levels. (b) In the case of top-down control, predation plays a role in determining the distribution of biomass across trophic levels. In a three-level system, herbivores (2°) are suppressed by predators (3°), which allows accumulation of plant (1°) biomass. Addition of 4° controls the biomass of 3°. As a result, herbivore biomass (2°) increases, leading to a reduction in plant biomass (1°).

their prey, and that these effects subsequently cascade down food chains to impact primary producers (fig. 11-2b). This proposition ran counter to the dominant paradigm that nutrients and/or environmental factors limited plant communities and biomass, which, in turn, constrained higher trophic levels (compare fig. 11-2a, b). Hairston et al. (1960) has since inspired research directed toward the role of predators and resources as determinants of the abundance of trophic levels in a variety of ecosystem types (Polis and Strong 1996; Schmitz 2010). To illustrate, if top-down factors dominate, removal of predators from a three-level system should produce an increase in herbivore biomass, and a decrease in plant biomass. Alternatively, if removal of predators does not cause an increase in herbivore biomass, this indicates bottom-up control, and we might expect that increasing plant productivity would produce an increase in herbivore and predator biomass.

Simple food chain models have played an important role in ecology by generating testable predictions and are often consistent with observations from natural systems (Terborgh and Estes 2010). However, trophic levels can also be heterogeneous, and the addition of grazers to a system may cause a compensatory shift toward grazer-tolerant plants rather than an overall biomass reduction (Leibold 1989). Interestingly, descriptive food webs focusing on network structure offer the paradoxically different view that food webs are immensely complex—with hundreds of species and trophic links, rampant omnivory, and intraguild predation (Dunne et al. 2002; Bascompte 2009). Moreover, the prevalence of behavioral or "trait-mediated" interactions highlights the power of nonconsumptive effects (e.g., fear of predators) in food webs (Schmitz 2010). Although food chain models undoubtedly simplify trophic interactions, they are often useful, and it is important to consider when and whether additional complexities are important in driving system dynamics.

One way that food web theory has built on the food chain concept is through the study of subsets of interacting species within a system. In the rocky intertidal, Robert Paine's (1966) seminal food web experiments demonstrated that predation by the Ochre sea star (*Pisaster ochraceus*) on competitively dominant prey reduced competition for space, thereby allowing persistence of inferior competitors. This work highlighted the role of predators in maintaining prey diversity by mediating interspecific competition (fig. 11-3a). Paine labeled *Pisaster* a keystone species due to its role in structuring the community. The implication was that a few species play central roles in structuring ecosystems (Lawton 2000).

The question of what governs the stability of ecosystems has long been a key motivating question in ecology (Elton 1927). Early food web studies depicted relatively static interactions among organisms that were presumed to fluctuate near equilibrium. Today our view of food webs is more dynamic in both the nature of interactions and the consequences of these interactions for organisms. Although ecosystems often persist in a specific state for long periods of time, it is also recognized that shifts in species interactions can lead to rapid and potentially undesirable changes in ecosystems (chap. 2). Furthermore, positive feedbacks can make systems resilient against attempts to reverse these undesirable changes (Scheffer et al. 2001; Suding and Hobbs 2009). Indeed, restoration ecologists have written extensively about the role that feedbacks play in restoration design—often the actions needed involve reinforcing or weakening a feedback in order to shift the system toward the more desirable state, for example, Zedler (2013).

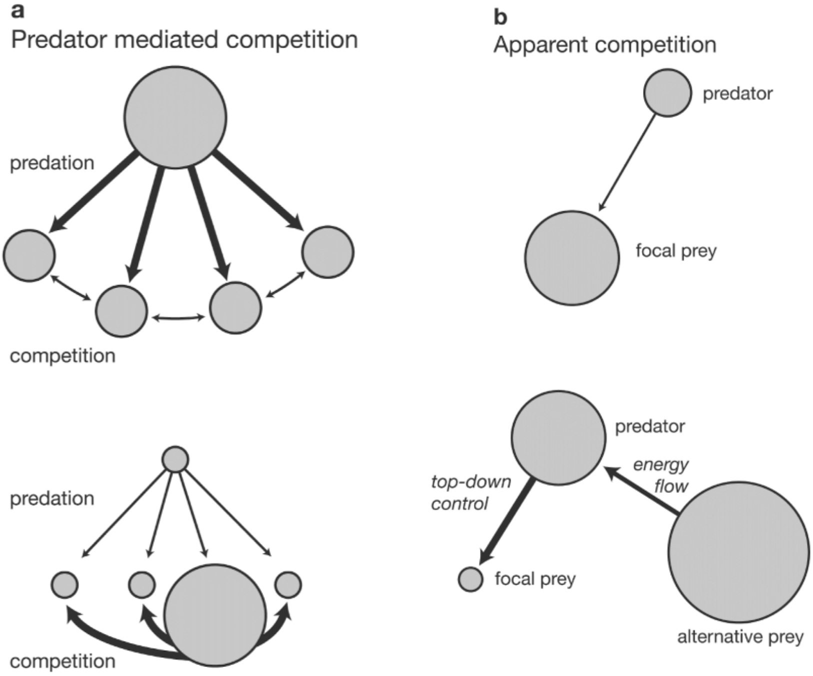

Figure 11-3. Examples of complex food web interactions. Upward arrows represent energy flow pathways; downward arrows represent top-down control. Arrow width represents the strength of the trophic linkage. (a) Predator-mediated competition. High-predator biomass suppresses densities of prey taxa, reducing competition among prey. Reduction of predator biomass allows increased prey biomass, thereby increasing competition among prey and domination by the superior competitor taxa. (b) Apparent competition. The predator consumes the focal prey (top panel). Addition of a highly productive alternative prey increases predator biomass, causing greater predation rates on the focal prey than in the absence of alternative prey (bottom panel). The consequence is elevated predator biomass and decreased biomass of focal prey.

The diversity-stability debate is a well-known research theme related to food webs (McCann 2000). Early studies noted that species-poor ecosystems were more likely to undergo severe fluctuations. For example, monocultures appear more susceptible to pest outbreaks, and islands are more susceptible to species invasion (Elton 1958). These observations led to the conventional wisdom that more species and more complex food webs beget stability (MacArthur 1955). In contrast, May (1973) found that species-rich mathematical food web models were less stable than simple models, thereby challenging ecologists to more carefully consider how food web configuration affects stability (Rooney and McCann 2012). Recent research considers the importance of interaction strengths. Theory suggests that weak food web interactions can dampen oscillations among strongly interacting organisms (Rooney and McCann 2012). Understanding the connections between food web structure and stability remains an active area of research that has relevance for ecological restoration (McCann 2000; Thebault and Fontaine 2010; Saint-Béat et al. 2015).

Application of Food Web Theory to Restoration Ecology

Restoration ecology has historically been based on a succession-driven, bottom-up view of ecosystems that has not generally incorporated food web perspectives. Even if restoration targets do not specifically involve the reestablishment of trophic linkages per se, there may be value in food web approaches because the dynamics of any species or community depend critically on interactions within and among prey and predators.

Food Chain Approaches

The loss of apex predators from aquatic and terrestrial environments is perhaps one of humanities most pervasive influences (Estes et al. 2011; Ripple et al. 2014b). Numerous studies demonstrate that changes at the top of the food web can have powerful cascading effects, with implications for process, function, and resilience of ecosystems (Estes et al. 2011). Top-down effects and predation are widely recognized as key processes in the maintenance of biodiversity and ecosystem function (Terborgh and Estes 2010; Estes et al. 2011), highlighting the value of restoring or maintaining predation regimes as a component of ecological restoration. Below, are several examples where ecosystem restoration was viewed through the lens of a food chain model.

The importance of simple food chain interactions in ecosystem restoration has been well described for aquatic ecosystems. Human-induced eutrophication caused by nutrient loading is a critical problem affecting lakes, resulting in algal blooms, oxygen depletion, and loss of submersed aquatic vegetation (Carpenter et al. 1998). Although nutrient reductions are an obvious approach for improving water quality, food web manipulations can also play a role. The trophic cascade hypothesis was conceived to explain unexplained variance in relationships between nutrient levels and phytoplankton (algae) biomass in lakes, by postulating that changes in predator abundance can "cascade" down the food chain to affect phytoplankton (Carpenter et al. 1985). This realization led to the use of biomanipulation, particularly piscivorous (fish-eating) fish stocking as a lake restoration tool (Hansson et al. 1998). Temperate lakes generally function as four trophic level systems comprising phytoplankton, zooplankton, planktivorous fish, and piscivorous fish (Carpenter et al. 1985). Protecting or augmenting populations of piscivores can reduce planktivore biomass, releasing zooplankton from predation, thereby increasing zooplankton grazing rates and decreasing algal biomass. One important way that humans may have amplified the effects of eutrophication has been the reduction of piscivorous fishes due to overfishing and habitat alteration (Post et al. 2002). Along these same lines, restoration of filter-feeding bivalves and oyster reefs offer a means of improving water quality (Beck et al. 2011; Gedan et al. 2014).

In Atlantic Coast salt marshes, predation has traditionally been assumed to be unimportant in regulating marsh plant (*Spartina*) productivity. This view has been challenged by work in mid-Atlantic U.S. marshes demonstrating an important role of periwinkle (*Littoraria*) herbivory in regulating *Spartina* production and biomass (Silliman and Bertness 2002). This suggests that efforts to restore salt marsh communities may benefit from not only restoring hydrology and improving abiotic conditions for plant growth (i.e., nutrient enhancements), but may also be hastened by efforts to manipulate food webs or by tolerating the spread of nonnative predators (green crabs) that prey on marsh grass herbivores (Bertness and Coverdale 2013). For example, augmenting or protecting blue crabs, a major predator of *Littoraria*, appears to benefit *Spartina* restoration efforts (Silliman and Bertness 2002).

The importance of food chain dynamics are being revealed for terrestrial systems (Ripple et al. 2014b). The rapid suburban development in coastal canyons of southern California has diminished and fragmented natural habitats. The mesopredator release hypothesis was proposed to explain the dramatic decline of scrub-breeding birds in these fragments. Crooks and Soulé (1999) reported that coyotes (*Canis latrans*), the top predator in the system, have been extirpated from all but the largest habitat patches. Sites lacking coyote support large numbers of mesopredators (raccoon, grey fox, striped skunk, opossum, domestic cat), which are effective predators on birds and other small vertebrates. An increase in abundance of mesopredators following coyote extirpation in habitat patches explains the recent avifauna declines in these habitat fragments. Based on this work, efforts to restore the avifauna would benefit from managing bird predators, perhaps in combination with efforts to improve bird habitat.

Reintroduction of wolves (*Canis lupus*) into the Greater Yellowstone Ecosystem in the 1990s provided unique insights into the role of food web interactions in structuring the ecosystem. Riparian ecosystems in the Greater Yellowstone Ecosystem (and much of the western United States) have undergone declines over the past century (Beschta and Ripple 2009). An important aspect of this decline has been the recruitment failure of riparian trees such as native cottonwoods and aspens. While a number of explanations have been examined, food web interactions appear to play a key role in maintaining riparian vegetation structure (Beschta and Ripple 2009; Painter et al. 2015). Wolves were extirpated from Yellowstone in the 1920s, which coincided with riparian tree recruitment failure. The reintroduction of wolves has reduced abundance and altered the foraging behavior of elk (*Cervus canadensis*). Woody plants are now recovering from past unimpeded browsing by herbivores (Beschta and Ripple 2009; Painter et al. 2015). Regeneration of riparian vegetation is having far-reaching implications for the broader ecosystem, including increases in beaver, bison, and avifaunal communities (Ripple and Beschta 2012). Reduction of elk has also led to an increase in berry-producing shrubs, which appears to be benefitting grizzly bears (Ripple et al. 2014a). Finally, there are consequences for aquatic ecosystems, including stabilization of streambanks and strengthened linkages between riparian and riverine habitats (Beschta and Ripple 2012).

Complex Interactions

The above examples illustrate how simple food chains provide useful models for informing ecological restoration. Yet chain-like interactions do not accurately describe many systems, which are often considerably more complex. Here we illustrate the value of recognizing predator-mediated competition (fig. 11-3a) and apparent competition (fig. 11-3b) in a restoration context. In addition to food webs being complex, energy and nutrients also move across habitat boundaries, and can have important dynamic implications (Polis et al. 2004; Richardson and Sato 2015). Top-down control can be dampened or reinforced by resource subsidies from outside the focal habitat, which can cascade to lower trophic levels (Baxter et al. 2005; Richardson and Sato 2015). Recognition of the importance of landscape context and cross-habitat linkages represents an important conceptual shift in food web ecology, with implications for the provisioning of ecosystem services and ecological restoration (Richardson and Sato 2015).

An example of apparent competition in natural systems is the introduction of the brown tree snake (*Boiga irregularis*) to Guam (Savidge 1987). This introduction has caused the near complete elimination of the island avifauna. A simple predator-prey (snake-bird) model would predict snake populations to decline following local extirpation of the avifauna. But *Boiga* are generalist predators, readily consuming alternative prey such as small mammals and lizards. Because of this, *Boiga* has maintained high population densities, even after eliminating bird populations. In effect, the availability of alternative prey sustained high *Boiga* populations through the avifaunal crash, thereby preventing avifaunal recovery.

Islands provide strong evidence for the importance of food web interactions when conducting ecosystem-level restoration. The eight California Channel Islands off the coast of southern California have been the subject of intensive restoration efforts. During much of the nineteenth and twentieth centuries, Santa Cruz Island supported nonnative populations of cattle, sheep and pigs, which adversely impacted the native plant community. Restorationists initiated a program to eradicate cattle and sheep. Following the decline of these two nonnative herbivores, European fennel (*Foeniculum vulgare*) rapidly became the dominant plant species on the island (Zavaleta et al. 2001). This improved the plant forage base for feral pigs, resulting in an increase in pig numbers. Feral pigs have subsequently devastated native plant communities as a result of their digging and grubbing (Power 2001). These interactions would not have been predicted from a simple herbivore-plant model, as they involve direct and indirect interactions among a mix of native and nonnative plants and herbivores.

Food web interactions involving predators on Santa Cruz Island also have restoration significance (Roemer et al. 2001; Roemer et al. 2002). Santa Cruz Island historically supported two carnivores—the endemic (and endangered) island fox and the island spotted skunk. Introduction of feral pigs in the mid-nineteenth century expanded the prey resource base, ultimately allowing the island to be colonized by golden eagles from the mainland. Golden eagles became significant fox predators, and the endemic island fox declined dramatically (Roemer et al. 2002). In turn, skunk populations increased due to competitive release from island fox. Recognizing these more complex food web interactions was key to the subsequent restoration of these island ecosystems (Knowlton et al. 2007). Ultimately, both pigs and eagles had to be removed to allow recovery of the endemic island fox (Collins et al. 2009).

Melero et al. (2014) cautions that restoration of multiple-invaded ecosystems should explicitly consider the interactions between nonnative predators and prey. Following escape from fur farms, American mink (*Neovison vison*) are now established in many areas outside of North America. Crayfish comprise a large portion of mink diets, and mink often reach higher population densities in areas with high invasive crayfish densities. The authors argue that mink will be harder and more costly to eradicate in areas where consumption of nonnative crayfish elevates mink densities. The authors recommend use of information on interactions among nonnative species in the planning of restoration and ecosystem management.

Spatially Linked Food Webs

Because islands are isolated, they tend to be free from the heavy influence of landscape context that can complicate restoration at mainland sites. In addition, islands are conducive to whole-ecosystem experimental approaches to restoration, allowing comparisons between experimental and reference ecosystems (Donlan et al.

2002). Yet the majority of restoration projects occur on mainland systems, meaning that restoration sites are not isolated, but rather are nested within a broader landscape context (Ehrenfeld and Toth 1997). For example, while the boundaries of a wetland restoration site may be easily delimited, this target ecosystem is connected in diverse ways to its surrounding landscape. Nutrients and consumers may be imported or exported from the wetland via streams, while mobile consumers (mammals, birds, insects) move across the wetland boundary. Consumers may be dependent on the restoration site to satisfy some needs, and areas outside the restoration site for others (i.e., feeding grounds, reproductive areas, refuge from predators). While resource managers may have some control over what happens within the boundaries of the restoration site, the broader linkages to the surrounding landscape are likely beyond their control. A food web approach recognizes linkages beyond the boundaries of the restoration site, and includes the broader landscape and ecosystem context of ecological restoration (Ehrenfeld and Toth 1997; Richardson and Sato 2015).

A dramatic example in which the dynamics of distinct habitats are linked by mobile consumers is that of snow geese (*Chen caerulescens*), which migrate between arctic breeding grounds in Canada and wintering grounds in the central United States. (Jefferies 2000; Jefferies et al. 2004). Intensification of agriculture and fertilizer use in the central United States during the past century has shifted snow geese wintering grounds from coastal marshes to agricultural areas. This has subsidized snow goose populations, allowing a 5% annual increase in the population. The effects of this population explosion are readily evident in the coastal breeding habitats around Hudson Bay, Canada, approximately 5,000 km from their winter feeding grounds, producing what has been described as a spatially subsidized trophic cascade (Jefferies et al. 2004). Goose overabundance has intensified grazing and grubbing in breeding grounds. Local impacts range from decreased plant cover and productivity, to the transformation of intertidal salt marshes to bare mudflats—a process involving positive feedback mechanisms analogous to that of desertification (Jefferies 2000; Jefferies et al. 2004). Subsequent changes in ecosystem processes, as well as increased reproductive success of arctic foxes (Giroux et al. 2012), and declines in bird and insect communities have been documented (Jefferies et al. 2004). Restoration of breeding ground habitat would likely necessitate wholesale changes in agricultural management practices in the United States, an unlikely prospect considering the remoteness of the impacted habitat and the vast spatial separation between the two areas. This is a clear example of how the dynamics of spatially separated habitats can be linked (chap. 4), and highlights the need to better understand landscape-level food web linkages (Polis et al. 2004).

In agricultural systems, arthropod predators such as lady beetles, wasps, and spiders are important mobile consumers. The essence of biological control of insect pests in forest or agricultural systems relies on predators inducing trophic cascades to increase crop yields. Yet, modern agricultural landscapes are often dominated by large expanses of intensively managed annual crops, where it can be difficult for predators to maintain adequate populations to suppress pests (Tscharntke et al. 2012). Restoration of nonagricultural ("natural") habitats as reservoirs for predators in the landscape (Landis et al. 2000) relies on the concept that food webs in unmanaged, nonagricultural areas are linked to agricultural habitats through the movement of mobile predators. In sum, restoration of ecosystem services such as biological control or pollination in agricultural landscapes can be enhanced by understanding the factors that affect landscape-level food webs linkages (Dreyer and Gratton 2014).

Invasions and Reintroductions

Biological invasions are of global concern because of mounting economic and ecological costs (Lodge et al. 2006). Nonnative species can pose major barriers to achieving restoration goals, which are often focused on native species and communities. Yet with accumulating numbers of introduced species, eradication may not be compatible with restoration goals due to food web interactions involving native and nonnative species (case study box 11-1). In addition, nonnative species are not always considered harmful. In the Laurentian Great Lakes, nonnative species have adversely affected native biodiversity, though food chains comprising introduced species now support valuable sport fisheries, and the native predators in these systems are reliant on nonnative prey (Eby et al. 2006). Indeed, nonnative species are sometimes used for achieving desired restoration goals and providing ecosystem functions (Schlaepfer et al. 2011). This does not negate the adverse impacts of invasive species, and reliance on nonnative species warrants thoughtful consideration of costs, benefits, and other constraints to restoration (Schlaepfer et al. 2011).

Once established, many undesirable invasive species are difficult to control since they tend to be *r*-strategists, with high reproductive rates, broad environmental tolerances, and high dispersal abilities (Elton 1958). In addition, systems subject to anthropogenic disturbance, the very sites that often require restoration, tend to be more invasible (Chytry et al. 2008). Invasive species may themselves be an agent of disturbance that can promote further invasions, leading to what has been termed invasional meltdown (Simberloff and Von Holle 1999; chap. 8). A meta-analysis evaluating interactions among invasive animals highlighted the fact that combinations of invasive species can interact to either amplify or mitigate each other's impacts in ecosystems (Jackson 2015). The challenges that invasive

Case Study Box 11-1
Invasive Species on Islands
Apparent Competition and Hyperpredation

Oceanic Islands: The native biota of many island ecosystems evolved in the absence of strong competition and predation, and as a result, islands are often rich in endemic species. Consequently, these insular systems tend to be deeply affected by introduction of nonnative species, particularly mammals. Conventional wisdom would suggest that the undesired invasive should simply be controlled as a part of ecological restoration. Yet addition of these invasive species can lead to complex food webs comprising a mix of interacting native and invasive species spanning multiple trophic levels. This creates opportunities for unexpected consequences of invasive species management and control.

Supporting theory: Apparent competition

Bob Holt and colleagues (1977; 1994) greatly advanced the theory of apparent competition, defined as two species interacting indirectly through a shared common predator. As an example, consumption of prey A benefits the predator, thereby leading to increased predation rates on prey B.

Expected outcomes and progress: Numerous studies have highlighted the role of complex interactions such as apparent competition in ecological restoration. Smith and Quin (1996) found that declines of Australian island-dwelling mammals were most severe on islands containing both nonnative predators (cats, foxes) and nonnative prey (rabbits, mice). To explain this, they suggested "hyperpredation," whereby nonnative predators were maintained at high levels due to consumption of nonnative prey, thereby increasing predation on native prey. There have since been several examples: introduction of feral pigs increased predation by native eagles on an endangered fox in the California Channel Islands, and introduced rabbits increase mammal predation on native dryland lizards in New Zealand. Apparent competition and other complex food web interactions are increasingly considered as a factor in species endangerment, and for conservation efforts more broadly.

References: Holt 1977; Holt and Lawton 1994; Smith and Quin 1996.

species pose for large-scale restoration efforts is well illustrated in the Columbia River Basin where recent calls have suggested that it would be prudent to identify and maintain the most productive and resilient food webs (i.e., those food webs with the capacity to buffer and recover from mild perturbations). Such food webs may contain both native and nonnative species that collectively retain function, productivity, and resilience into the future (Naiman et al. 2012).

Several salmonid species have been widely introduced throughout the world. These species have generally been viewed as "desirable" nonnatives since they provide valuable recreational fisheries. As the broader ecosystem and food web consequences of these introductions have been documented, this perspective is shifting toward a more cautious view of nonnative salmonid introductions (Cucherousset and Olden 2011). A notable example of food web interactions involving nonnative salmonids and native species in a restoration context can be seen in the Colorado River below Glen Canyon Dam in the southwestern United States. The population size of the native humpback chub (*Gila cypha*) has declined precipitously due to multiple factors, including predation by introduced rainbow trout (*Oncorhynchus mykiss*). Stable isotope and dietary studies suggest that suppression of nonnative trout should have a positive effect on native fishes (Whiting et al. 2014). In response, restoration efforts have focused on the removal of rainbow trout and other nonnative fishes, which corresponds with increased survival and recruitment of juvenile native fishes (Coggins et al. 2011).

Although salmonids are common nonnative species, these same trout species are sometimes endangered or extirpated in their native range due to loss of habitat, water quality degradation, exploitation, obstructions to migration, and nonnative species (Gustafson et al. 2007). Not only are trout viewed as "sensitive," but theory indicates that extinction risk increases with body size and trophic level, and that top predators are vulnerable to harvest and habitat degradation (Pimm 1991), making them particularly difficult to recover or reestablish (Neubauer et al. 2013). Indeed, for a species reintroduction to succeed, reintroduced individuals must survive at low population levels, and successfully reproduce in spite of predators, competitors, and pathogens. Although these are the same challenges faced by invasive species, this highlights the need to better understand food web interactions involving nonnative and native species in the context of ecological restoration.

Human alteration of physical processes in ecosystems may also have important food web implications. Restoring or maintaining natural flow regimes is critical for maintaining the integrity of riverine ecosystems (Poff et al. 2010). In Pacific Northwest rivers, human alteration of stream flow patterns has disrupted food web interactions. In response, there has been interest in how linkages between flood disturbance and food chain length in rivers could guide the restoration of riverine food chains (Power et al. 1996), though food web concepts have not been widely applied to stream restoration (Lake et al. 2007). In unregulated streams in the southwestern United States, the natural flooding regime has allowed the continued persistence of native fishes, despite the presence of nonnative predatory fishes (Gido et al. 2013). Similarly, the occurrence of seminatural flow regimes in dammed rivers during high precipitation years resulted in greater dominance of native fishes. Recognition that natural flow regimes promote the persistence of desired native species has been the basis for many large-scale flow releases on the Colorado River and elsewhere around the world (Olden et al. 2014)

Food Web Assembly

Ecological communities are not static entities, but rather are dynamic in composition (chap. 2). Community ecologists have examined whether ecological assembly rules and the order of species introductions govern the composition of ecological communities (chap. 9). Relatively few studies have examined food web assembly involving interacting species across several trophic levels (Thornton 1996), and more generally, a lack of empirical and observational studies has hindered our understanding of food web assembly (Fahimipour and Hein 2014). Simulation models of food web assembly have been equivocal with regard to how food web complexity influences resistance to invasive species (Drake 1990b; Lurgi et al. 2014).

Microcosm studies generally find that changing the sequence of species introduction can produce very different community outcomes (Robinson and Dickerson 1987; Drake 1990a). For example, a species that is competitively dominant under one set of circumstances may be unable to establish given a different assembly scenario (Drake 1990a). Further, mesocosm experiments have found that arrival order can influence the flux of material through different trophic pathways—an important component of ecosystem function. Assembly of grassland food webs was found to be regulated by both spatial conditions and trophic relationships (Harvey and MacDougall 2014). Generalist guild establishment was more dependent on spatial isolation of patches whereas specialists tend to establish in larger patches with more diverse plant communities. Though the applicability of food web assembly to ecosystem restoration efforts remains uncertain, this work suggests that species diversity, food web connectivity, and introduction sequence are likely to be important considerations (for more on assembly theory, see chap. 9).

An example of food web assembly concepts being incorporated into ecological restoration involves lake restoration efforts in Ontario, Canada. Following the successful control of industrial sulfur emissions in the region, lake pH has improved to levels (pH > 5.5–6.0) capable of supporting top predators such as lake trout (*Salvelinus namaycush*) and smallmouth bass (*Micropterus dolomieu*). The success of predator reintroduction has been examined in acid-recovering Ontario lakes. Trout recovered rapidly in lakes with few fish species, while in species-rich systems, lake trout were slow or unable to reestablish. This suggested that community attributes or reintroduction order (priority effects) played a role in the recovery of this species. In contrast, reintroduced smallmouth bass established rapidly, regardless of community composition (Snucins and Gunn 2003). Smallmouth bass have well-documented predatory impacts on forage fishes and adverse competitive impacts on lake trout (Vander Zanden et al. 1999). Restoration of fish assemblages in these lakes will require further attention to priority effects and the order of species reintroductions. In acid-recovering lakes, lake trout should be reintroduced early in the reassembly process (Snucins and Gunn 2003), although such a strategy may limit the subsequent chance of successfully establishing native prey fishes that are vulnerable to lake trout predation.

New Food Web Tools and Ecological Restoration

A common goal in restoration ecology is to reestablish impaired or lost functionality in ecosystems. Species are essential building blocks of communities, and reestablishing their interactions is critical to restoring function to degraded ecosystems (Gray et al. 2014). Restoration of food web interactions is a potential restoration goal that incorporates aspects of ecosystem structure and function and is starting to be used as a restoration monitoring tool (Wozniak et al. 2006; Kovalenko et al. 2013). Thus, in addition to monitoring for the presence or absence of species, identifying what critical interactions need to be restored and whether this has occurred is increasingly recognized in restoration ecology. Unfortunately, identifying species interactions is challenging, especially in species-rich communities, or when organisms have cryptic life stages (e.g., parasites). As a result, indirect approaches to elucidating trophic interactions are becoming widespread and can provide insights on the nature, diversity, and strength of interactions among species (Traugott et al. 2013).

Use of stable isotope techniques to infer trophic flows in food webs is widespread (Peterson and Fry 1987). Ratios of stable isotopes ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) vary predictably from resource to consumer tissues. Differences in plant $\delta^{13}C$ are preserved in consumer tissues, such that $\delta^{13}C$ is an indicator of the sources of carbon in food webs. In contrast, protein biosynthesis and catabolism tend to excrete the lighter N isotope, resulting in a 3%–4‰ enrichment of $\delta^{15}N$ from prey to predator. Nitrogen isotopes are used to infer trophic position of consumers (Vander Zanden and Rasmussen 2001).

Stable isotopes provide a powerful tool for monitoring and evaluating food web linkages, greatly facilitating the incorporation of food web approaches into restoration ecology (Wozniak et al. 2006; Kovalenko et al. 2013; Howe and Simenstad 2015). For example, Gratton and Denno (2006) used stable isotopes to monitor arthropod food webs in New Jersey salt marshes that had been restored to *Spartina* following the extirpation of invasive *Phragmites*. The trophic position of most consumers including the top predatory spiders were indistinguishable from those in reference *Spartina* habitats with no history of *Phragmites* invasion (fig. 11-4), indicating that trophic interactions among arthropod consumers had been largely reestablished in restored habitats in less than five years. Stable isotope data suggested that consumers used resources primarily from the habitat where they

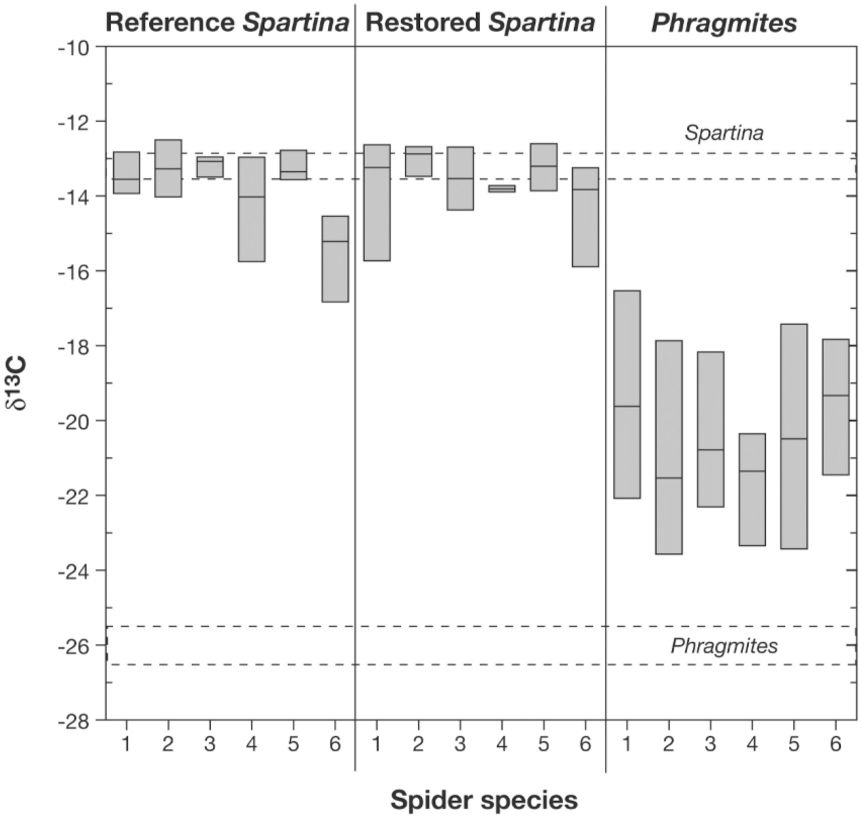

Figure 11-4. δ^{13}C stable isotope box-plot (median and interquartile range) of dominant spider predators from reference *Spartina*, restored *Spartina*, and *Phragmites*-dominated habitats within the Alloway Creek Watershed Restoration site (Salem County, New Jersey, US). Dotted lines indicate the ranges of the basal resources (*Phragmites* or *Spartina*) in each habitat. Spiders in restored habitats are feeding on *Spartina*-based resources (herbivores and other predators) and are indistinguishable from the same species found in reference habitats while *Phragmites*-collected spiders are feeding on non-*Phragmites* based resources, likely detritivores. Spider species are (1) *Tetragnatha* sp.; (2) *Pachygnatha*; (3) *Grammonota trivittata*; (4) *Hentzia* sp.; (5) *Clubiona* sp.; (6) *Pardosa* sp. Based on Gratton and Denno (2006).

were collected, and that as habitats were restored, predators integrated into local food webs.

Stable isotopes have been used to assess the restoration of southern California salt marshes (Kwak and Zedler 1997). Marsh-derived algae and vascular plants, particularly *Spartina*, are important energy sources for invertebrates and fish (Kwak and Zedler 1997; Desmond et al. 2000), supporting the idea that these habitats should be managed as a single ecosystem. Mitigation and restoration projects in southern California coastal areas have focused either on the creation of basin or channel habitat for fishes, or alternatively, the creation of coastal salt marshes as habitat for endangered birds. Although both are valid restoration targets, restoration of habitat for fishes and endangered birds may have erroneously been viewed as a competing objective (Kwak and Zedler 1997). Considering the food web linkages between these two habitats, restoration might more productively focus on the creation of integrated channel-tidal salt marsh systems to accomplish both restoration objectives.

Food web approaches are also valuable for assessing the restoration potential of freshwater ecosystems. Vander Zanden et al. (2003) characterized historical food web changes in Lake Tahoe (California, US) using stable isotope analysis of contemporary and preserved museum specimens. The introduction of nonnative freshwater shrimp (*Mysis relicta*) and lake trout disrupted pelagic food web structure. These two nonnatives are thought to limit the restoration potential of native Lahontan cutthroat trout (*Oncorhynchus clarkii henshawi*) in Lake Tahoe. Food webs in two nearby headwater lakes are relatively intact despite some nonnative species introductions, and stable isotopes indicate that food webs in these lakes resemble that of Lake Tahoe prior to nonnative species introductions (Vander Zanden et al. 2003). These relatively unaltered lakes are ideal candidates for Lahontan cutthroat trout reintroduction, and provide an opportunity to examine whether historical food web niches are regained when species are reestablished (Vander Zanden et al. 2003). The above studies demonstrate the value of stable isotopes as a tool for documenting how food webs have been altered, identifying energy sources for key species, and assessing food web recovery as systems move along restoration trajectories. Newer approaches such as compound-specific stable isotope analysis appear to be more accurate and robust to assumptions for inferring trophic position and hold great promise in the analysis of food web structure (Chikaraishi et al. 2009).

The molecular revolution has made DNA-based techniques more available to ecologists for reconstructing the diets of consumers (Pompanon et al. 2012; Clare 2014). By amplifying genes that are common to a range of potential prey, for example, insects prey for bats (Clare et al. 2011), and comparing sequences to existing DNA libraries of known species, it is possible to reconstruct the presence or absence of particular species within the diet of a consumer. These approaches are becoming more widespread and provide insights into the feeding associations of insects on plants (García-Robledo et al. 2013), predators on prey (Piñol et al. 2014), parasites on hosts (Hrcek et al. 2011), and pollinator visitation of flowers (Keller et al. 2015). In general, molecular-based approaches tend to identify many more species interactions than were previously recognized, forcing us to fundamentally reconsider how food webs are structured (Wirta et al. 2014). One key limitation of these approaches is that they tend to reveal the presence-absence of interactions. This makes it challenging to understand the relative importance of food web links, though semiquantitative methods (e.g., the proportion of individuals that feed on a particular diet item) can be used to infer the energetic importance of food web links (Clare 2014). Despite some limitations, the novel insights provided by molecular methods can complement traditional approaches and provide a more complete picture of food web.

Areas of Research Need and Opportunity

While the field of ecological restoration builds on key areas of ecological theory such as community succession, population biology, and alternative stable states, other areas, including food web ecology, are only now being integrated into ecological restoration (Memmott 2009; Montoya et al. 2012). In this chapter, we have discussed how consideration and understanding of food webs can contribute to ecological restoration. Here, we identify some of the challenges and opportunities likely to be encountered in the application of food web ecology to ecological restoration.

Food Web Experiments and Adaptive Management

In some ecosystems, predation is critical in structuring ecosystems, while in other ecosystems habitat and resource availability drive ecosystem dynamics. How can we identify ecosystems in which predation and top-down forces are important for structuring the food web? Experimental manipulations of consumers and resources can be used to examine this, though in many systems the necessary manipulations are not practical or feasible. Observational studies and a “natural history” understanding of a system can provide some basis for identifying what factors are responsible for structuring a food web, though important food web interactions may simply not be apparent without experimentation. In the absence of experimentation, there remains a need to understand whether ecosystems are dominated by top-down (predation) or bottom-up (productivity) forces, how these factors interact, and the role of indirect and other complex food web interactions. The above issues are difficult to resolve because ecological restoration projects are typically carried out at the ecosystem level, while much of ecology is based on small-scale, highly replicated experiments. Can we scale up from small-scale experiments to the management and restoration of real ecosystems? Small-scale experiments suffer from “cage-effects,” whereby the results are artifacts of experimental conditions. Findings cannot be generalized or “scaled up” to real ecosystems. Small-scale approaches are also likely to fail to capture relevant food web processes such as cross-habitat linkages, complex trophic interactions, and the role of mobile predators. One obvious alternative is to conduct large-scale, whole-ecosystem manipulations (Carpenter et al. 1995). Restoration projects provide unique opportunities for whole-ecosystem experiments within an adaptive management, "learning-by-doing," framework (Holl et al. 2003). Such experiments speed the accumulation of knowledge about food webs and the response of ecosystems to management actions, and hasten the application of ecological knowledge to restoration (Donlan et al. 2002). In addition, ecological restoration can improve basic understanding of food webs and inspire new directions in food web theory with more direct relevance to ecosystem management (Palmer et al. 1997).

The Backdrop of Nonnative Species and Global Change

Although the restoration potential of many ecosystems may be high, accelerating species invasions may severely limit prospects for achieving restoration goals (Donlan et al. 2003). Combined with global climate change, it is certain that existing food webs will be torn apart, and new food webs will be reassembled (Lawton 2000). The "rules of engagement" in food webs and ecosystems will change, yielding completely new outcomes and interactions. Restoring ecosystems within the context of the shifting backdrop of climate change and nonnative species seriously confounds the task at hand, necessitating a more complete incorporation of food web, landscape, and ecosystem perspectives. Restoration ecology draws increasingly from the field of invasion biology, and is demanding improved methods for controlling undesirable nonnative species. Perhaps a more critical challenge will be to find ways to manage ecosystems so as to maintain native species and ecosystem services in the face of invasive species. In some cases, reliance on nonnative species may be crucial for promoting restoration of ecosystem services and energy flows to higher trophic levels, and food web approaches will figure prominently into assessing the value and viability of such efforts (Schlaepfer et al. 2011).

Closing Remarks

The study of food webs is a long-standing and rapidly expanding subfield of ecology with the goal of understanding and predicting multispecies interactions. Though ecologists recognize the interconnectedness of species in ecosystems, new tools and new paradigms are allowing advances in our understanding of food web interactions, particularly the role of predation and indirect effects in structuring ecosystems. Restoration of food web interactions may not necessarily follow restoration of the plant community or physical habitat features (i.e., the "field of dreams" paradigm—that is, "build it, and they will come" [Palmer et al. 1997]). While restoration of habitat is critical, it is not guaranteed that the desired consumer taxa will recolonize and food webs will assemble as expected. Invasive species can be a barrier to achieving restoration goals. We present several examples in which food web interactions affect ecosystem attributes, with important implications for ecological restoration. Viewing restoration at the whole-ecosystem level and incorporating a food web perspective can contribute in a real way to ecological restoration efforts. We offer that further advances will derive from restorationists incorporating "food web thinking" into restoration projects, and treating restoration projects as ecosystem experiments (see also chap. 13). Food web ecology has demonstrated the value of more holistic approaches for understanding species and ecosystems, lessons that will undoubtedly contribute toward efforts to restore ecosystems.

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PART III

Ecosystem Processes and Restoration Ecology

Chapter 12

Nutrient Dynamics as Determinants and Outcomes of Restoration

Sara G. Baer

Theory and Application

- Revegetation, managing ecological drivers, changing land use practices, wetland mitigation, and increasing the interaction between flowing water and benthic substrates or riparian ecotones are examples of restoration practices that alter nutrient dynamics.
- Plant nutrient use and plant input-output theory provide a valuable framework for how plants, soil, and their feedbacks influence nutrient dynamics.
- The 'resource ratio hypothesis' and 'fluctuating resource hypothesis' can be used to steer changes in nutrient dynamics that determine restoration outcomes.
- Ecological stoichiometry, progressive nutrient limitation, soil carbon saturation, and nutrient spiraling are key concepts that can be applied to achieve nutrient endpoints of restorations.

Human exploitation of natural resources for energy, the production of fertilizer, species invasions, and land-use change for food, fiber, and urban expansion have altered the global cycling of three elements that comprise a large majority of biomass: carbon (C), nitrogen (N), and phosphorus (P). The combustion of fossil fuels has increased the concentration of CO_2 (carbon dioxide) in the atmosphere, which contributes to global warming (IPCC 2014). Anthropogenic land use change has also altered the global C cycle, with an estimated net loss of 96 Gt of C from ecosystems over the last millennium that has increased atmospheric CO_2 by 20 ppm (Pongratz et al. 2009). Humans have altered the global N cycle by increasing fixation, emissions, and availability of biologically reactive forms of N (Gruber and Galloway 2008). Land-cover change and associated nutrient pol-

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lution from fertilizer inputs, livestock production, and urban activity are major sources of N and P responsible for eutrophication of surface waters (Carpenter et al. 1998) and growing hypoxic zones at the mouths of major rivers (Diaz and Rosenberg 2008). Further, human and livestock demand for P threatens the future of food security because the terrestrial reservoir of P (apatite rock) is finite, globally imbalanced in its distribution, and costly to extract (Elser and Bennett 2011).

Ecological restoration is considered the “low hanging fruit” in mitigating many negative impacts humans have had on global C, N, and P cycling. Land restoration is a means to offset increasing atmospheric CO_2 that is more cost effective, manageable, and lower risk than sequestering liquefied CO_2 geologically, or stimulating the biological pump and transfer of C to the ocean floor (Lal 2008). Furthermore, promoting C sequestration on land improves many other aspects of environmental quality, including nutrient conservation. The link between restoration and C sequestration is of such interest globally that its discussion appears multiple times in this book (e.g., see chap. 13). Wetland restoration is vital for reducing N and P inputs into surface waters (Mitsch et al. 2001), and provides benefits of sediment entrapment, flood control, and biodiversity (Hey et al. 2012). Restoration strategies that promote C sequestration and nutrient conservation in terrestrial and wetland systems, as well as nutrient spiraling (repeated cycles of uptake and mineralization by benthic biota over short distances) in streams, have the potential to help offset many global changes to the C, N, and P cycles. In these ways, nutrient dynamics are endpoints for restoration. Nutrients can also act as determinants of restorations if they prevent achieving restoration goals through inadequate or excess supply. This chapter reviews biogeochemical principles underlying the cycling of major nutrients that are either manipulated to achieve restoration goals or change in response to restoration, and the application of ecological theory to steering nutrient dynamics as determinants and endpoints of restoration. Plant ecophysiology also plays an important role in the cycling of nutrients in soils, as discussed in chapter 6.

Key Principles of Biogeochemistry for Ecological Restoration

Quantitative relationships between C, N, and P exist for many levels of biological organization within an organism, and as a result, variation in biota (e.g., among major taxonomic groups, trophic levels, and species) results in different demands and limiting status of these nutrients in ecosystems (Sterner and Elser 2002). Thus, knowledge of factors influencing inputs, transformations, and outputs of nutrients in restored ecosystems is needed to address how their dynamics act as determinants or endpoints of restoration.

Stoichiometry

The cycling of C, N, and P in ecosystems is influenced by the need for all living things to maintain and synthesize biomass. Molecules, cellular structures, and cells differ in their ratios of C:N:P, which are constrained by limited combinations of elements and how they interact (Sterner and Elser 2002). Stoichiometry describes a quantitative relationship (constrained ratio) between elemental constituents in a chemical substance and when more than one substance makes up a molecule. For example, *C-rich molecules* function largely in energy storage. Fatty acids, lignin, sugars, starches, glycogen, and structural polysaccharides (e.g., cellulose) contain no N or P. An increase in these biomolecules within an organism raises the C:N and C:P ratios without changing the organism's N:P ratio (Sterner and Elser 2002). *Nitrogen-rich molecules* such as amino acids are used to synthesize proteins. Different cellular composition results in varying demands for N among organisms. For example, peptidoglycan in the cell walls of bacteria is 12.7% N (C:N of 2.5), whereas chitin in the cell walls of fungi is 6.9% N, with a C:N ratio more than twice that of peptidoglycan (Sterner and Elser 2002). Nitrogen concentration also varies among plants with different photosynthetic pathways. Plants with the C_3 photosynthesis pathway allocate about 26% of their N to the carboxylating enzyme, ribulose bisphosphate carboxylase (RUBISCO), whereas plants with the C_4 photosynthesis pathway allocate only 5%–10% to RUBISCO (Evans 1989). *Phosphorus-rich molecules* include ATP, nucleic acids, phospholipids, and bone (hydroxyapatite).

Because molecules, organelles, cells, and organisms differ considerably in their elemental composition, the composition of species and their stoichiometry influence nutrient cycling (Elser and Urabe 1999). A classic example is the limitation of phytoplankton growth by N or P, depending on the composition of dominant zooplankton with different body N:P ratios. If zooplankton N:P ratio is low, then there will be a high N:P supply ratio and phytoplankton will become P-limited; the opposite process occurs if the zooplankton N:P ratio is high (Sterner et al. 1992). Thus, requirements for cellular growth influence how organisms interact with their environment and other organisms, for example, consumer-driven nutrient recycling (Elser and Urabe 1999).

Collective components of ecosystems can also exhibit constrained C:N:P ratios and provide insight into the nature of nutrient limitation. The "Redfield ratio" describes a nearly constant C:N:P ratio of 106:16:1 in planktonic biomass and dissolved organic matter pools throughout the world's oceans (Redfield 1958). This ratio has been critical to understanding marine biogeochemical cycles and will serve to test the efficacy of feedbacks controlling nutrient cycling in response to human-caused global changes (Gruber and Deutsch 2014). Changes in the availability of nutrients can shift whole system nutrient limitation. For example, atmospheric deposition of N has increased N:P ratios in many lakes, shifting nutrient limitation of phytoplankton growth from N to P (Elser et al. 2009). "Redfield-like" ratios also exist for foliar N:P ratios and vary with latitude corresponding to climate, soil age, weathering, and nutrient availability (Reich and Oleksyn 2004). There is surprising consistency in total soil and soil microbial biomass C:N:P ratios at a global scale (Cleveland and Liptzin 2007). Constrained C:N:P ratios of 186:13:1 for soil and 60:7:1 for the soil microbial biomass may be a useful tool in assessing nutrient limitation and processes responsible for nutrient limitation in ecosystems.

N Cycling

Applying fundamental principles of N cycling to reduce excess N or promote accrual of N through restoration requires understanding microbial metabolic pathways responsible for transformations of N (fig. 12-1). Oxygen availability affects whether conditions favor oxidation or reduction of N, with anaerobic conditions favoring reduction pathways. In aquatic systems, oxygen availability is determined by photosynthesis, nutrients, biological oxygen demand, substrate particle size, and hydrology. In soil, oxygen availability is influenced by factors that affect moisture: climate, texture, topography, soil structure, organic matter content, and plant water use. In all environments, oxygen favors aerobic cellular respiration (oxidation of reduced C in organic matter to CO_2), ammonification (mineralization of ammonium [NH_4^+] from organic matter), and nitrification (oxidation of ammonium to nitrate [NO_3^-]). In soil, the rates of these processes increase with microbial activity, corresponding with an increase from 10% to 60% water-filled pore-space (Linn and Doran 1984). Controls on ammonification are the same as those that regulate decomposition: temperature, moisture, pH, and substrate quality (i.e., C:N and lignin:N ratios). Nitrification is a two-step process, where the oxidation of NH_4^+ to NO_2^- (nitrite), followed by NO_2^- to NO_3^-, are performed by specific and different genera of chemoautotrophic bacteria (Meyer 1994). Nitrification is an aerobic, pH-sensitive, and energy yielding metabolic pathway coupled with the fixation of C. Two gaseous byproducts of nitrification are NO (nitric oxide) and N_2O (nitrous oxide) (Williams et al. 1992). In the absence of oxygen, some facultative anaerobic bacteria use NO_3^- as an alternate electron acceptor for cellular respiration. This pathway, known as dissimilatory nitrate reduction or denitrification, involves the reduction of NO_3^- to dinitrogen gas (N_2), also known as atmospheric or molecular N. Like nitrification, NO and N_2O are produced during denitrification (Knowles 1982). Thus, denitrification is a process that removes

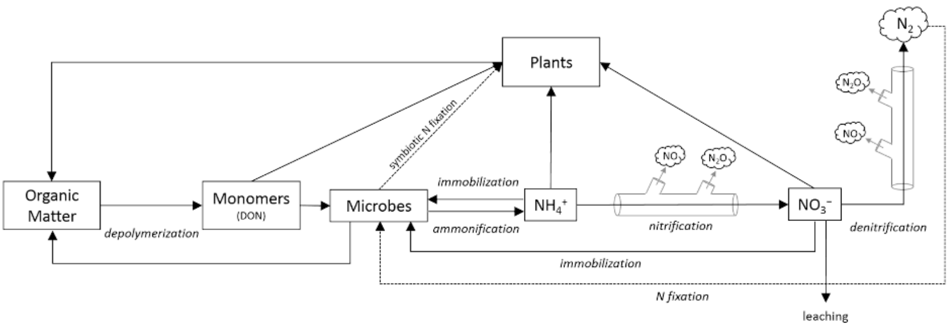

Figure 12-1. Schematic of major pools and transformations of N among plants, microbes, and organic matter in ecosystems (modified from Davidson 1991 and Schimel and Bennet 2004).

N from the ecosystem. Requirements for this pathway to occur include anaerobic conditions (or microsites), a supply of NO_3^-, and bioavailable organic C for microbial oxidation to synthesize ATP.

A perceived negative trade-off of restoring wetlands is the production of greenhouse gases (GHG) with more heat-trapping ability than CO_2. Nitrous oxide is inert in the troposphere, so it has a very long residence time in the lower atmosphere. Eventually, N_2O mixes with the stratosphere, where it reacts to produce NO, which destroys ozone—the gas that protects Earth from harmful ultraviolet radiation (Warneck 2000). Methane (CH_4) is another GHG produced under reducing conditions (i.e., low oxygen and high organic substrate availability) that characterize wetland soils. There is, however, evidence that CH_4 emissions are “trumped” by C sequestration during wetland restoration. Further, N_2O production from restorations on former agricultural land will likely be less than that produced from marginal croplands that wetland replaces, leading to lower fractional yield of N_2O produced in wetlands relative to downstream systems (Hey et al. 2012).

P Cycling

The primary input of P into terrestrial ecosystems is through the weathering of apatite, which is facilitated by the production of organic acids from plant roots and fungi. The availability of P in soil is pH-dependent (most available at neutral pH) and varies with stages of ecosystem development (Walker and Syers 1976). As ecosystems develop and weathering proceeds, mineral-containing P is exhausted and the fate of inorganic P depends on pH. In acidic soil ($pH < 5.5$), P precipitates with iron (Fe) and aluminum (Al). Once captured within crystalline Fe and Al oxides, P becomes occluded and is not readily available to biota. In alkaline soils (pH > 7), P precipitates with calcium (Ca). Inorganic (nonoccluded P) can be adsorbed onto soil particles through different mechanisms and made available, but P availability generally becomes increasingly limited as ecosystems mature (Walker and Syers 1976). As organic matter accumulates, biota rely largely on internal recycling of P, facilitated through the production of extracellular phosphatase enzymes. The production of organic acids by biota can prevent precipitation of P with Fe and Al, which keeps P in solution for biotic uptake. Organic and adsorbed P can be mineralized or desorbed, respectively, to result in "internal eutrophication" (internal loading) of aquatic ecosystems. Mitigating P pollution is challenging due to the few microbial transformations, numerous chemical reactions, and unlike N, no natural mechanism for complete removal of P from the system. Occlusion and sedimentation of P are the only processes that greatly reduce P availability.

Theoretical Logic of C and N Interactions in Ecosystems

Plants vary in nutrient use efficiency (NUE; C assimilated per unit N), which influences the quality (C:N ratio) of plant inputs to soil (Vitousek 1982). Plants exhibit several strategies to conserve N by reusing N atoms (e.g., resorption of N prior to litterfall or being evergreen) or increasing access to N through associations with mycorrhizae. *Plant N use theory* predicts that plant litter quality feeds back to influence the rate of nutrient cycling and primary productivity (fig. 12-2). In fertile (high-N) sites, the theory predicts that plants will produce high quality (low C:N ratio) litter to result in high internal N supply (N mineralization rate and availability of inorganic N) and plant growth (positive feedback). In low-N systems, the same plants are predicted to produce less decomposable low quality (high C:N ratio) litter to result in less internal N supply (low N mineralization rate and limited N availability) and lower productivity (Hobbie 1992). Positive feedback would also be expected in fertile and infertile sites if different species dominate due to variation in NUE (fig. 12-2a and 12-2b). Plants can even change site fertility through feedback according to the same mechanisms, as demonstrated for sites invaded by species with different tissue C:N ratios than resident species (Ehrenfeld et al. 2005). Negative feedback can occur if an ecosystem has a closed N cycle (with a fixed amount of N) and contains plant species that vary in NUE and growth rate. In this scenario, plants that grow rapidly will dilute their internal N pool with more biomass (high NUE) relative to slow growing species and result in a negative effect on plant growth (Tateno and Chapin 1997).

Plant N use theory has been challenged with respect to the direct role plants play in short-term feedbacks on N cycling through their litter quality (Knops et al. 2002) and in the context of nonsteady state conditions such as restoration (Baer

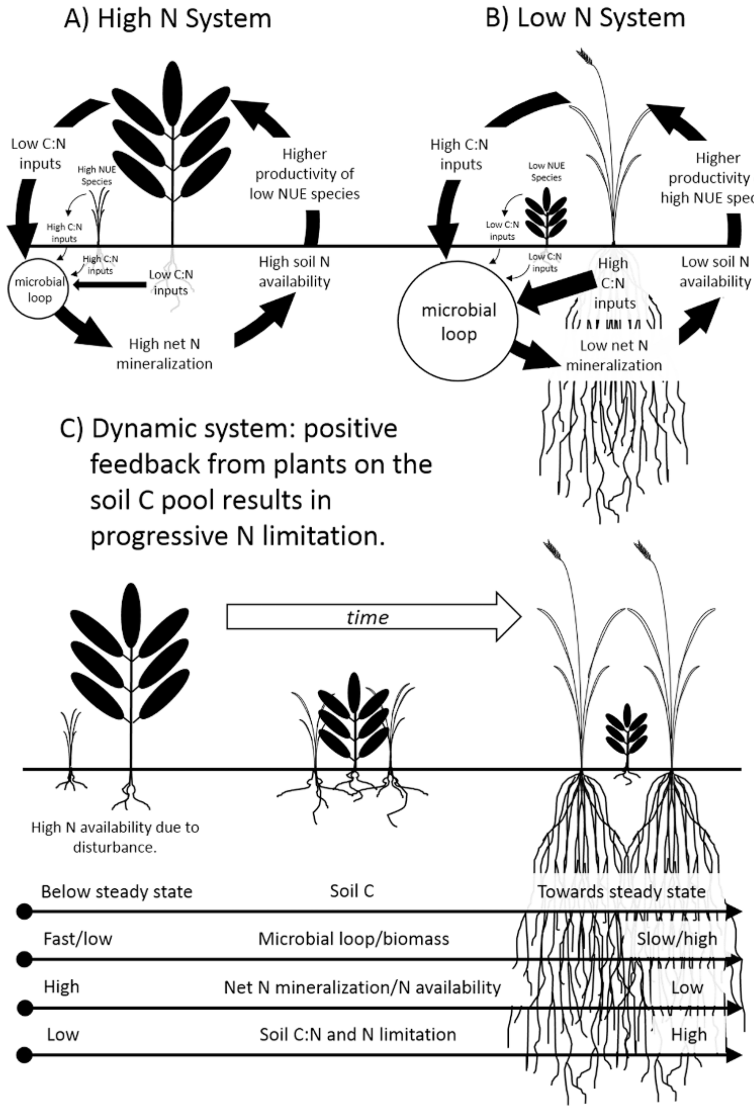

Figure 12-2. Illustrations of potential plant-soil feedbacks. (A) In a high-N system, there is high-N supply for plant growth and high productivity of species with low nutrient use efficiency (NUE) that input high-quality (low C:N ratio) organic matter into the soil to result in net N mineralization and high N supply for plant growth. (B) In a low-N system, species with high NUE and low tissue N concentration dominate and input low quality organic matter (high C:N ratio) into the soil to result in immobilization of N in the microbial biomass and reduced N supply from soil for plant growth. (C) Ecosystem nutrient status can change during restoration. If disturbance has reduced soil C stocks and left high N availability, low NUE species could be favored initially. As plant communities develop over time, C accrues in the soil and microbial biomass to result in progressive N limitation that can favor species with high NUE.

and Blair 2008). There is evidence that much of the N in plant litter is retained (not immediately mineralized) for a period of time, which would slow feedback to plant growth. Nitrogen in plant litter would first be immobilized by the microbial biomass (microbial N loop). A lag would be expected in the effects of litter quality on N supply to plants because it must first cycle through the soil organic matter pool. The immediate effect of plants on N mineralization would be C inputs promoting immobilization, and the strength of negative feedback would increase with plant productivity and inputs of C belowground. This is also applicable to dynamic state changes that occur during restoration on formerly cultivated land with initially high availability of nutrients and low levels of soil C, resulting in a succession of species based on their resource requirements (fig. 12-2c).

Plant input-output theory suggests that the immediate effects of plants on N cycling in soil occur through more direct mechanisms (Knops et al. 2002). Some plants acquire N independently from the soil organic matter pool through associations with N-fixing bacteria (fig. 12-1). Plants can also influence new inputs of N received from atmospheric deposition through their architecture and canopy interface with the atmosphere, taking up inorganic and leaching organic forms N (Lovett 1994). Direct uptake of N by plants reduces inorganic N lost from soil through leaching. Fire volatilizes N in aboveground plant tissue, so plants that change fire regimes can affect N return to soil through litter inputs. Plant communities can also affect N availability through their influence on the composition and function of soil microbial communities, for example, populations of nitrifiers (Hawkes et al. 2005). Lastly, plants directly influence N cycling by taking up bioavailable organic forms of N, that is, depolymerized monomers (amino acids, amino sugars, nucleic acids, etc.) cleaved from organic matter by extracellular enzymes (fig. 12-1). The degree to which plants depend on uptake of mineral or monomer forms of N, however, will depend on site and microsite fertility (Schimel and Bennett 2004).

Nutrients as Determinants of Restoration Outcomes

Nutrients can determine restoration outcomes by influencing the relative growth of target and nontarget species, as predicted by ecological theory. The *resource ratio hypothesis* predicts which species will dominate during secondary succession as consequence of changing relative ratios of resource availability over time (Tilman 1985). The hypothesis was developed in the context of light and N availability and assumes the following: (1) these resources are inversely related, (2) species vary in their competitive superiority for acquiring light and N, and (3) total soil N reflects the supply for plant growth. As in restoration sites, secondary succession can occur on nutrient-rich or nutrient-poor soils. On very nutrient-poor soil, the succession of species should reflect that predicted for primary succession: early successional species will be better competitors for N and be replaced by species that are better competitors for the progressively more limited light resource relative to N over time. The rate of succession is hypothesized to increase with soil fertility. In nutrient-rich soil, the maximal growth rates of plants influence the successional sequence. If a superior N competitor also has a higher maximal growth rate, the successional sequence in nutrient-rich soil will reflect that of primary succession and secondary succession on nutrient-poor soil. If maximal growth rates of all species are the same, then a late successional species (better competitor for light) will dominate from the onset. Which resources and to what extent resources are limiting at the onset of restoration depend on the type of disturbance that has degraded the environment. Plant competition theory can be applied to steer the relative growth of species by directly manipulating limiting resources, managing the environment to change resource limitation, or selecting species to reintroduce based on their resource requirements or functional traits (Funk et al. 2008). The resource ratio hypothesis underlies more specific hypotheses in ecology applied to establishing self-sustaining communities in severely disturbed sites, promoting the growth of native species in communities invaded by undesirable species, and rapidly achieving communities dominated by later successional species in ex-arable soil, as influenced by nutrient deficiency and surplus.

Nutrient Deficiency

Some restoration sites can be too deficient in nutrients to sustain plant growth (Bradshaw 1997) or achieve a canopy-cover restoration goal. For example, intertidal marsh habitat constructed from sandy dredge spoils did not provide self-sustaining tall canopies of *Spartina foliosa* without annual N addition (Lindig-Cisneros et al. 2003), demonstrating an "irreversible transition" (Hobbs and Norton 1996). Mined land also often contains soil properties that limit plant growth. Severely compacted soil contains low oxygen availability and biological activity. Soil ripping is commonly used to aerate mined land soil and stimulate microbial activity that releases nutrients from soil for plant growth. Mining can also cause soil acidification, which affects nutrient solubility, microbial activity, and microbial-mediated nutrient transformations sensitive to pH, that is, nitrification and nitrogen fixation. Soil pH can be raised through addition of calcium carbonate ($CaCO_3$ or lime), but additional measures may be required to facilitate the recovery of soil microbial populations. Application of nutrient-rich substrates (e.g., organic matter, topsoil, mushroom compost, or biosolids) are used to increase soil nutrient status (available and slow-release forms); improve soil structure and water holding capacity; bind trace elements; provide an immediate energy source for soil microbial activity; minimize nutrient loss through runoff and leaching; and, in some cases, supply propagules and mutualists needed for revegetation (Larney and Angers 2012). In theory, resource input will rapidly move a low-energy, nutrient-poor substrate to a condition where dynamic community reorganization can commence and plant-soil feedbacks can develop.

Silva et al. (2013) documented a highly synergistic effect of resource input (biosolid application) to mined land in Brazil that otherwise remained devoid of vegetation (case study box 12-1). The biosolid application resulted in rapid plant establishment, accrual of C in soil, and intrasystem cycling of nutrients. The stable isotope signature of C ($\delta^{13}C$) was used to identify the source of C increasing in soil across the fourteen-year restoration chronosequence. The isotopic signature of C in soil can reflect organic matter inputs from plants with different photosynthesis pathways because RUBISCO has a greater affinity for $^{12}CO_2$ (the lighter isotope) and discriminates against $^{13}CO_2$. Plants with the C_4 photosynthetic pathway discriminate less against the heavier isotope of C because they close their stomates more to conserve water. A result of this mechanism increase water use efficiency is that C_4 plants have a different (less negative) $\delta^{13}C$ signature than C_3 plants (Farquhar et al. 1989). Silva et al. (2013) found that exotic C_4 grasses were primarily responsible for the initial and rapid accumulation of C across the restoration chronosequence. The stable isotope signature of N ($\delta^{15}N$) in plant tissue was used to identify the source of N for plant growth. Because the N-fixing enzyme (nitrogenase) in bacteria that converts N_2 to NH_3 exhibits only slight discrimination between $^{14}N_2$ and $^{15}N_2$, plants associated with symbiotic N-fixing bacteria have $\delta^{15}N$ signatures close to that of the atmosphere (~ 0 or slightly negative). Plants not associated with N-fixing bacteria obtain N from the soil and show a much wider range of positive $\delta^{15}N$ signatures (Garten and Van Miegroet 1994). Leaf $\delta^{15}N$ signatures in the C_4 grasses studied by Silva et al. (2013) revealed that N supply to plants shifted from the biosolid source in the recently restored land, to that more derived from N-fixing plants in the intermediate-aged restorations, to N supplied from soil organic matter derived from the invasive C_4 grasses that excluded native species in the oldest restorations. This study exemplifies the role of nutrient manipulation as a necessary and effective means to initiate ecosystem development in nutrient-poor soil. In accordance with the resource ratio hypothesis, maximum diversity occurred at intermediate restoration age and ratio of limiting resources, but the pulse of high resource availability favored exotic invasive grasses (better competitors for N) at the expense of native species. Developing plant-soil feedbacks led to the persistence of the invasive species in this restoration site.

Case Study Box 12-1

Understanding Ecological and Biogeochemical Processes Driving Ecosystem Restoration

By Lucas C. R. Silva, Timothy A. Doane, Rodrigo S. Corrêa, Vinicius Valverde,
Engil I. Pereira, and William R. Horwath

Brasilia, DF, Brazil: In central Brazil, a single application of nutrient-rich biosolids (sewage sludge) prompted the spontaneous revegetation of abandoned mines that had been barren for many decades following disturbance.

Supporting theory: Resource-ratio biodiversity enhances ecosystem function theories.

The resource-ratio theory of succession explains how the supply of limiting resources determines whether competing species can coexist and, if not, which species will be excluded during successional trajectories. In such trajectories links between biodiversity and ecosystem function can be expected.

Expected outcome: It was hypothesized that organic nutrient inputs in degraded mined substrates would prompt the establishment of plants originating from the regional species pool. It was expected that synergistic effects of substrate restoration and plant colonization would promote soil development and C accumulation, initiating a process of natural succession.

Progress: Diverse plant communities colonized the previously barren mined sites after a single application of nutrient-rich biosolids. Plant colonization caused rapid accumulation of soil C in chemically and physically stable pools, quickly surpassing the amount applied as biosolids. The highest C accumulation was observed during the period of highest plant diversity (>30 species; year 3–6), declining significantly with the exclusion of native species by invasive grasses (year 9–14), although remaining greater than soil C levels found in pristine forest and savanna ecosystems of the same region.

Case Study Box 12-1. A mined site before and after soil restoration in central Brazil corresponding to (from *left* to *right*) the 1960s, 2011, application of organic matter, incorporation of organic matter, and restored 0, 0.5, 3, 6, 9, and 14 years. Photos courtesy of Rodrigo S. Corrêa.

Case Study Box 12-1 continued

Long-term outcomes: After fourteen years, invasive grasses contributed >65% of the total accumulated soil C, stabilized into iron-coordinated complexes, which served as nuclei for microbial formation of soil aggregates. However, the highest rates of C accumulation were observed during the period of highest plant diversity, declining significantly with the increasing dominance of invasive grasses. Invasive grasses are abundant throughout the region and their dominance in these sites was favored by increased soil fertility. Over time, their progressive dominance was found to be associated with a steady decline in the concentration of soil N and P per unit of accumulated C, attributed to a decline in the quality of litter inputs. At the end of the experiment, soil C accumulation remained much greater than levels found in undisturbed ecosystems of the same region, although on a declining trajectory. These results illustrate the importance of interdependent ecological and biogeochemical processes, as well as the role of plant-soil interactions in determining the success of restoration efforts.

References: Silva et al. 2013, 2015.

Role of Nutrients in Invaded Environments

Invasive species colonize a wide variety of environments in part by exploiting unused nutrients. The *fluctuating resource hypothesis* predicts that disturbance makes a community susceptible to invasion by increasing gross resource supply relative to resource uptake (Davis et al. 2000). Plant trait data provide some support for this hypothesis. For example, some invasive exotic species have faster growth strategies and higher foliar N:P ratios in disturbed sites relative to native plants in disturbed sites (Leishman et al. 2007). A review by Ehrenfeld (2003) also showed a tendency for invasive species to produce more biomass with higher litter quality (low C:N), coinciding with higher net N mineralization rates (mostly due to nitrification) and increased N availability in soil. Invasive species also colonize sites with low resource availability. Their invasion of such habitats is attributed to higher resource-use efficiency (C assimilation per unit of resource) than native species in the same environment (Funk and Vitousek 2007). This may explain inconsistencies in the ability to control invasive species through nutrient manipulations. Whether invasion is a result of high or low nutrient use, changes in nutrient dynamics and development of feedbacks can lead to alternative stable states (Suding et al. 2004; Prober and Lunt 2009; case study box 12-2). Consequently, highly invaded ecosystems can be very challenging to restore, and in some cases, the cost of restoration should be weighed against potential gains from other conservation strategies (Casazza et al. 2016).

Case Study Box 12-2

Plant-Soil Feedbacks Lead to Alternative Stable States in Australian Grassy Woodlands

By Suzanne Prober, CSIRO Land and Water Flagship, Australia
Ian Lunt, Charles Sturt University, Australia

Temperate woodlands, southeastern Australia: When temperate grassy woodlands are grazed regularly by livestock, the naturally dominant Kangaroo Grass (*Themeda triandra*) and many native forbs are replaced by other native grasses and exotic annuals. At the same time, soil nitrate levels change from being consistently low to seasonally high. When livestock are removed, the perennial Kangaroo Grass sward does not usually recover. Instead elevated soil nitrate levels support the persistence of exotic annuals.

Case Study Box 12-2. After three years, untreated plots remained dominated by exotic annuals despite seeding with Kangaroo Grass (A), whereas Kangaroo Grass established densely in sugar treatments, leading to longer term suppression of soil nitrate and exotic annuals (B).

Supporting theory: Alternative stable states

Shifts in underlying ecological processes during ecosystem degradation can result in alternative stable states. In such cases, ecological barriers can constrain recovery even after degrading processes are removed, and active interventions to remediate ecological processes may be needed to restore the initial state.

Case Study Box 12-2 continued

Expected outcome: We hypothesized that woodland ground-layers dominated by Kangaroo Grass, and woodland ground-layers dominated by invasive exotic annuals, represent alternative stable states of temperate grassy woodlands, controlled by plant-soil feedbacks on N cycling. We proposed that in the invaded state (1) interventions to suppress soil nitrate (using sugar addition) would suppress exotic annuals and facilitate reestablishment of sown Kangaroo Grass, and (2) Kangaroo Grass would take up soil nitrate and restore ecological resistance to invasion by exotic annuals.

Progress and long term outcomes: The sugar treatment temporarily suppressed seasonal peaks in soil nitrate levels and limited the growth of exotic annuals. Within three years, Kangaroo Grass dominated the sown sugar plots, whereas it established poorly in the nonsugar plots. Soil nitrate was restored to consistently low levels (<3 mg/kg) where Kangaroo Grass established a dominant sward, but increased in plots without Kangaroo Grass after sugar addition ceased. Similarly, exotic annuals were far less abundant in plots with Kangaroo Grass than in other plots. These results demonstrate that long-term resistance to exotic invasion in these woodlands can be restored by facilitating the transition from a stable state dominated by exotic annuals to the alternative state dominated by the keystone native perennial, Kangaroo Grass. More generally, the study demonstrates that some stable degraded states can be restored to more desirable states by remediating key altered ecological processes

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References: Prober et al. 2002, 2005, 2009; Smallbone et al. 2007, 2008; Prober and Lunt 2009.

Reducing Excess Nutrients in Soil

Increased nutrient availability can reduce diversity through strong productivity responses of a few species at the expense of rare species, native species, and those associated with N-fixing microorganisms (Suding et al. 2005). Atmospheric deposition and agricultural inputs of N can leave a legacy of high nutrient availability and nitrification rates in soil (Flinn and Veland 2005). Fundamental principles of N and P cycling can be applied to reduce nutrient availability in soil as a means to restore native and diverse plant communities. Several efforts to reduce P availability have aimed to promote plant species diversity in ex-arable lands (Walker et al. 2004). Methods used to reduce P availability in soil include haying or cropping to promote off-take; addition of Al or Fe (ferric) sulfate to immobilize P through adsorption; and deep cultivation or addition of organic inert materials to dilute available and total P nutrient pools. Manipulating soil C has been used to reduce N availability, with the goal of favoring later successional, target, or restored species and leaving less N for volunteer, exotic, or invasive species to exploit. Incorporating sugar, sawdust, or organic matter with a very high C:N ratio can effectively reduce available N in formerly agricultural soil because the microbial community tends to be C-limited in long-term cultivated soil with depleted C stocks. Carbon addition causes the microbial biomass to grow, immobilize N, and leave little available N (Baer et al. 2003; fig. 12-3a, c). Baer et al. (2004) showed that variation in N availability led to differential establishment of a dominant grass in restored prairie, resulting in higher diversity and community similarity to never-cultivated prairie under low N conditions (fig. 12-3d, e). Reduction in available N through C addition at the onset of restoration has also been shown to reduce establishment of exotic/invasive species and favor recovery of native/desired species, but this is not a consistent response (Perry et al. 2010). Outcomes of this practice may depend on the functional disparity and variation in nutrient requirements of the exotic versus native species, the duration of N immobilization by the microbial biomass, the extent to which the total soil C pool has been reduced by disturbance, the degree to which the microorganisms are C-limited, and the propagule supply of target and nontarget species. Effects of nutrient manipulation on community divergence and diversification often lessen over time (Pywell et al. 2002). This may result from the absence of strong priority effects (a type of historical contingency where prior arrival of a species affects the trajectory of community development) in assemblages that establish in response to variation in available nutrients or propagule limitation (Foster et al. 2011).

Immobilizing N through C addition may not be realistic on a large scale. Other means to reduce N availability include the use and harvest of cover crops with high N demand, carefully timed burning, or haying (Vasquez et al. 2008), but these practices are not universally effective. Multiple processes may need to be manipulated to initiate and sustain the trajectory of community change toward a desired state. In an invaded Australian woodland, establishment of a native tussock grass with low N requirements was achieved using a combination of C addition and burning to promote N limitation, coupled with alleviated dispersal constraints through propagule supply (Prober and Lunt 2009, case study box 12-2). The combination of manipulations was key to maintaining low N availability and reducing the cover of exotic species that competed with the target species.

Nutrients as Restoration Endpoints

Accumulating or reducing nutrients represent endpoints for restoration where their levels are known to fundamentally alter the structure, functions, and services of natural ecosystems. Changes in pools and fluxes of nutrients in ecosystems generally coincide with other disturbances, the most globally widespread of which are agricultural. For watersheds (chap. 14), reducing nutrient loads is a restoration goal where improving water quality is a priority and possibly mandatory (e.g., meeting total maximum daily load limits); elsewhere nutrient accrual can

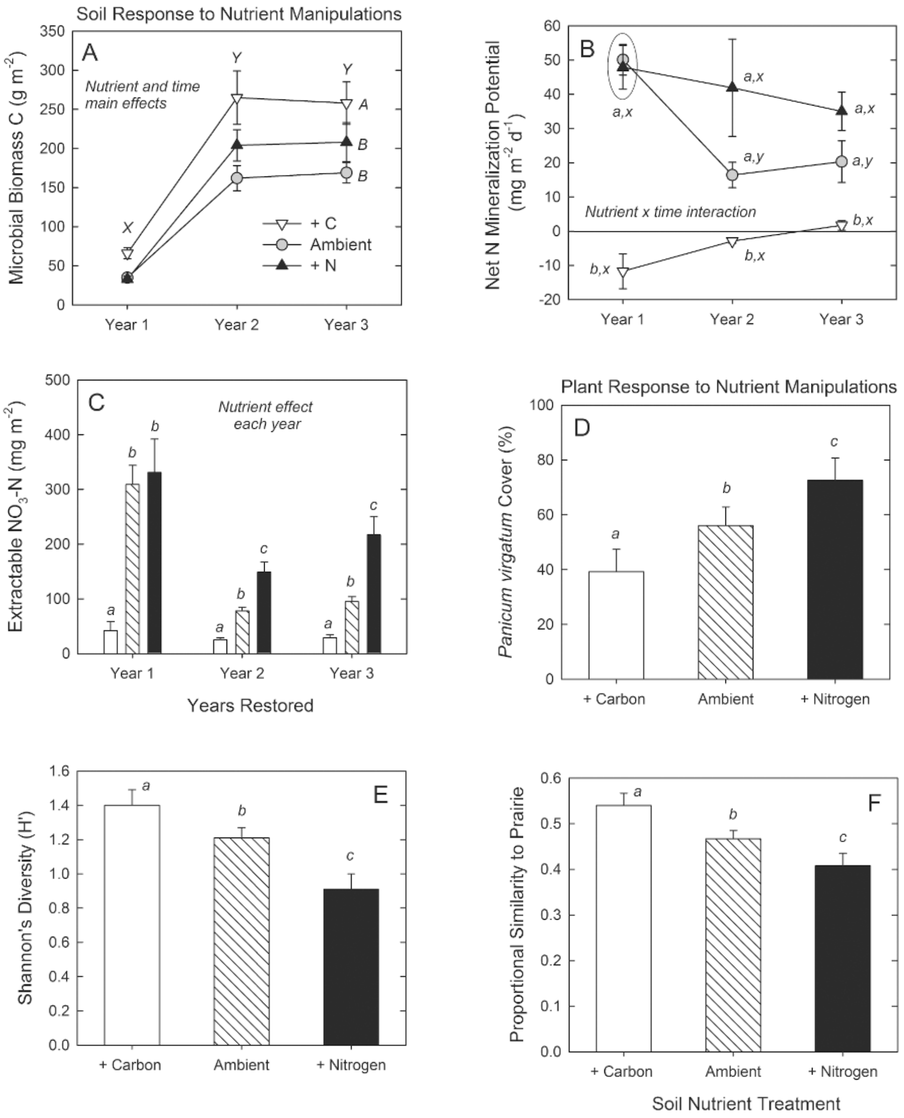

Figure 12-3. Effect of soil C and N amendments in prairie restored on (A) microbial biomass; (B) net N mineralization rate; (C) inorganic N availability; (D) cover of a dominant grass, *Panicum virgatum*; (E) plant diversity; and (F) plant community similarity to never-cultivated prairie. Incorporating sawdust (+ Carbon) increased the microbial biomass, immobilized N, and reduced available NO_3-N relative to ambient (control) and fertilized (+ Nitrogen) soil. High N availability in soil promoted *P. virgatum* cover, reduced diversity, and resulted in a restored community least similar to never-cultivated prairie. Differences among treatments within a year indicated by letters a through c. In panels A and B, differences among years within a treatment indicated by letters x through z. Uppercase letters indicate significant main effects. Means accompanied by the same letter were not significantly different ($\alpha = 0.05$). (Figures adapted and redrawn from Baer et al. 2003 and 2004).

be an indirect benefit from practices aiming to conserve soil (e.g., C sequestration). Ecological theory is relevant to steering desired nutrient outcomes through restoration.

Eugene Odum's *strategy of ecosystem development* (1969) was formulated with the intent to apply principles of succession as "a basis for resolving man's conflict with nature," meaning the maintenance of protective, productive, multi-use, and urban-industrial environments. This theory predicts that changes in organic matter and nutrient cycling accompany shifting bioenergetics during succession (fig. 12-4). At the onset of ecosystem development, gross primary production (GPP) exceeds respiration (R) to result in the accumulation of biomass. As an ecosystem matures, the GPP:R ratio approaches one, biomass stabilizes, nutrient cycles close, intrasystem nutrient cycling increases, and nutrients are increasingly conserved (Odum 1969). Where disturbance has reduced organic matter storage, developing plant communities will impart a positive feedback on C accrual (Ehrenfeld et al. 2005). As C accumulates in an ecosystem, so does biological demand for limiting nutrients, that is, *progressive nitrogen limitation* (Luo et al. 2004). Promoting C accrual is instrumental in conserving N and P on land, which reduces their export into aquatic systems. Thus, managing restored lands and riparian ecotones to maximize N and P conservation may require maintaining these ecosystems in a biomass- and nutrient-accumulating state.

Carbon Sequestration

Carbon sequestration is the accrual and long-term storage of organic matter in ecosystems; it is the net result of greater C inputs (products of photosynthesis) than outputs (decomposition). Organic matter inputs must become stabilized (not susceptible to decomposition) for C to become sequestered. Organic matter stabilization mechanisms include chemical protection through sorption to minerals, physical protection in soil aggregates, and biochemical protection through recalcitrance (Six et al. 2002). Carbon sequestration in soil is limited by the cumulative behavior of stabilized and unprotected (bioavailable) C pools. As more C is stabilized, soil becomes saturated with C and has a lower capacity to sequester C. *Soil C saturation theory* was developed from the asymptotic relationship observed between C inputs and soil organic C stocks across a variety of agroecosystems (Six et al. 2002). The theory predicts that soil with a greater C saturation deficit has a higher capacity to accumulate C relative to soil with C stocks closer to saturation (Stewart et al. 2007). The application to restoration is that sites with more degraded soil C stocks have a high potential for providing this ecosystem service, as affected by climate, mineralogy, vegetation, and history of disturbance.

Overgrazed and formerly cultivated lands generally contain soil C stocks be-

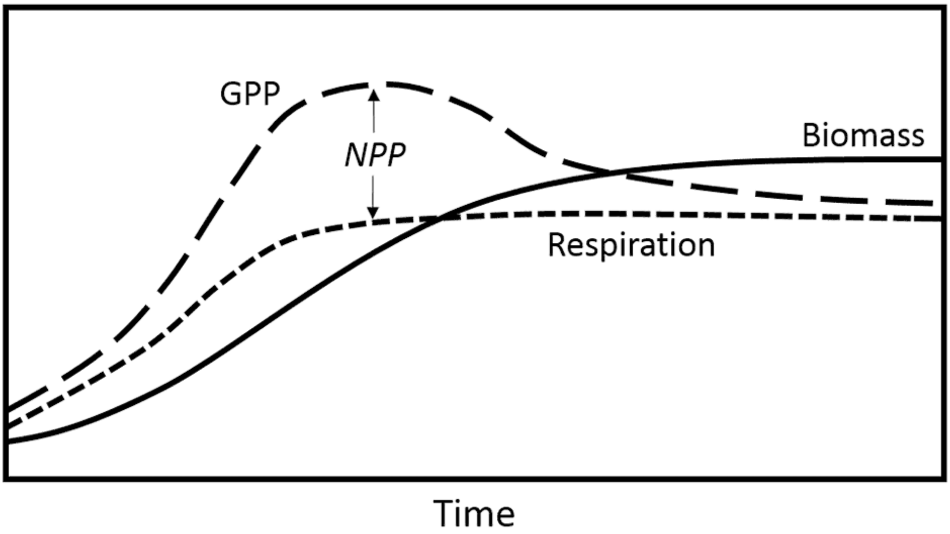

Figure 12-4. Generalized model of the strategy of ecosystem development based on forest succession. As an ecosystem develops, gross primary production (GPP; long dashed line) exceeds ecosystem respiration (R; short dashed line) to result in increasing net primary production (NPP; region between GPP and R) and accrual of total biomass (solid line). As ecosystems mature, nutrient cycles close, organic matter accumulates, internal nutrients are increasingly supplied from detritus, and overall nutrient conservation increases. Modified from Odum (1969).

low historical steady state conditions. Overgrazing lowers soil C stocks through reduced plant productivity (inputs). Degraded rangelands have the capacity to sequester C in soil through better management (e.g., adjusting stocking rate and destocking during drought) and plant improvements (Morgan et al. 2010). Tillage reduces soil C by disrupting soil aggregates and exposing organic matter to decomposers (Mann 1986). Over fifty percent of forested area in eastern North America and Europe have aggraded on formerly cultivated land, and lower soil C stocks can be evident 90–120 years following agricultural abandonment, relative to sites with no history of cultivation (Flinn and Vellend 2005). Establishing perennial vegetation in agricultural lands has been advocated as a means to conserve soil, sequester C, and help mitigate increasing CO_2 in the atmosphere (Lal et al. 2011), but recovery rates of total soil C stocks following these ecosystem state changes are highly variable (Post and Kwon 2000; McLauchlan 2006). Knowledge of soil C stocks and saturation deficit, quantity and quality of inputs from developing vegetation, and potential stabilization mechanisms (physical, chemical, and biochemical) could be used to ascertain the potential for C sequestration in soil. For example, a comparison of grasslands restored under the same regional climate conditions and composition of species, but on contrasting soil textures, showed no change in soil C in very sandy soil and an accrual of C in silty clay loam soil, the latter corresponding with recovery of the microbial biomass and soil aggregate structure (Baer et al. 2010). Within a similar soil texture, a comparison of restored grasslands in the US Midwest to South Africa attributed more rapid C accumulation in South Africa to greater soil C saturation deficit (Baer et al. 2015).

Forests have long been considered a potential sink for atmospheric CO_2. Sequestration of C aboveground occurs as forests develop from young to mature states. Planting forests in regions where they formerly occurred has the capacity to sequester significant amounts of C aboveground (Fang et al. 2001), but this would be a short-lived phenomenon and only briefly delay CO_2 accumulation in the atmosphere (Vitousek and Matson 1991). Carbon sequestration in forest biomass and soil is variable, site dependent, and requires adequate soil fertility (Oren et al. 2001). There is little consensus on how forest management changes soil C and its accrual into stable pools (Jandl et al. 2007), but a meta-analysis demonstrated that N-fixing species were associated with increases in soil C, and gains in soil C occurred following their invasion after fire (Johnson and Curtis 2001). The production of charcoal stabilizes C through its chemical recalcitrance and sorption to minerals, which protect this form of "black carbon" from microbial degradation. Another meta-analysis of afforested lands found previous land use (ex-arable soil), climate (tropical and subtropical), and forest type (deciduous hardwoods and N-fixing species in the understory or as a plantation) as significant factors affecting soil C accrual (Paul et al. 2002).

It is often not possible to select sites for restoration that will maximize nutrient accrual or processing. Rather, practitioners are usually challenged to improve the structure and functioning of a site where a restoration opportunity exists. Under these circumstances, plants represent the primary means of maximizing C sequestration. A *plant-trait-based approach to C sequestration* (De Deyn et al. 2008) is an application of theory to promote this process based on the evolutionary trade-off between plant growth rate and the amount and quality of organic matter that plants input to the soil. Short-lived plants, with inherently high relative growth rates, tend to input relatively large amounts of easily decomposable litter to soil. Long-lived, slow-growing plants, however, tend to input low quantities of more recalcitrant litter to soil (Chapin 2003). Plant traits affecting C accumulation are those that maximize inputs from primary productivity and minimize loss via soil respiration (De Deyn et al. 2008). Plant traits influencing primary productivity include life history strategy, water and nutrient use efficiency, and associations with soil mutualists. Plant-based controls on decomposition that are directly beneficial for C sequestration include production of recalcitrant compounds such as lignin, polyphenols, and tannins; high root:shoot ratio; and toxin exudation to reduce the "priming effect"-stimulated activity and decomposition of recalcitrant substrates by soil microbes in response to root exudates (Dijkstra et al. 2006). Although N-fixing plants produce litter with high N content, there is evidence that they increase C sequestration and N accrual in restored soil (Fornara and Tilman 2008; Hoogmoed et al. 2014). Plants may indirectly benefit C sequestration in soil if species favor different microbial communities (fungal- versus bacterial-dominated). Compared to bacteria, fungi have higher C:N ratios, respire less C per unit biomass (high C use efficiency), produce more recalcitrant necromass, and are more instrumental in the formation of soil aggregates that protect C inputs (Rillig 2004; Six et al. 2006). Recovery of fungal biomass in restored soil coincides with C accumulation in large soil aggregates that their hyphae help form (Bach et al. 2010).

Reducing N and P Loading

The productivity of many natural (undegraded) ecosystems is limited by N and/or P, resulting in watershed retention of these nutrients. Human modifications to the environment have increased the export of biologically available forms of N and P from the terrestrial to the aquatic environment, which can be "too much of a good thing" by causing eutrophication and hypoxia. Because of this, reducing nutrients is a common desired endpoint for watershed restoration (chap. 14). Hydrologic change generally accompanies large-scale conversion of land to row-crop agriculture, which can result in the export of more water carrying high nutrient and sediment loads to aquatic ecosystems (Schilling and Drobney 2014). Increased nutrient loading in freshwaters is a result of (1) nutrient export from streams draining crop, livestock, and urban environments; (2) changes to stream morphology that increase flow and reduce nutrient-laden water interaction with the benthos; (3) loss of riparian zones; and (4) direct export of water and nutrients from drained wetlands. As a result, there is a growing N and P pollution problem in aquatic ecosystems.

Restoring riparian vegetation reduces nutrient export from land to aquatic systems. The effectiveness of riparian ecotones in nutrient mitigation depends on the nutrient and how it is delivered to streams (surface runoff versus subsurface flow). Phosphorus is predominantly delivered to streams in particulate or dissolved forms through surface runoff, whereas N is delivered as NO_3^- primarily through subsurface flows (Sharpley and Syers 1981; Sharpley et al. 1992). Changes in land use that reduce erosion, no-till agriculture for example, will reduce particulate P inputs into aquatic systems. The role of riparian zones in P abatement is through deposition and sorption processes, the latter determined by equilibrium reactions. If P concentration in water is high, then P will be adsorbed into particles, as affected by clays, pH, Al and Fe oxides, redox potential, organic matter, and calcium carbonate ($CaCO_3$). In general, N and P in surface runoff are effectively removed over short distances through riparian buffers (Vought et al. 1994). Uptake by vegetation and denitrification are the two primary mechanisms responsible for the reduction of NO_3^- in subsurface flow. Increased surface roughness by vegetation reduces the velocity of overland flow, which increases the residence time of water for infiltration, plant uptake, and microbial processes that remove N. The successional state of riparian vegetation also influences nutrient fluxes, as young or aggrading forests have more demand for nutrients as biomass accumulates (Osborne and Kovacic 1993). Riparian areas can become less efficient in nutrient removal over time (Hanson et al. 1994). Thus, management of riparian buffers may be needed to maintain plant demand for N and P (biomass accumulating state) and bioavailable C for denitrification to maximize nutrient abatement.

Riparian protection, restoration, and reconnection are used to reduce nutrient loads to streams. Channelization, canalization, impermeable surface, and drainage (e.g., tile or ditch) all increase stream energy. High flows can lead to bank incision and development of riparian zones that are disconnected from their streams (chap. 14). Restorations that reconnect streams with riparian ecotones involve engineering stream cross-sections to reduce excessive force, promote overland flow, and increase water residence time with heterogeneous substrates. These activities have been shown to promote denitrification and reduce NO_3^- in streams and groundwater (fig. 12-5; Kaushal et al. 2008). The potential for riparian reconnections to reduce nutrient loads depends on the timing of flows carrying high N loads coinciding with when flows interact with their riparian zones, the amount of bioavailable C for denitrification in soil, and the degree of N limitation in riparian vegetation and soil (Orr et al. 2007).

Carefully positioned created wetlands have the potential to remove significant amounts of reactive N and P in surface water (Mitsch et al. 2001; Hey et al. 2012). Wetlands reduce reactive N concentrations in water through plant uptake and denitrification. Phosphorus is removed from water in wetlands through plant uptake, sedimentation, chemical precipitation, and adsorption, but the primary mechanism is through accretion (the development of soil/sediment from organic debris deposition containing assimilated P). The effectiveness of wetlands in mitigating nutrients exported to large rivers requires conducive hydrologic conditions and depends on their proximity to high concentration sources of reactive N and P. Slow moving, shallow water wetlands close to upstream sources of reactive N and P (e.g., agricultural watersheds, drainage outflows, and wastewater treatments facilities) will be most efficient at nutrient abatement. Because reactive N and P concentrations become dilute with increasing discharge, proportionally more wetland area will be needed reduce the same amount of N and P downstream (Hey et al. 2012). There are several configuration innovations of constructed wetlands to enhance N removal by manipulating circulation, supply of electron donors, mi-

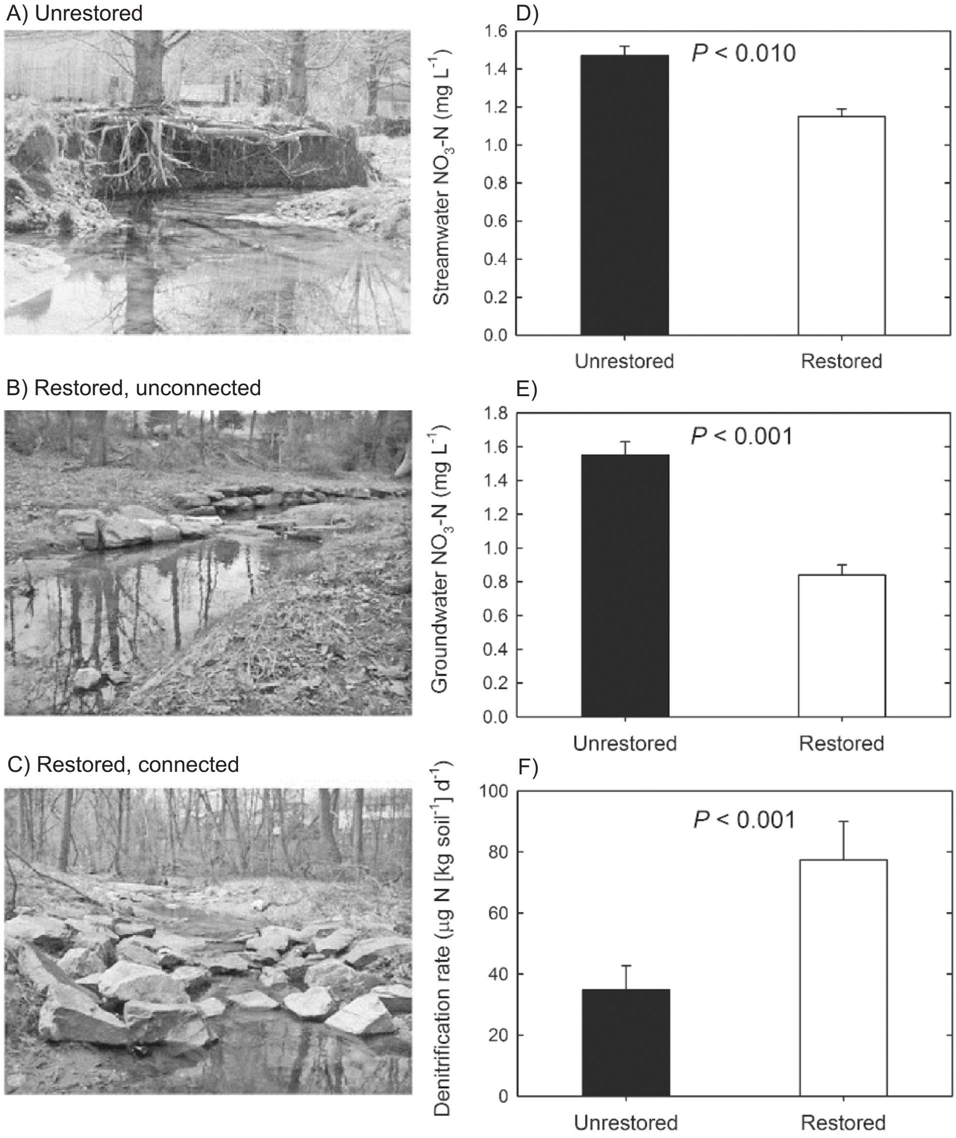

Figure 12-5. Images of (A) an unrestored stream reach with extreme bank incision; (B) a restored stream reach with bank armoring to reduce channel incision—but not connected to the riparian zone to enable rapid drainage away from commercial property; and (C) a stream reach restored to dissipate erosive force using step pool, meandering, and cross-section engineering to increase connection within the riparian ecotone. Concentrations of NO$_3$-N were significantly lower in (D) surface water and (E) groundwater of the restored reaches relative to the unrestored reaches. (F) Mean in situ soil denitrification rate was higher in restored than unrestored reaches; restored reaches connected to the riparian ecotone had higher denitrification rates than unconnected restored reaches. Panels A–C reproduced with permission from Kaushal et al. (2008); panels D–E drawn from data in Kaushal et al. (2008).

crobial communities, and surface area for biofilms and vegetation (floating mats), which could mitigate more N with less land (Wu et al. 2014).

In-Stream Nutrient Processing

Reducing nutrient export from upstream to downstream ecosystems requires intervention to promote *nutrient spiraling* (Newbold et al. 1983). Increasing water residence time with benthic substrates enables reactions that remove nutrients to occur, also called the residence to reaction time ratio (Hill et al. 1998). Low order (headwater) streams are particularly important for N retention through spiraling because there is a high ratio of substrate surface area to volume of water relative to higher order streams. Restoration that slows stream energy in headwater reaches can significantly reduce the volume of water and nutrients exported downstream. For example, installation of debris dams and weirs can restore stream connectivity with the hyporheic zone, a region where surface and groundwater mix that contains heterogeneous interstitial flow paths in subsurface sediment. Hyporheic zones contain hotspots depleted in dissolved oxygen and redox conditions that favor denitrification (Merill and Tonjes 2014). Several features of streams can be used to predict denitrification potential: (1) sediment quality, as it affects surface area for bacteria, retention of organic matter, and water residence time; (2) flow, as it affects residence time and reducing conditions; and (3) flooding, if it increases connectivity with riparian areas containing highly organic hydric soils (Merill and Tonjes 2014). Managing in-stream processing of N, however, will not compensate for N inputs into most agricultural streams (Inwood et al. 2005). Reducing N inputs to streams from the landscape will be required to significantly reduce the flux of N that leads to hypoxia at the mouths of major rivers.

Restoring Large Eutrophic Ecosystems

Restoring ecosystems that are eutrophic as a result of human modification to the landscape requires complex strategies formulated from a deep knowledge of how changes in nutrient dynamics influence ecological processes and feedbacks. Restoration of the Florida Everglades exemplifies this challenge (Noe et al. 2001). Historically, the Florida Everglades was an oligotrophic, low-gradient wetland ecosystem limited by P due to the absence of underlying P-containing minerals and hydrology determined primarily by rainfall. Surface water mixes with groundwater that has passed through limestone, where high pH and Ca concentrations limit P availability. The Florida Everglades has experienced major changes to hydrology and P loading (in soluble reactive form) from canals draining agricultural fields and urban developments. Enrichment is heterogeneous on the landscape, and comparisons of ecosystem structure and function between P-enriched and unenriched areas have revealed that calcareous periphyton play a major role in the uptake of P and that their senescence contributes to the removal of P through accretion. Calcareous periphyton further affect P cycling by increasing pH during periods of photosynthetic activity. This causes a reduction in the partial pressure of soluble CO_2, crystallization of $CaCO_3$, and precipitation of P with Ca-containing compounds. Enrichment of the ecosystem with even low levels of P coincides with a reduction in calcareous periphyton mats and the degree to which water is saturated with $CaCO_3$, both of which are instrumental to P removal and limitation. Areas enriched with P also experience an increase in the abundance of the native cattail, *Typha domingensis*. Relative to other macrophytes, this species has high tissue P concentration and is less efficient at P resorption. This results in the production of P-rich detritus, from which P can be more readily mineralized. Thus, P enrichment promotes a positive feedback in the cycling of P. Knowledge of the impacts of P enrichment on the structure and functioning of this ecosystem made reducing P loading a major focus for legislation that aimed to restore the Florida Everglades (Noe et al. 2001). The Florida legislature passed the Northern Everglades and Estuaries Protection Program in 2007, with the intent of restoring and protecting water resources for the state by expanding the Lake Okeechobee Protection Act, which was passed in 2000 (Office of Ecosystem Projects 2013). A primary goal of the original and expanded legislation is to reduce P loading. Plans to achieve total maximum daily loads include implementing more on-farm best management practices to reduce P inputs and export, as well as the creation of thousands of acres of constructed wetlands to treat stormwater (Sklar et al. 2005).

Closing Remarks

Humans have increased reactive N and P pools in the environment. Excess nutrient supply can reduce plant community resistance to invasion. Further, communities invaded by species with different growth and nutrient requirements can change nutrient cycling rates and soil microbial communities to promote their persistence. Knowledge of feedbacks between plants and soil biota, as they affect or are affected by nutrients and possibly other consumers, should improve the ability to restore heavily invaded ecosystems. Reactive forms of N and P are often highly available on land that has been used for crop production or overgrazed, and correspondingly, soils with lower C stocks. High levels of residual nutrients generally promote growth of early successional and sometimes invasive species. The consequence of this for restoration will depend on whether plant-soil feedbacks develop, or priority effects prevent a target species composition from being achieved. Soil amendments that increase bioavailable C have been used to reduce N availability, inhibit growth of undesirable species, and promote establishment of later-successional species and diversity. Limitations of C addition include the short duration of microbial immobilization of N, high variability in plant and community response, and feasibility at large scales. Manipulating processes that promote nutrient limitation through plant uptake and microbial immobilization (e.g., fire), managing land to promote off-take (e.g., cover crops, biomass removal), and adding propagules of species with high nutrient use efficiency may be required to shift plant species composition and enhance nutrient conservation at large scales. Nutrients that are not retained in the terrestrial environment can be abated in riparian ecotones and wetlands. Here, processes that maintain a biomass-accumulating (successional) state are critical for plant uptake of N and P. Riparian zones can be engineered to increase the residence time of water to promote nutrient removal through uptake by the biota and denitrification. Carefully positioned constructed wetlands also represent a means to significantly reduce N and P loading in streams through plant uptake, P burial, and N loss through denitrification. Slowing stream flows can prolong water residence time and foster reactions with the benthos to take up and remove N and P. Where eutrophication persists, restoration will require knowledge of landscape factors contributing to nutrient loads and processes limiting their removal in ecosystems. A plan to reduce nutrient inputs from urban developments and agricultural lands will require an investment in waste and stormwater treatment and widespread implementation of better farm management practices. A growing understanding of changes in ratios of C:N:P, and how changes in N and P affect ecosystems, has made restoration practitioners better equipped to deal with nutrient excesses as well as deficiencies.

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Chapter 13

Recovery of Ecosystem Processes: Carbon and Energy Flows in Restored Wetlands, Grasslands, and Forests

Erika Marín-Spiotta and Rebecca Ostertag

Theory and Application

- Wetlands, grasslands, and forests are carbon-rich ecosystems. Their restoration can offset some of the carbon emissions from land use and land cover conversion through the enhancement of carbon storage in plant biomass and in soil organic matter.
- Rates of the accumulation of carbon in biomass and soils and of the recovery of other ecosystem processes during restoration are influenced by climate, historical disturbance regimes, management, and species traits and interactions.
- Restoration efforts toward the goal of recovering ecosystem processes may differ from management for restoring original species composition, as, typically, ecosystem structure can recover faster than species assemblages. Further research on species effects on ecosystem processes can improve assessment of the success of ecosystem function restoration projects.

Human perturbations of the global carbon (C) cycle have altered greenhouse gas concentrations in the atmosphere, with consequences for Earth's climate. After fossil fuel emissions, changes in C fluxes from terrestrial ecosystems via changes in land cover are the second largest source of anthropogenic carbon dioxide (CO_2) in the atmosphere (Houghton et al. 2012). The restoration of ecosystem processes has garnered attention for the potential to contribute to C sequestration and climate mitigation, in addition to providing ecosystem services, such as habitat for biodiversity, watershed protection, and erosion control. Wetland restoration, for example, is promoted to improve aquatic ecosystem nutrient regulation, hydrologic flow and coastal stabilization (Meli et al. 2014).

In this chapter we briefly introduce the concepts of C and energy flow in ecosystems (for a more thorough discussion, see Chapin et al. [2012]). We focus on

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how restoration efforts of wetlands, grasslands, and forests can target the recovery of above- and belowground ecosystem processes related to biomass production, C sequestration, and greenhouse gas emissions reductions. We provide examples of how the removal and reinstatement of disturbance types and regimes can affect ecosystem processes, and finally we discuss challenges and opportunities for restoration in a changing world.

We use the term *recovery* to encompass improved abiotic conditions in reference to a more degraded state, which does not necessarily imply recovery of the original conditions. This distinction is important because the recovery of some structural properties and ecosystem functions can occur during natural secondary succession well before the return of the previous species composition (Guariguata and Ostertag 2001; Martin et al. 2013). Likewise, vegetation cover may return to predisturbance levels, but ecosystem processes may differ from reference sites (e.g., Lugo and Helmer 2004). We also distinguish between passive and active restoration practices, which differ in the intensity of human inputs. Passive restoration usually involves natural regeneration with little or no intervention, whereas active restoration includes interventions such as planting, seeding, soil amendments, manipulations of plant density and cover, and removal or reintroduction of individual species (Holl and Zahawi 2014).

Carbon Ecosystem Stocks and Flows

The main biological processes controlling C accumulation and loss and energy transfers in terrestrial ecosystems are photosynthesis and respiration. During photosynthesis, primary producers (autotrophs) reduce CO_2 from the atmosphere into organic compounds for biomass growth and energy storage. The total amount of C fixed during photosynthesis for an entire ecosystem is *gross primary production* (GPP), which is influenced by multiple factors (fig. 13-1).

Respiration releases energy via the oxidation of organic compounds. The net C gain by primary producers, or *net primary production* (NPP), is the difference between GPP and autotrophic respiration. The balance between GPP and all C losses from respiration, including that of consumers (heterotrophs), is *net ecosystem production* (NEP). The breakdown of organic matter (OM) through decomposition is an important form of heterotrophic respiration that results in trophic energy transfer and recycling of C and nutrients. *Net ecosystem carbon balance* (NECB) represents the total amount of C accumulation in an ecosystem through primary and secondary (higher trophic levels) production, minus all losses from plant, animal, and microbial respiration, lateral and vertical exports of dissolved, gaseous, and particulate organic and inorganic C (e.g., diffusion, leaching), and disturbance events (e.g., fire, erosion) (fig. 13-2).

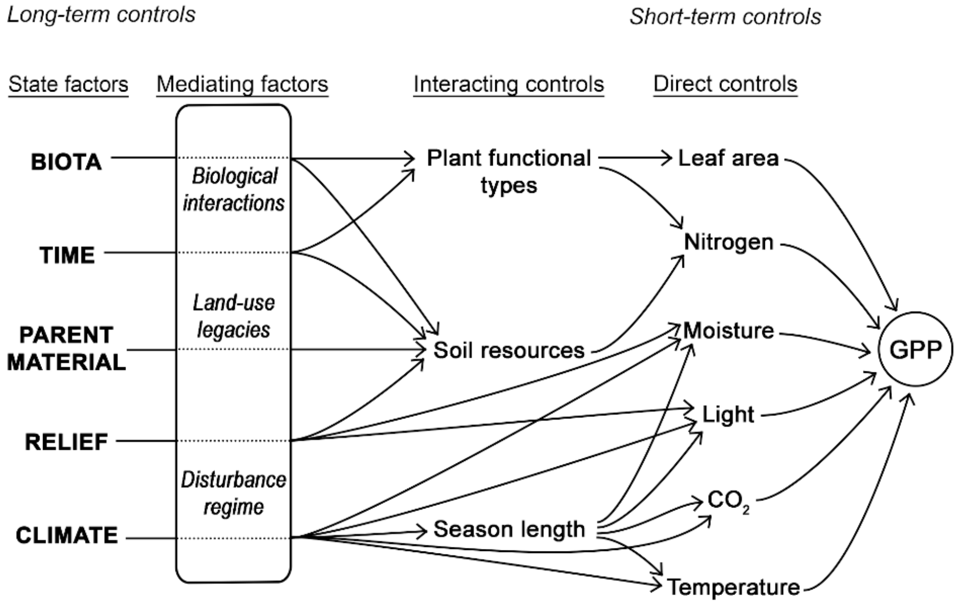


Figure 13-1. Gross primary production (GPP) is controlled by a hierarchy of physiological and environmental factors that exert short- and long-term influence on spatial and temporal variability in photosynthetic rates. Direct controls on GPP include leaf area and nitrogen content, which themselves are influenced by interactive controls, such as plant functional types. Other direct controls are soil resources, which vary spatially and temporally within and across ecosystems, and environmental factors, such as soil and air moisture, temperature and variations in day length and temperature. Short-term factors and interactive controls are influenced by long-term controls, represented by ecosystem state factors, which drive differences among biomes. In the context of restoration, the effects of state factors on interactive and direct controls are mediated by alterations to biological interactions, land use legacies and disturbance regimes resulting from past human activities, as well as contemporary management efforts. Modified from Chapin et al. (2012).

The C budget of an ecosystem is affected by the balance of C inputs and C outputs and can be expressed by a simple donor-controlled model:

$$\frac{\partial C}{\partial t} = Inputs - kC$$

where $\partial C/\partial t$ is the rate of change in C content over time and kC represents the output term, which includes the standing stock of C and a decay constant, k. In nonsteady state systems, C accumulates when the rate of inputs exceeds outputs and/or the rate of outputs decreases, either by a reduction in the standing stock or a decrease in turnover time ($1/k$) (see Torn et al. 2009). Identifying differences

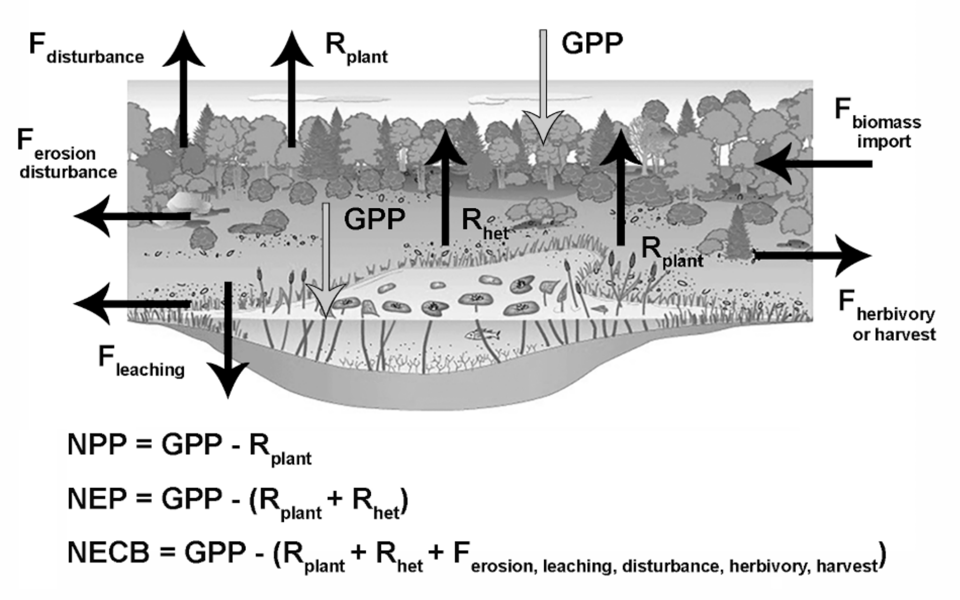


Figure 13-2. Major ecosystem carbon (C) fluxes (F) in a landscape that includes forests, grasslands, and wetland areas. Gross primary production (GPP) represents the major input flux of C into an ecosystem through photosynthesis by terrestrial and aquatic plants. Some of this C is lost via autotrophic respiration (R_{plant}). The remaining is represented by net primary production (NPP), which is commonly measured as the accumulation of plant biomass C in an ecosystem. Carbon gained through primary production is also lost via heterotrophic respiration (R_{het}) by animals and microbes through cellular metabolism and decomposition processes: the balance is net ecosystem production (NEP). Taking into account all C loss pathways allows for estimation of net ecosystem carbon balance (NECB). NECB is a measure of organic and inorganic C accumulating in an ecosystem after accounting for all losses. Losses of ecosystem C include gaseous, dissolved, and particulate C from all respiration processes, physical and chemical losses through leaching, erosion, and disturbance events, such as fire and biomass removal via herbivory and harvest.

between stocks and fluxes is especially important for quantifying whether an ecosystem is acting as a C sink or source. Changes in ecosystem processes over time alter the balance of C inputs and outputs.

OM is the main form of energy storage in terrestrial ecosystems; hence, the amount of biomass in an ecosystem is a common metric for assessing ecosystem function. In forests, for example, C stocks in plant biomass commonly are estimated as 50% of dry biomass, which can be measured directly by harvesting, or indirectly via allometric equations and remote sensing.

Carbon storage in an ecosystem can increase through C transfer into stocks with longer turnover times, such as long-lived woody biomass or soil organic matter (SOM), a heterogeneous mixture of plant, animal, and microbial residues in different stages of decay (Schmidt et al. 2011). SOM is an important contributor to soil fertility as a source of plant nutrients and of energy for decomposers, and through its high water-holding capacity and enhancing effects on soil structure. In calcareous soils and in arid ecosystems, substantial amounts of C can exist in inorganic forms.

Ecosystems differ in the allocation of C to different compartments. In grasslands the largest stocks exist belowground in root biomass and SOM, whereas in forests, large amounts of C are stored in aboveground biomass. Coarse woody debris and lianas can also contribute considerable C stocks in forests. In wetlands, C accumulates in organic-rich soils and sediments formed by the partial decomposition of plant debris under low oxygen conditions.

The potential for restoration to effectively remove C from the atmosphere and store it in ecosystem stocks depends on NPP and the residence time of C in each stock. For example, an actively growing forest can sequester C as trees grow and the amount of C fixed is greater than C lost via respiration and decomposition. A forest in C balance, or steady state, may also store C if the residence time of C in the largest stocks is long. Over its lifetime, a forest may transition from a C sink to a source, as respiration overcomes production (but see Stephenson et al. 2014).

The C balance of an ecosystem can be altered abruptly as a consequence of disturbance events, such as insect outbreaks or fire, which can result in catastrophic C losses (Flower and Gonzalez-Meler 2015; Kasischke et al. 2013). Fire suppression activities in fire-prone forests can lead to the accumulation of large fuel loads that increase the risk of severe fires and greater losses of ecosystem C (Hurteau and Brooks 2011; Swetnam and Falk 2015). A growing literature indicates that the short-term C cost of treatments such as thinning and prescribed burning has a substantial net benefit in terms of stabilizing large C pools in old forest stands. This example illustrates trade-offs between disturbance regimes, management options, and ecosystem processes.

Restoring Ecosystem Processes

Restoration efforts often target the following ecosystem processes: NPP (commonly measured as a change in aboveground biomass + litterfall), biogeochemical cycling, and water and nutrient availability (see chap. 12 for a discussion of nutrient dynamics). To restore these processes requires understanding of the factors that enhance, modulate, and inhibit succession rates (Walker et al. 2007). Management practices and time scales of restoration projects must acknowledge that success is in part related to how much is known about an ecosystem, and on the interactions between species and ecosystem processes.

Repeated sampling of the same site is one of the best ways to evaluate whether restoration targets are met and maintained over time (Osenberg et al. 2006). A more commonly used method for assessing restoration success is to use paired sites, where sites under different treatments are compared to a reference site, usually to undisturbed or more natural conditions, or to a degraded site. A chronosequence approach is common for measuring long-term (decadal to a century) dynamics of ecosystem processes. An important assumption of this method is that the patterns observed across sites varying in age are comparable to those occurring at one site over time. In severely disturbed sites, successional trajectories may lead to alternative states compared to what would be predicted under less intense or frequent disturbances (Walker et al. 2010). The availability of reference sites and measurements over appropriate time scales are important challenges in assessing restoration efforts.

Evaluating the recovery of a site is difficult, in part because of the subjectivity and site-specificity of restoration goals (Bakker et al. 2000; Higgs 1997). Some patterns do emerge from recent meta-analyses of restoration studies. In a synthesis of eighty-nine studies, restored site conditions were significantly improved over degraded sites for biodiversity, supporting and regulating ecosystem services (Rey Benayas et al. 2009). Compared to reference sites, however, restored sites had reduced levels of biodiversity and ecosystem services. In a wetland meta-analysis, biogeochemical cycling was greater in restored than in degraded sites, but still less than in natural wetlands (Meli et al. 2014). Another meta-analysis found C storage and plant diversity gains in restored agroecosystems (Barral et al. 2015).

We combined data from these three meta-analyses to evaluate the effect of restoration on C cycling processes. The data revealed a consistent pattern of improved conditions in restored sites relative to degraded conditions, but not the full recovery of undisturbed ecosystems (fig. 13-3). The response ratios of restored sites relative to degraded conditions were always greater than relative to the reference—for forest, wetlands and grasslands (fig. 13-3). Often (e.g., agroecosystems) there were no reference sites because entire landscapes had been converted. Overall, this analysis suggests that restoration is a useful approach for increasing C storage across landscapes, but greater sample sizes are needed to reveal ecosystem-specific effects (fig. 13-3).

The outcome of restoration efforts can vary with management approaches. Decisions on species selection for restoration often have to be made with incomplete information about species' characteristics and interactions. If C storage is a primary restoration goal, then choosing species with traits that support C gain is essential. Maximizing C storage can result in trade-offs in reduced species or functional diversity, or fidelity to native community composition. Pichancourt et al. (2014) presented a decision framework for maximizing biodiversity and C stocks and demonstrated that the greatest C storage could be achieved at intermediate levels of plant functional diversity in upland environments. In a restoration project

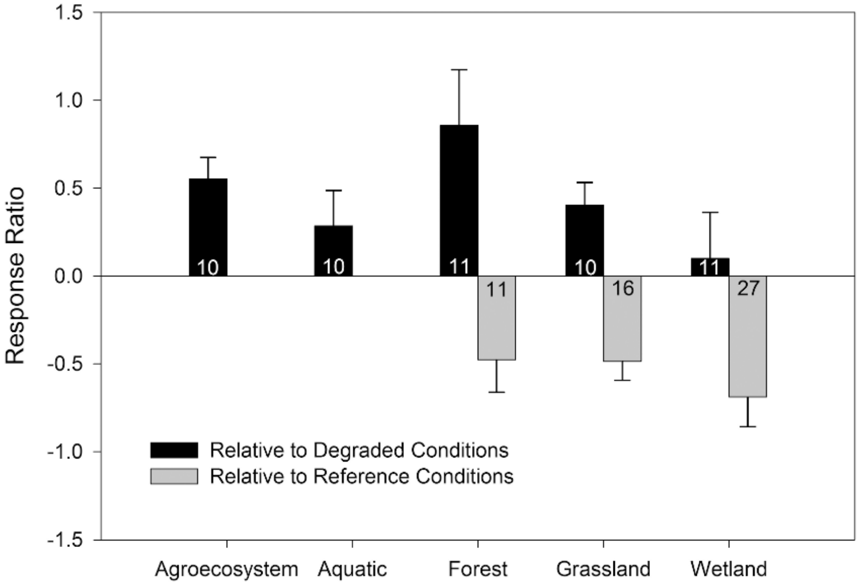


Figure 13-3. Comparison of response ratios from meta-analyses reporting data on carbon measurements after restoration (means + SE). Data courtesy of J. M. Rey Benayas, used in Rey Benayas et al. (2009), and from Meli et al. (2014) and Barral et al. (2015). The response ratio is the natural logarithm (ln) of the restored site relative to degraded conditions (black bars) or reference conditions (gray bars). Sample sizes are indicated inside bars. Data are not included for agroecosystems and aquatic ecosystems relative to reference conditions due to limited sample size. Variables used in the analysis were those identified to explicitly measure C or organic matter: soil C, percent of organic C, microbial biomass C, dissolved organic C, C concentration in water, organic acid C in pore water, C in roots, and soil C mineralization rate. Analysis of variance showed no significant differences in response ratios among the three vegetation types, which are the focus of this chapter: forests, grasslands, and wetlands. However, for these three ecosystem types, the response ratios relative to the degraded sites are always greater than relative to the reference conditions (paired t-test, $t = 6.00$, $df = 2$, $p = 0.0267$).

in Hawaii, Ostertag et al. (2015) proposed selecting species based on C storage potential and their redundancy or complementarity in life history traits (see chap. 8, case study box 8-1). Other models apply a response-and-effect framework, wherein response traits that influence community assembly and affect traits emphasizing ecosystem processes are considered (Laughlin 2014). These models represent efforts to apply ecological theory of the relationships between species and ecosystem function to restoration practice.

A restoration focus on ecosystem processes can be consistent with the maintenance of cultural landscapes that continue to be shaped by human use. Root-Bernstein and Jaksic (2013) described an example from Chile where multiple ecosystem services could be maintained by embracing a landscape's long history of human use. The *espinal*, an extensive silvopastoral system that harbors many endemic species, is currently threatened by agricultural expansion. Perceptions of overgrazing by low-income rural communities and of invasion by *Acacia* trees frame the *espinal* as degraded beyond the point of recovery, facilitating the way for land conversion. Root-Bernstein and Jaksic (2013) challenge these perceptions and provide innovative management practices aimed at restoring productivity of the *espinal*. These practices meet the dual goals of sustaining the silvopastoral ecosystem's economic and cultural value and protecting it from conversion to cropland or urbanization.

Restoring Wetland Ecosystem Processes

Wetlands are areas that are permanently or temporarily submerged by fresh, salty, or bracken water and include boreal peatlands to tropical mangroves, marshes, bogs, fens, swamps, and floodplains (Moreno-Mateos et al. 2012). Wetlands store large amounts of C due to high rates of NPP and slow decomposition and provide important fish nursery habitat (Zedler and Kercher 2005). Wetlands contribute to coastal stabilization and also help regulate the input of pollutants into aquatic ecosystems. For example, high organic C content and low oxygen supply make wetland soils ideal places for microbial denitrification, which reduces the leaching of nitrates that can cause eutrophication of aquatic ecosystems but produces nitrous oxide (N_2O), a potent greenhouse gas.

Wetlands are some of the most threatened ecosystems because of their location at interfaces between terrestrial and aquatic ecosystems, areas also attractive for economic development. In many parts of the world, organic-rich soils of peatlands, bogs, and fens have been drained for agricultural use or harvested as a source of household fuel. Estimates of global wetland conversion vary, but on average, almost 80% of estimated wetland area in 1700 has disappeared (Davidson 2014). Despite the importance of mangroves, peatlands, and other wetland ecosystems in the global C cycle, they are not included in global estimates of land change-induced greenhouse gas emissions (Houghton et al. 2012). Mangrove forests are some of the most C-rich wetlands, due to exceptionally high storage in deep organic soils and in woody biomass (Donato et al. 2011). Large uncertainties surround estimates of C emissions from the destruction of mangroves globally, but these are likely to be significant.

Rates of recovery following disturbance for wetland ecosystems vary. A historical analysis of mangrove areas on the Caribbean island of Puerto Rico found that despite large losses of spatial coverage due, initially to agricultural pressures, and more recently to urbanization, some mangrove forests did recover (Martinuzzi et al. 2009). This recovery was attributed to local agricultural abandonment and subsequent wetland protection laws. Ecosystem type, disturbance history, and restoration actions explained differences between restored and degraded sites in a meta-analysis of seventy wetland studies (Meli et al. 2014). Levels of biodiversity ecosystem services were greater in restored wetlands compared to degraded, yet supporting and regulating ecosystem services remained lower than in natural wetlands. Differences between restored and natural wetlands were primarily attributed to specific restoration practices.

Alterations to hydrological flow that result from manipulation of wetlands transform nutrient, carbon, and energy dynamics (also see chap. 14). The cultivation of drained wetlands leads to rapid losses of SOM and to soil subsidence. Carbon that may have been accumulating for 1,000s and 10,000s of years can be respired on time scales of decades to a century. A global meta-analysis of >600 sites found that hydrologic features such as water level, flooding regime, and water storage were more readily restored than biogeochemical functions or species composition (Moreno-Mateos et al. 2012). Rates of recovery for ecosystem processes were faster in larger wetlands (>100 contiguous ha) in warm and wet climates compared to smaller wetlands in cooler climates. Even after the recovery of hydrologic regimes in restored and created wetlands, C storage was 50% lower than in reference sites, and soil nitrogen concentrations were also depleted (Moreno-Mateos et al. 2012). A ten-year study in Thailand found differential species survival of mangrove plantings, yet all species fared better when flooding conditions were restored through an excavation pretreatment (Matsui et al. 2012). These studies demonstrate that an active approach (e.g., reinstating hydrological flow) may be necessary for successful wetland restoration.

The role of wetland restoration in C sequestration is controversial because of highly variable rates of C accumulation in restored or reconstructed wetlands, and because wetlands can also be large sources of CH_4, with a global warming potential twenty-five times more potent than CO_2 (Zedler and Kercher 2005). A study measuring natural and constructed wetlands reported large variability in the balance between C sinks and sources, with greater fluxes in tropical than temperate sites (Mitsch et al. 2012). Using a dynamic C model, the authors estimated that it would take three hundred years for long-term C sequestration in wetland soils and sediments to compensate for CH_4 emissions.

Wetlands exemplify interactions among ecosystem processes that can result in trade-offs in the provisioning of ecosystem services. Despite this, a recent analysis of the peer-reviewed literature revealed few studies examining these interactions in the context of restoration (Kimmel and Mander 2010). More quantitative studies of C changes during restoration and natural succession of wetland ecosystems will improve management and understanding of their role in the global C cycle.

Such studies should take into account changes in above- and belowground stocks and fluxes and their sensitivity to changes in environmental conditions, such as water levels, salinity, and temperature.

Restoring Grassland Ecosystem Processes

The world's grasslands have suffered losses in their spatial extent and productivity due to overgrazing, cultivation, and fire suppression that promote woody encroachment (Briggs et al. 2005). Temperate grasslands, savannas, and shrublands have the greatest ratio of habitat conversion to protected habitat, making them a critical terrestrial biome for restoration (Hoekstra et al. 2004). Given the economic importance of grasslands, restoration efforts have focused on improving productivity for livestock and habitat structure for wildlife. Efforts for rehabilitating grasslands have focused also on the potential for deep-rooted grasses to sequester C below ground.

The conversion of grassland to agriculture worldwide has contributed to atmospheric C emissions by enhancing SOM decomposition. The cessation of agricultural practices that disrupt soil structure, such as tillage, allow for the recovery of soil aggregate formation processes that are influential in the accumulation and persistence of C in grassland soils (O'Brien and Jastrow 2013). The amount of aggregate-associated SOM has been proposed as a sensitive measure for ecosystem restoration (Six and Paustian 2014). Grassland restoration can accumulate C in soils (Post and Kwon 2000), yet there is little evidence that formerly cultivated prairies can recover all soil C lost during agricultural use (DeLuca and Zabinski 2011).

Widespread prairie restoration efforts in the United States started in the mid-1980s with the Conservation Reserve Program (CRP), which compensated farmers for taking agricultural land out of production. Through the CRP, millions of acres of former agricultural land were seeded with native and nonnative grass species. Many of these landscapes have recently been plowed again for bioenergy crop cultivation (Gelfand et al. 2011; Lark et al. 2015), highlighting the vulnerability of long-term restoration efforts to changes in land use prioritization.

CRP lands have provided useful information about the factors that may influence the trajectory and rates of recovery of ecosystem components during restoration. Site age was found to be the most important predictor of SOM gains across a forty-year prairie chronosequence in Minnesota (McLauchlan et al. 2006). In Wisconsin, Kucharik (2007) found that the accumulation of soil C with increasing prairie age was short-lived and did not differ with soil type, suggesting a need to better understand site-specific factors. Others have found significant effects of soil texture on soil C accumulation rates during restoration (Baer et al. 2010).

Response rates for above- and belowground C stocks may be decoupled from each other during restoration and natural succession. In Illinois, aboveground biomass C and N recovered decades before soil stocks (fig. 13-4) (Matamala et al. 2008). Soil C and N accrual was related to vegetation type (C3 versus C4 grasses) and soil moisture but not to plant diversity (O'Brien et al. 2010). In a Minnesota study, the belowground response to prairie establishment on former cropland was independent of differences in aboveground productivity of vegetation treatments (McLauchlan et al. 2006).

Herbivores play an important role in shaping grassland ecosystems by influencing the temporal and spatial distribution of biomass and nutrients (Burke et al. 2008; Piñeiro et al. 2010). Experimental manipulations in North American tallgrass prairie and South African grasslands have found positive effects of grazing and fire on grassland productivity (Buis et al. 2009).

Both the removal and introduction of herbivores are used in grassland restoration, with domestic grazers replacing wild herbivores. The extirpation of many of the world's megafauna has led proposals for the reintroduction (or "rewilding"; Donlan 2005) of large mammalian herbivores in the grassland and steppe biomes of North America and Eurasia. In other cases, changes in grassland NPP are blamed on overgrazing, leading to policies to remove traditional livestock herders from grasslands (Butt and Turner 2012). The introduction of goats for grassland restoration is particularly controversial in areas, like islands, where grazing has not been a part of the historic disturbance regime. Regional differences in scientific and cultural perceptions of historical populations of native grazers can also make these practices controversial.

Grazing can negatively affect belowground NPP. In the semiarid steppes of Mongolia, soils from sites where grazing had been excluded for over thirty years showed reduced respiration rates compared to continuously grazed sites and greater amounts of particulate OM, which contributes to soil aggregate formation and C protection from decomposition (Wiesmeier et al. 2012). A meta-analysis of grazing effects on soil C revealed large differences in the response of C3- and C4-dominated grasslands under different rainfall regimes (McSherry and Ritchie 2013).

Large herbivores have been an important part of the C cycle in many natural grasslands for millions of years, and their reintroduction and exclusion can alter biogeochemical cycles and ecosystem feedbacks to climate change (Tanentzap and Coomes 2012). A better understanding of historical grazing regimes, duration and intensity of contemporary grazing, and of interactions among grazing and fire and site-specific environmental factors, such as rainfall regime, soil properties, and nutrient availability, will improve predictions of the response of grasslands to restoration.

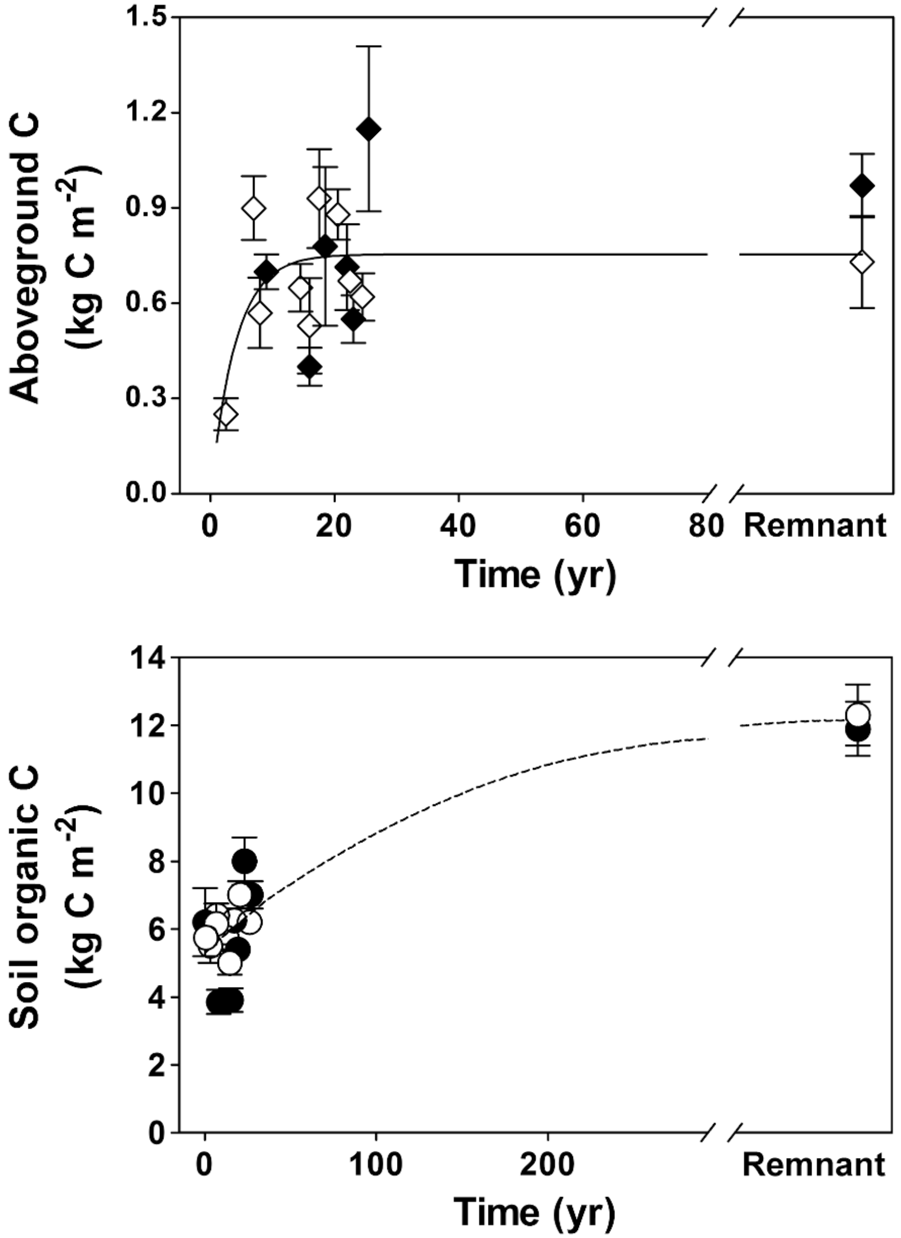


Figure 13-4. Above (a) and belowground (b) carbon stocks can show different rates of recovery after abandonment of agricultural use. In a chronosequence of actively restored prairies in Illinois, US, vegetation biomass achieved levels found in remnant prairies in less than 15 years, whereas soil carbon stocks were estimated to take more than a century to recover to precultivation levels. Restoration management included seeding and burning. Modified from Matamala et al. (2008).

Restoring Forest Ecosystem Processes

Worldwide, forests store some of the largest C stocks of all terrestrial biomes (Pan et al. 2013). Reforestation provides an opportunity to reverse some proportion of anthropogenic C emissions from land-use change (Houghton et al. 2012), although the amount of C accumulated during forest recovery can vary widely. Here we compare C storage under passive and active restoration methods. We address the literature on tree plantations only when directly relevant to restoration, such as a treatment in an experiment or for ameliorating soil conditions, because in many cases plantation forestry represents an agricultural land use.

The rate of structural change and C accumulation during restoration can be predicted from successional chronosequences. The extensive literature on natural forest regeneration after agricultural abandonment generally shows rapid recovery of forest structure, which is most commonly measured as stem density, basal area, and aboveground biomass. In the Brazilian Atlantic forest, basal area of actively restored riparian forests recovered to that of old-growth forests in twenty years, but stem density recovered more slowly (Suganuma and Durigan 2015). A number of studies have taken advantage of restoration plantings to examine C dynamics over time, by developing allometric equations for planted species (e.g., Giday et al. 2013; Nogueira et al. 2014). This approach introduces uncertainties (table 13-1) (Shimamoto et al. 2014), especially in highly diverse tropical forests given that species-specific equations may not be available and many published models are biased toward late-successional, large trees. Models that simulate changes in vegetation and C in response to management, fire, herbivory, and climate change are available for many temperate forests (Keane et al. 2011; Caldwell et al. 2013; U.S. Forest Service 2013; Wang et al. 2013; chap. 17).

Questions about the importance of species richness and composition in ecosystem processes dominate the ecological literature on C outcomes of restoration. In a modeling study, simulations of extinctions of tree species with different functional traits led to sixfold differences in estimates of aboveground C in a tropical forest (Bunker et al. 2005). In Jiangxi, China, a long-term experimental restoration project found that monocultures performed similarly to a more diverse forest, despite individual species effects (Wei et al. 2013).

Other studies demonstrate species differences. For example, in Atlantic forests in Brazil, four treatments were sampled ten years after establishment: low diversity plantings (five species), high diversity plantings (forty-one species), native forest, and a control (passive restoration) (Nogueira et al. 2011). Soil C did not differ among treatments, but the low diversity plantings had greater litter C than the control. In a study in southern China, biomass C was greatest in a naturally regenerating forest and smallest in a *Camellia* plantation, with pine stands having intermediate values (Zheng et al. 2008).

TABLE 13-1.

Differences in allometric equations developed from different forests can cause discrepancies in biomass carbon estimates, leading to uncertainties in measurements of forest recovery targets during restoration efforts. This example, modified from Shimamoto et al. (2014), compared the range (minimum–maximum) of biomass carbon (Mg C ha^{-1}) results from four different equations on the same data set to estimate carbon accumulation in three forests in the Atlantic forest of Brazil varying in age since restoration planting.

Allometric Model Reference	Diameter at Breast Height (cm)	Biomass C by Forest Age (Mg C ha^{-1})		
		7–20 years	21–40 years	41–60 years
Chave et al. (2005)	5–156	16.6–153.7	121.3–296.0	319.7–737.3
Scatena et al. (1993)	2.5–57	20.3–161.2	124.2–278.0	254.5–540.0
Brown (1997)	5–148	20.0–241.0	183.7–403.7	365.1–750.3
Chambers et al. (2001)	5–130	36.1–443.3	340.0–771.4	692.7–1461.2

Species effects on ecosystem processes can be deliberately used to facilitate restoration. For example, nitrogen-fixing trees can stimulate NPP and C recovery rates through increased soil N availability. In fifteen-year-old mixed-species restoration plantings on former pastures in Australia, total soil C increased under some N-fixers (Hoogmoed et al. 2014). Shimamoto et al. (2014) measured the effects of ten forest species that varied in life history traits on aboveground biomass accumulation under assisted natural regeneration and in late successional forests in the Atlantic forest in Brazil. Fast-growing species accumulated more C in the first thirty-five to forty years, after which they were overtaken by slow-growing species. Based on expected successional changes in the proportion of pioneer versus nonpioneer species, the authors recommended using species representing a mixture of life histories to maximize C gain during restoration, rather than just focusing on fast-growing species.

Restoration experiments provide insights into the positive effects of active restoration methods. In Spain, planting islets of oak on abandoned cropland increased soil C by 25% compared to passive restoration (Cuesta et al. 2012). In a Costa Rican experiment in tropical premontane rain forest, soil C did not differ among control plots under natural regeneration and two planting treatments with the same four species, one in which trees were planted as islands, and another where trees were planted in plantation-style rows (Holl and Zahawi 2014). Plantations had greater aboveground biomass accumulation of the planted species and less seedling damage than did the islands, but they were also more expensive to manage (Holl et al. 2011; Holl and Zahawi 2014). In some cases, active restoration practices may not fare much better than natural succession. Understanding where low-input or unassisted regeneration may recover ecosystem processes at the same or faster rates as unassisted restoration would help reduce costs.

The effectiveness of restoration practices may vary from site to site and from ecosystem to ecosystem. The intensity of past human use, disturbance regime, and degree of ecosystem alteration from an undisturbed reference site can influence the rate of recovery and the need for different restoration strategies (fig. 13-5) (Chazdon 2008; Sasaki et al. 2011). Past land use can leave a legacy on ecosystem processes; the duration of this legacy varies with intensity of human activities, disturbance regime, and site-specific factors. In mixed tree plantations in the Himalayas, C stored in vegetation and soil was initially greater at the abandoned agricultural site than at the highly degraded forest site that had experienced logging, fire, and grazing; but after twenty years, the two sites had similar C accumulation rates (Semwal et al. 2013).

Mining is particularly destructive as soils have to be reconstructed before vegetation treatments are initiated. A study in the Canadian boreal forest biome found no effect of site reclamation methods (e.g., amendments with peat and mineral soils, tailing sands, or overburden) or planted tree species on soil nutrients, SOM chemistry, and microbial composition (Quideau et al. 2013). All treatments, however, retained distinct properties compared to undisturbed soils. After twenty-five years, reclaimed sites showed some evidence of recovery of biogeochemical processing, yet microbial community composition appeared to lag behind. More studies with long time frames are needed to make general conclusions about the effectiveness of different restoration methods.

Role of Fire in Ecosystem Carbon Dynamics and Restoration

A full exploration of the ecological role of fire as an intrinsic and extrinsic disturbance and its application in restoration is beyond the scope of this chapter (see Bowman and Murphy 2010). Instead, we will outline briefly how fire affects major ecosystem C pools and processes and highlight examples from wetlands, grasslands, and forests. Fire has been at the center of policy conversations about climate as fires contribute large amounts of CO_2 and CH_4 to the atmosphere (Wiedinmyer and Neff 2007) and are predicted to increase in frequency and severity as a consequence of climate change. Fire also is used globally as a land-clearing agent and is thus tied closely to land-use change C emissions (Houghton et al. 2012).

Fires result in short-term ecosystem C losses from direct biomass combustion and delayed emissions from the decomposition of biomass killed during the fire

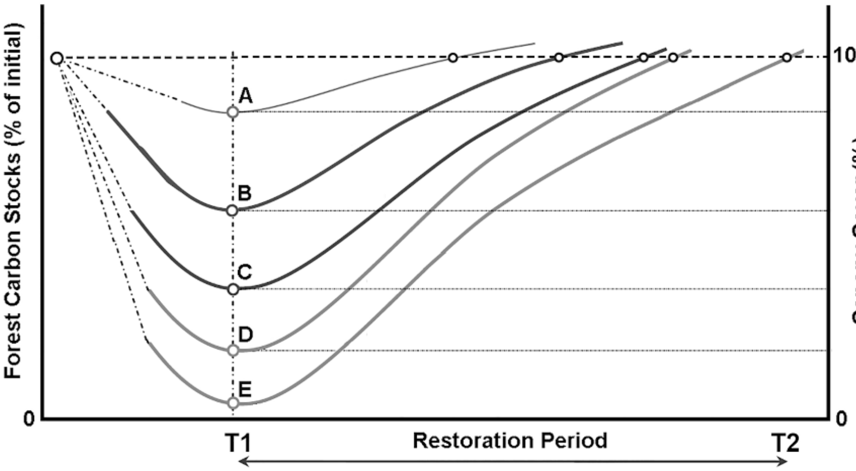


Figure 13-5. Trajectories of recovery of forest carbon stocks and canopy cover during restoration are predicted to differ based on degree of forest degradation (A–E). Slightly degraded sites (A) will recover forest structure more quickly and require fewer restoration efforts. Critically degraded sites (D) will take longer for recovery via natural succession (passive restoration) or require greater management efforts (active restoration) to regain initial forest structure. From D to E, the land is considered deforested and not just degraded. Modified from Sasaki et al. (2011).

(Hurteau and Brooks 2011). Severe fires can reduce long-term C storage by shortening the longevity of large and old trees and by influencing the rate of recovery and the C sink potential of forests (Pan et al. 2013). For example, in the Amazon, forest C accumulation rates were halved in sites that experienced five fires or more compared to sites without fire (Zarin et al. 2005). At the same time, fire suppression can lead to increased risk of ecosystem C losses in the future, as discussed earlier.

Fires can stimulate and depress NPP through its effects on SOM and nutrient availability. The net long-term effects of fires on belowground C pools are conflicting. Fires contribute to the loss of organic C from soils and to the storage of C in long-lived pools via the accumulation of pyrogenic C (DeLuca and Aplet 2008; Santín et al. 2016). Ultimately, larger and more frequent fires can disrupt successional trajectories and result in ecosystem replacement, with consequences for C (Bond-Lamberty et al. 2007).

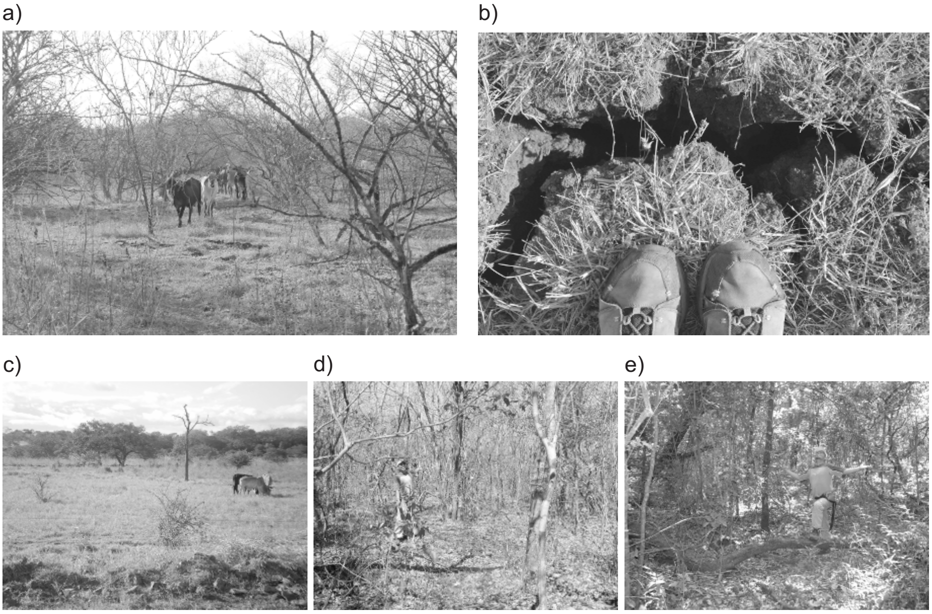
Land clearing for agriculture has introduced fire to ecosystems that did not burn in preindustrial times, such as wetlands and wet tropical forests. In Indonesia, oil palm establishment on peat swamp forests has increased ecosystem C losses from fire via emissions to the atmosphere and increased fluxes of dissolved organic C to rivers (Moore et al. 2013). The introduction of pastures in many tropical for-

Case Study Box 13-1
Predictors of Aboveground Biomass in Regenerating Tropical Dry Forests

By Rebecca Ostertag, Jennifer S. Powers, and Erika Marín-Spiotta

Tropical dry forests, Guanacaste, Costa Rica: The tropical dry forest biome worldwide has experienced severe fragmentation and destruction due to agricultural conversion and livestock production. Fire is used to maintain forage grasses, which resprout quickly after fire and prevent the regeneration of woody species.

In northwestern Costa Rica, careful management of fire and grazing is leading to the recovery of some secondary forests. These forests encompass several vegetation types that vary in their degree of deciduousness and species richness, and differ in recovery rates. Understanding the factors that can predict aboveground biomass on a landscape scale is useful for the recovery of habitat for biodiversity and for carbon management.



Case Study Box 13-1: Restoration of seasonally dry tropical forests of northwestern Costa Rica. (a) Cattle pastures are one of the dominant land uses replacing tropical forests worldwide. Whereas many ecosystems have evolved with large populations of herbivores, the introduction of domestic livestock into new regions can slow down recovery of woody species. The introduction of fire-prone pasture grasses also introduces a positive fire feedback that inhibits forest succession. (b) Forest regeneration is especially challenging in soils, such as the Vertisols pictured, where the clay minerals can be sensitive to compaction by cattle and to drying out events that cause the soil to crack and heave, affecting seedling regeneration. Fire suppression and the removal of cattle can facilitate forest restoration (c–e). An increase in stem density, aboveground biomass and canopy closure is evident 12 (d) and 60 years (e) after pasture abandonment. Photos courtesy of Jennifer S. Powers.

Case Study Box 13-1 continued

Supporting theory: Role of functional traits in ecosystem function
In order to identify what factors influence biomass recovery, Jennifer S. Powers from the University of Minnesota and her colleagues established eighty-four plots in two conservation areas in Costa Rica. Plots were stratified to encompass different vegetation types, stand ages, and soil properties. In contrast to the chronosequence approach, stratified sampling allows for identifying the relative importance of multiple predictors and scaling up to the landscape scale, rather than just along a temporal axis. This geographic approach is important as environmental factors are known to affect ecosystem processes, resulting in wide ecosystem and biome differences from place to place. Data on tree species abundances and trunk diameter were combined with species-specific data on plant functional traits including wood density, leaf nutrients and specific leaf area, to see whether tree species with different functional traits and carbon storage potential occur on different soils. The study will test whether ecosystem processes are a function of the traits and biomass of the dominant species present, such that a given process could be predicted by the community-weighted mean of all plant traits (or biomass production) of the species in the community.

Expected outcome: Aboveground biomass as an indicator of carbon stocks is predicted by stand age and related to the combination of edaphic properties, plant functional traits, and plant diversity.

Progress: Using advanced quantitative techniques (structural equation modeling), stand age was still the single best predictor of aboveground biomass, explaining 46% of the variation. The addition of soil pH and functional traits helped to explain up to 58% of variation in biomass. The large amount of unaccounted for variation in biomass stocks will require examination of additional variables to improve forest recovery predictions at landscape to regional scales.

Long term: As the plots age, successional changes in plant communities, aboveground biomass, and soil carbon stocks will provide key information about the role of environmental factors and climate variability on carbon accumulation and diversity. Current efforts are aimed at identifying tree species that can be used as restoration plantings to accelerate succession in pastures where intense grazing has resulted in soil compaction, and the cracking structure of the soils makes planting and watering efforts challenging.

References: Díaz et al. 2007; Calvo-Alvarado et al. 2009; Powers et al. 2009; Becknell and Powers 2014.

est regions has resulted in a positive feedback that maintains the dominance of fire-adapted grass species (Brooks et al. 2004). In those cases, active fire suppression is required for forest restoration (see case study box 13-1).

The use of fire may place restoration efforts and C sequestration goals at odds with each other. Fire is employed as a common restoration treatment in North American prairies to control woody plants (Briggs et al. 2005). While fire can stimulate NPP immediately following burning, repeated fire can result in large

C losses. In a modeling study, Martin et al. (2015) evaluated trade-offs between restoration practices targeting C accumulation and biodiversity conservation. Prescribed burning and thinning used to restore habitat for an endangered woodpecker resulted in reduced ecosystem C stocks (fig. 13-6) but was projected to protect fire-prone forests from future C losses. These examples illustrate complex interactions between disturbance and ecosystem processes and the need to identify restoration priorities, incorporate ecological history, and evaluate all possible outcomes when determining appropriate management.

Translating Restoration Ecology into Practice and Policy

In principle, restoration efforts can be consistent with global initiatives aimed at enhancing C storage in terrestrial ecosystems and reducing emissions from land-use change (e.g., REDD+ or payment for environmental services [PES]) (Alexander et al. 2011). An accurate accounting of C gains and losses and an identification of appropriate time scales for restoration are necessary for synergy between C sequestration and restoration efforts (Neßhöver et al. 2011). If restoration projects are undertaken with participation and buy-in of local communities, there is a greater possibility for investment in infrastructure, knowledge building, and jobs (e.g., seed collection, planting, monitoring, and verification) (Alexander et al. 2011). Restoration can be managed to improve livelihoods (Semwal et al. 2013), conserve biodiversity (Alexander et al. 2011), and help society and ecosystems adapt to climate change (Locatelli et al. 2015).

Numerous challenges remain before restoration is successfully implemented into C compensation schemes and vice versa. Foremost, restorative land use has to be valued more than alternative extractive uses (Barr and Sayer 2012; Semwal et al. 2013). More consideration needs to be given to the economic costs and benefits to all stakeholders (L'Roe and Naughton-Treves 2014), to the ethical and political context of restoration and REDD+ schemes (Meijaard and Sheil 2011), and to questions about land tenure and governance (Robinson et al. 2014).

Even if forest restoration is valued as a way to stem forest cover loss, controversies remain over the benefits of planting different types of forest. For example, forest C offset payments on Hainan Island, China, resulted in the replacement of natural forests by monospecific plantations (Zhai et al. 2014). In Brazil and other parts of the world, tree planting is occurring at the expense of natural grasslands (Veldman et al. 2015). Promotion of planted forests for climate mitigation also needs to take into account site and species-specific properties to minimize negative effects, such as soil C losses or reduced streamflow (Hodgman et al. 2012; Ponette-González et al. 2014) or changes in evapotranspiration and radiative properties that may affect precipitation and energy balance (Kirschbaum et al. 2011).

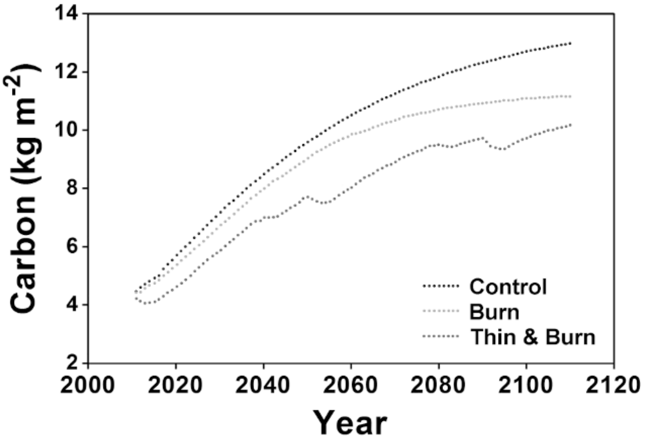


Figure 13-6. Management practices used to restore forest habitat for wildlife conservation can result in trade-offs for carbon sequestration. The effects of three treatments on forest ecosystem carbon stocks were compared using a forest simulation model: (1) control (no management), (2) prescribed burning to maintain existing habitat for an endangered woodpecker species, which requires low-density stands of longleaf pine with open understories, and (3) thinning and burning to increase woodpecker habitat. Figure modified from Martin et al. (2015).

More work is needed to better understand vegetation effects on climate to reduce unintended feedbacks that may offset climate benefits of ecosystem C uptake.

Interactions among ecosystem processes that result in positive or negative feedbacks among ecosystem products and services raise additional questions about market-driven restoration efforts. For example, the potential for selling ecosystem services of a restored wetland, such as habitat for biodiversity, C storage, and nitrate reduction as independent commodities increases the likelihood for ecosystem losses to be underestimated (Robertson et al. 2014).

Closing Remarks

A changing environment makes achieving specific restoration targets a challenge (Harris et al. 2006; Sutherland et al. 2009). Ecosystem processes are sensitive to changes in climate and climate variability (chap. 17), as evidenced by observed changes in NPP and NEP in response to increased temperature or to drought events (e.g., Ruppert et al. 2014). Rates of C accumulation during forest succession are influenced by climate and rising CO_2 (Marín-Spiotta et al. 2008; Anderson-Teixeira et al. 2013). Changes in ecosystem processes in response to climate can occur due to changes in the physiological activity of producers, consumers or decomposers and to species replacement. Feedbacks between terrestrial ecosystem processes and climate at a global scale are still poorly understood and are one of the main sources of uncertainty in projections of future atmospheric CO_2 and warming (Field et al. 2007; Friedlingstein et al. 2014).

Restoration targets also shift over space and time as our understanding of ecological history evolves, including the recognition of historic disturbance regimes and ancient humans' role in shaping ecosystems (Jackson and Hobbs 2009). Observed temporal shifts in the geographic distribution of ecosystems to past climatic change, as a result of alterations in species movement and productivity, suggest that ecosystem boundaries are flexible (e.g., Mayle et al. 2004). Mangroves and other coastal wetlands provide examples of inherently dynamic ecosystems whose spatial distribution has fluctuated on human time scales in response to anthropogenic pressures and to rising sea levels (Alongi 2011). Understanding the drivers and magnitude of variability in ecosystem processes is important for informing restoration efforts and C payments.

Ecological history is key for understanding successional trajectories and their response to future disturbance, especially in landscapes in different states of recovery from past human use, which characterizes much of our terrestrial biosphere. Human activities can leave long-lasting legacies on species composition and ecosystem processes, such as C storage and nutrient cycling (Lugo and Helmer 2004; Zamorano-Elgueta et al. 2014). Recognition of the importance of land-use legacies, introductions of new species, and changing environmental conditions (e.g., climate change, nitrogen deposition) is embodied in the "novel ecosystems" concept (Hobbs et al. 2006; Radeloff et al. 2015). As with many concepts in restoration ecology, this term has stirred some controversy (Murcia et al. 2014), yet it is useful for recognizing that many landscapes exist in varying degrees of alteration and that restoration baselines and the feasibility of different management practices are constantly shifting (Hobbs et al. 2011; Higgs et al. 2014). The novel ecosystem concept may offer protection value to some ecosystems where resources do not exist for restoration to historical conditions, or where there are no longer any reference sites to serve as a target. The concept also provides opportunities for creative ways of thinking about ecosystem conservation and experimental approaches to recover ecosystem functions, such as the use of exotic species to facilitate succession (Ewel and Putz 2004; Ostertag et al. 2015). Closing existing gaps in our knowledge of species' roles in ecosystems remains an active area of research that will improve our understanding of interactions among species composition, richness, and ecosystem function.

As our environment continues to change in response to anthropogenic climate change, alterations to biogeochemical cycles, and species introductions and extirpations, restoring to a specific historical target can be cost-prohibitive. A diverse portfolio of management practices is especially important in the context of C sequestration, where the trade-offs between maximizing C gain, biodiversity, and other ecosystem services must be considered carefully.

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Chapter 14

Watershed Processes as Drivers for Aquatic Ecosystem Restoration

David Moreno-Mateos and Margaret A. Palmer

Theory and Application

- In many aquatic and terrestrial ecosystems, alteration of local water stores and fluxes is the primary factor that causes degradation.
- Hydrological restoration requires a holistic approach that considers watersheds as geomorphological units in which directional water flows connect vegetation, soils, groundwater, and surface waters.
- Restoration of soil infiltration capacity and hydraulic conductivity must often be accomplished before ecosystems recover.
- In their restored state, hydrologic fluxes have characteristic magnitudes, timing, and frequency; these have shaped the evolution of organisms in the region and may be critical to the ability of those organisms to grow and reproduce.

Understanding the fundamentals of water flux and storage is essential to restoration ecology. Watersheds capture, store, and release water, and the flow of water links ecosystems, transports organisms and material, influences temperature regimes, and drives many biogeochemical processes. Losses and gains of water in one part of a watershed—whether through evapotranspiration, infiltration, or runoff—can influence the ecological status of adjacent and even distant parts. Despite the critical role water plays in all ecological systems, the water cycle has been disrupted in many regions of the world. The water cycle is driven by solar energy and gravity, but is dramatically influenced by human activities including the overextraction of water for agriculture or urban use, deforestation, and flow regulation. In fact, one of the factors that most limits restoration outcomes glob-

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ally is inadequate water availability. Even in regions that historically had adequate rainfall, availability may be increasingly limited due to unsustainable extractive uses, a changing climate, or poor land management. Herding of livestock and intensive agricultural practices have caused desertification, which is one of the most difficult syndromes to reverse through restoration actions.

Repairing heavily degraded landscapes requires a watershed approach including an understanding of what factors control infiltration and associated hydrologic processes as well as their interactions and feedbacks with ecological processes such as plant growth and water use. Repairing degraded waterways, forests, grasslands, and wetlands requires knowledge on how plant species and soil microbial processes interact with hydrological processes. In short, understanding the water cycle and watershed processes is fundamental to ecological restoration regardless of the ecosystem type of interest and a landscape perspective is integral to this. As emphasized in chapter 4, the spatial configuration of parcels of land and water and how organisms and propagules move across the landscape are critical to ecosystem restoration. The same is true with aquatic ecosystems: position in the watershed and position relative to other ecosystems determine the timing and quantity of water that is delivered, as well as its quality.

In this chapter, we provide a brief overview of the water cycle: interception, infiltration, evaporation, and transpiration; surface water and groundwater storage; water flow paths (runoff) and soil infiltration; and atmospheric moisture (fig. 14-1). These processes are in turn linked to watershed dynamics, including how land cover influences the quantity, quality, and timing of water yields and fluvial processes (erosion and sedimentation). Watersheds are partially independent geomorphological units because internal cycling is stronger than external inputs and there are strong linkages between the movement of geological and biological materials and the movement of water. Throughout, we stress how and why they are relevant to restoration in practice and provide specific examples of each. There is a body of theory and many concepts related to the larger fields of hydrology, geomorphology, and watershed sciences and we encourage the reader to supplement this primer by delving into those fields; this chapter merely serves as an entry point for restoration ecologists.

Building from the first principles of watershed and hydrologic science, several concepts and governing equations are central to understanding the role of water processes in ecological restoration. Six equations predict infiltration, soil water storage versus groundwater recharge, and soil loss (table 14-1). The basic gas laws and the adhesive/cohesive properties of water inform the practice of hydrologic restoration. The former are relevant to evaporative losses of water from plants and wet surfaces, while the latter help explain soil moisture retention.

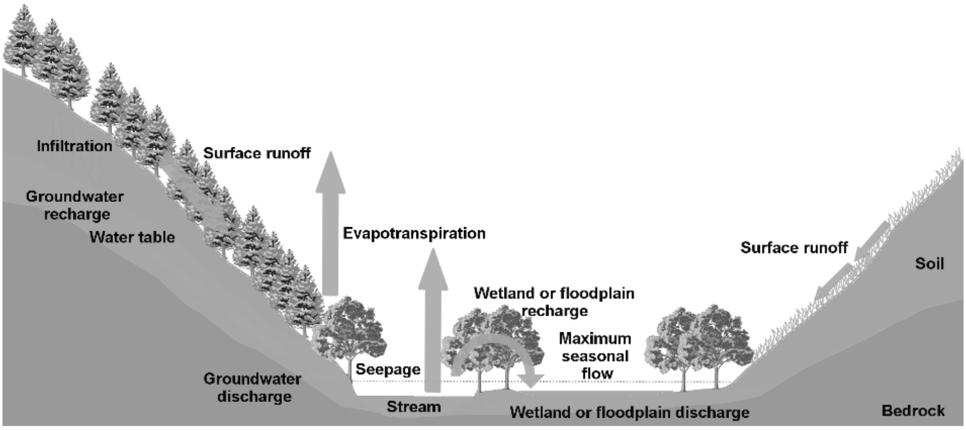

Figure 14-1. Recharge and discharge processes of streams and wetlands must be considered when restoring hydrologic dynamics at the watershed scale. Water table recharge and subsurface flow will replace overland flow as the dominant path of water to streams and wetlands when deforested or degraded hillslopes are reforested. Peak seasonal flows in free-flowing streams or restored hydrological flows can connect floodplains and wetlands with the main channel, allowing ground-water recharge and propagule dispersal.

Restoration of Governing Processes

Restoration requires a major focus on the soil system because of its importance to terrestrial vegetation and to water storage. Horizontal heterogeneity in soil moisture availability exerts a strong influence on plant community structure and biodiversity (Breshears et al. 2009). Combined with topographic complexity and vegetation characteristics (chap. 10), soil moisture influences runoff generation that drives hydrologic dynamics (Jencso and McGlynn 2011). Recovering the capacity of soils to absorb water may require mechanical “de-compaction,” nutrient additions, organic amendments, initial watering, and even the introduction of bioturbators, such as earthworms. Over time, soil hydrological conditions are then restored sufficiently to support plants, and the forces of gravity and capillarity action are able to move water to deeper soil layers. Restoring the vegetative cover, especially as forests, in turn increases porosity, water retention capacity, and hydraulic conductivity (Bonell et al. 2010; Buttle 2011; Perkins et al. 2012). Mycorrhizal amendments can further enhance nutrient acquisition by soils and assimilation by plants as well as increase water retention (Ohsowski et al. 2012). Recent research by Chen et al. (2014a) suggests that restoration actions can result in significant increases in the rate of water flow through soils even on highly degraded landscapes (fig. 14-2).

Table 14-1.

Examples of important concepts and governing equations that influence dynamics relevant to ecological restoration at the watershed scale.

Concept	Equation	Description
Water budget equation	$\Delta S = P - ET - Q - \Delta G$, where ΔS is the change in water storage as a function of precipitation (P) minus losses due to evapotranspiration (ET), runoff (Q), and deep groundwater seepage (G, could be inflows or outflows).	The amount of water stored in soils, aquifers, or the water table is influenced by evaporative losses from soils, water bodies, plants, and plant transpiration. It affects water yield (flow to surface waters) and is influenced by land use.
Interception	$I_c = P_g - T - S_f$, where I_c is the amount of water intercepted by the canopy, P_g the gross precipitation, T the throughfall, and S_f the stemflow.	The process of water interception by the canopy and how that water is partitioned among the plant assemblage structures. Typically as restoration from new forest planting proceeds, T decreases and S_f increases.
Soil infiltration	$F_c(\mathrm{t}) = f_1 + (f_o - f_l)\mathrm{e}^{-kt}$ (Horton's eq), where f is the infiltration capacity at time t, f_o is initial and f_c final infiltration capacity, and k is an empirical constant.	The process by which water on the ground surface enters the soil. It varies with soil texture, structure, surface features, amount of organic matter, depth of impermeable layers, and presence of macropores.
Soil hydraulic conductivity	$k = Q \cdot L / A \cdot \Delta H$ (Darcy's Law), where k is the soil hydraulic conductivity, Q the rate of water flow, A the cross-sectional area, ΔH the change in head, and L the length of soil column.	Soil attribute describing the ease with which water moves through pore spaces or fractures. It depends on the intrinsic permeability of the soil, which relates to its texture, composition, and structure.
Topographic index	$TI = \ln\ (A/\tan\ G)$, where A is the contributing area and G the slope gradient at a site.	Index that takes both local geometry and site location into account to measure the extent of flow accumulation at a given point on a topographic surface. It can be used to describe how soil moisture varies across the landscape.
Modified universal soil loss equation	$A = R \cdot K \cdot LS \cdot VM$, where A is the soil loss, R the rainfall erosive factor, K the soil erodibility, LS the topographic factor (slope length, steepness), and VM relates to land cover with subcomponents like canopy cover and presence of vegetation close to the ground.	Erosion is the process of relocation of soil and rock due to the action of water flow or wind. GIS and modeling facilitate predictions of soil erosion over a wide range of spatial scales.

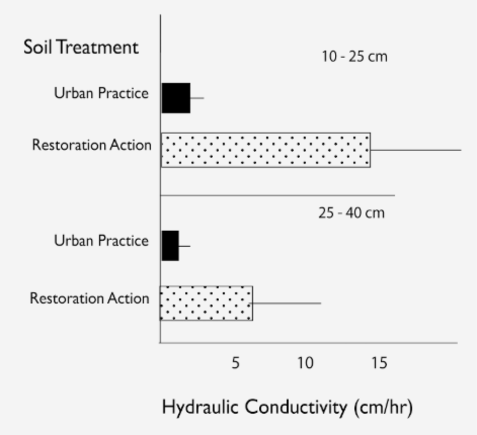

Figure 14-2. Restoration actions to improve the rate at which water flows through soil (hydraulic conductivity) can be critical to ecological recovery in areas with highly compacted soils, such as those in urban regions, mined areas, and some agricultural lands. Experiments demonstrated that deep tillage combined with organic amendments and tree planting ("restoration actions") greatly increased the saturated soil hydraulic conductivity (k_{sat}) compared to simpler restoration actions that only partially replace the A soil horizons. Modified from Chen et al. 2014a.

Infiltration and Soil Water Storage

Restoring more natural hydroperiods and associated biogeochemical processes in degraded watersheds is essential to the provision of water quantity and quality needed to support healthy ecosystems. The rate at which water enters the soil is influenced by rainfall (intensity, duration), characteristics of the land cover, and properties of the soil. Landscapes with dense plant canopies and broad leaves may intercept a large amount of rainfall, and much of what is not passed through the canopy as throughfall or stemflow may be lost due to evapotranspiration, depending on humidity, temperature, and wind conditions. Of that moving through the canopy, a fraction may be taken up by groundcover vegetation or stored in litter layers. Water infiltration into the soil due to capillary action and gravity is influenced by the presence of colloidal materials; soil pore space; and presence of macropores, organic matter content, and soil texture.

Land clearing reduces interception and infiltration so the most common restoration action is to revegetate. Planting of rapidly growing nonnative species may stabilize soils (García-Palacios et al. 2010); however, such species could reduce soil moisture enough to outcompete native species (Thaxton et al. 2012). Large-scale land clearing in the form of deforestation not only influences soil moisture by reducing infiltration but can also lead to changes in the rainfall amount, location, or distribution over time (Lawrence and Vandecar 2015). Replanting forests is now a major restoration enterprise, but how and if it increases net water storage is complex and controversial (box 14-1). For example, although deforestation may increase flooding risk because it reduces the water-holding capacity, reforestation may have negative effects on wetlands, through a decrease in the amount of water available to maintain wetland functions (Woodward et al. 2014). Thus, trade-offs may exist between restoring forests and restoring wetlands in the same watershed, and in some cases, restoring historical extents of both might not be possible.

Box 14-1
Water Yield and Forest Restoration: Not a Simple Story

Restoration of forests is a common environmental policy for recovering lost water resources. Most forest restoration for water programs are based on the assumption that forest area is a proxy for water-based ecosystem services. However, water flows that result from reforestation are rarely quantified. Empirical research on reforestation and water dynamics has been done at local scales—typically small watersheds where reforested areas clearly have higher soil infiltration rates. But since evapotranspiration is typically higher in forested areas, water yield to streams can change little or even decrease. There is little empirical evidence that total annual yields are increased, although forest restoration can change the seasonality of water yield—most often increasing dry season flows. Reforestation can provide water regulation benefits, meaning less variability in yields such that flooding is less likely following rainstorms. Presumably, variability is reduced with greater shallow subsurface storage capacity given more plant roots or macropores.

While wetlands and streams have been observed to dry up following deforestation, such observations have also followed forest restoration. In fact, deforestation and timber harvest may result in a rapid increase in water yield compared to nearby forested watersheds. This is largely due to a reduction in plant uptake of water and changes in evapotranspiration. While there are fewer data on deep recharge, it is possible that lower water interception and infiltration rates in deforested watersheds result in less water moving to deep storage; thus, more is available as streamflow. If, however, the deforested land is permanently converted to a high impact use (e.g., livestock, urbanization), then decreases in recharge are certain, so that eventually baseflow water yields may decline.

Modeling studies at regional and global scales suggest that deforestation will lead to decreases in rainfall largely due to changes in the distribution of evapotranspiration (less moisture returned to the atmosphere). If the reverse is true and forest restoration results in an increase in rainfall and perhaps eventual increases in water yield, two questions remain: Where will this precipitation fall, and will restoration at local scales scale up to help solve regional water problems? In sum, research thus far is simply inadequate to sort out the array of interacting factors that influence the effects of forest restoration across a variety of scales and locations.

References: Bruinjzeel 2004; Abjornsen et al. 2011; Roa-Garcia et al. 2011; Ellison et al. 2012; Perkins et al. 2012; Salemi et al. 2012; Gageler et al. 2014; Li et al. 2014; Ponette-González et al. 2014; Woodward et al. 2014.

Despite these complexities, forest restoration can enhance soil conditions, which in turn leads to increased infiltration rates with subsequent positive feedbacks to growth of the forest. On the island of Maui, Hawaii, less than 10% of the original dry forest remained when actions were taken to restore disturbed grassland to forest. Beginning in 1997, scientists, natural resource managers, and landowners worked together to restore a four-hectare tract of land. They fenced out grazing animals; removed an invasive grass; and replanted native grasses, shrubs, trees, and vines. After fourteen years, soil properties had changed significantly including a twofold increase in saturated hydraulic conductivity that further enhanced plant growth in this low-rainfall region (Perkins et al. 2012). Additionally, water infiltration rapidly reached depths of a meter or greater during the measurement period, leading scientists to suggest the potential for aquifer recharge (Perkins et al. 2014).

Water percolating to deeper soil layers or bedrock becomes groundwater and may recharge aquifers or flow along impermeable geological substrates in sedimentary formations or along subterranean crags and channels in calcareous rock formations (e.g., Karst). Groundwater recharge can also occur through seepage from lakes and ponds or from streams (fig.14-1). Recharge of aquifers and the water table is a core watershed process that must be tackled to achieve certain hydrological goals. Based on studies documenting increased stream flows following loss of vegetation (Brown et al. 2013) and increased soil infiltration rates following replanting (Perkins et al. 2012), watershed revegetation is commonly assumed to increase groundwater recharge (Buttle 2011; Perkins et al. 2012). However, the effect of terrestrial plant restoration on below groundwater storage is complex, and if it occurs, recharge takes a very long time (decades to millennia). For example, the enhanced recharge reported by Buttle (2011), was not verified in many other cases.

Studying groundwater dynamics in response to restoration is difficult because surface watersheds and subterranean watersheds do not always coincide. In sedimentary watersheds, groundwater flows may travel and emerge to create seepages, springs or wetlands, often many kilometers away or even in topographically independent watersheds (Toth 1963). This means that local restoration actions may not promote ecosystem recovery if the distant source of water is not restored or preserved as well.

Terrestrial-atmospheric interactions contribute to the complexity of hydrologic responses to restoration. Surface water, soil water, and water in the plant canopy evaporates to the atmosphere at rates varying with temperature, relative humidity, and wind speed. Vegetation, particularly forest cover, may retain and evaporate rainfall at rates ranging from 4% to >90% depending on forest type, rainfall intensity, or temperature (Crockford and Richardson 2000). The same vegetation will release water to the atmosphere via transpiration, regardless of the amount of rainfall. Losses due to evapotranspiration translate to decreased replenishment of groundwater and outflow, and thus reduced supply of water to downstream ecosystems and water bodies (Oishi et al. 2010).

Other hydrological and hydrometeorological processes may have local importance in some watersheds. For example, water is lost to the atmosphere through sublimation in boreal and alpine watersheds (Friesen et al. 2015). Elsewhere, fog water may provide up to 40% of the total water throughfall in watersheds (Ritter et al. 2008). Fog water captured by tree leaves is diffused through leaf cuticles, reducing root water uptake and reducing tree evapotranspiration in adverse seasons; or, it drips onto the soil and increases soil moisture (Ewing et al. 2009; Eller et al. 2013). As a consequence, fog water reduces water loss, which could potentially support groundwater recharge. For these reasons, restoring trees to capture fog water might be essential in some watersheds, but it may take long periods to reach predisturbance levels. A viable forest restoration strategy in some regions is to harvest fog water mechanically and use this to enhance survival of young seedlings until trees grow large enough to capture fog water themselves (Domen et al. 2014).

Runoff and Stream Flows to Support Aquatic Ecosystems

Water not infiltrating to deeper soil layers or bedrock becomes runoff, either above- or belowground, and flows downslope toward streams, lakes, wetlands, or the sea. Depending on regional geology, these processes may act at the entire watershed scale (e.g., in areas underlain by granite) or only subareas (e.g., in karstic watersheds). Runoff moves through a network connecting every topographic point in the watershed with the outflow (mouth). Thus, any action that affects the hydrological conditions or water quality at any point will have a downstream effect.

Largely due to changes in infiltration and soil storage capacity, water runoff to streams varies greatly in quantity, timing, and quality among landscapes subjected to different types and levels of human impacts. Thus, watersheds that are fully forested have significantly different discharge patterns compared to nearby urban or agricultural watersheds (fig. 14-3). The most difficult restoration challenges are associated with excessive runoff in urban regions with extensive pavement and compacted soils. In urban watersheds, peak stream flows during rainstorms can be much higher than in vegetated rural areas, and summer baseflows can be highly altered by reduced groundwater recharge (Fletcher et al. 2014). Direct runoff from impervious surfaces causes stream channels to incise, and stream biota are impoverished. As we describe later, restoration actions that focus only on in-channel structural changes (e.g., adding large boulders and constructing weirs to slow flows) have not been shown to recover urban stream ecosystems biologically

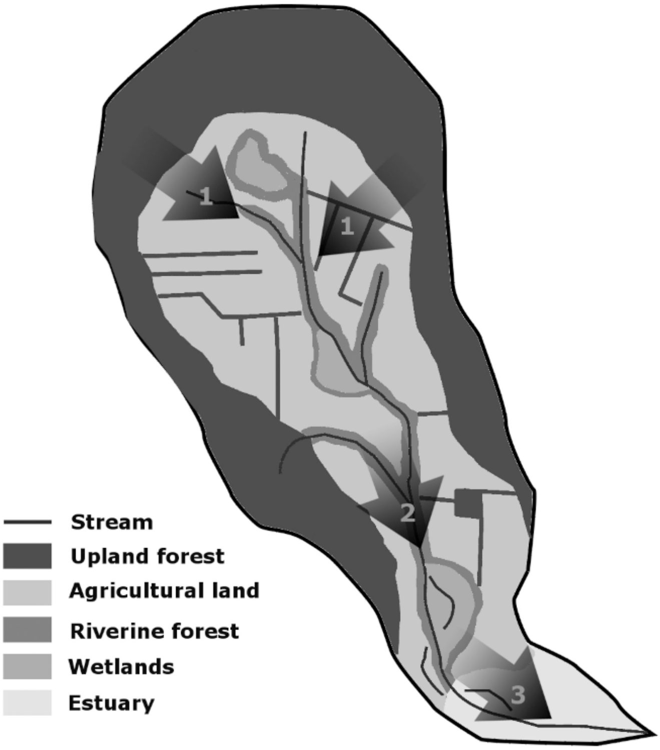

Figure 14-3. A three-step approach to watershed restoration. First, restore the headwaters' plant cover, forests, shrubland, grasslands, or mixed vegetation to restore processes such us soil retention, propagule dispersion, and nutrient cycling. Second, restore the intermediate stream reaches where agricultural areas are located by restoring hedgerows, forest patches, and riparian vegetation. This second phase may also involve restoring floodplains and inland wetlands. The aims are to reduce the impacts of agricultural production (e.g., reducing erosion and export of agricultural nutrients and sediments) and recover processes related to landscape connectivity (e.g., plant and animal dispersal). If the stream channel is incised or otherwise degraded to the point that ecological processes are impeded, a third phase could involve channel adjustments down to the delta, estuary, or other mouth geomorphology. This third phase could involve increasing in-channel heterogeneity (e.g., adding log-jams and boulders) and restoring estuarine hydrological gradients.

(Palmer et al. 2014). Current research suggests biodiversity loss in urban streams is driven by high levels of conductivity and metal pollutants that are washed into streams by excessive runoff (Vander Laan 2013). Watershed approaches are needed to reduce flows and minimize pollutant loads (Fletcher et al. 2014).

Reduction or elimination of vegetation by logging or agriculture also increases overland flows, which often increases soil erosion resulting in large inputs of sediments to downstream networks. Restoration of landscape vegetation has been shown to reduce runoff and the input of sediments to streams (Miller et al. 2015). The same happens when restoring riparian vegetation if the riparian cover aligns with the dominant flow paths (Weller and Baker 2014) and if there are no significant gaps in the riparian cover or gullies that cut through the cover. Restoration is also used to reverse the impacts of excessive groundwater pumping for consumptive uses. Large-scale restoration approaches include restricting pumping and constructing artificial wetlands and recharge basins near the river to return baseflows. These ecologically engineered systems must be strategically placed to provide appropriate depth to groundwater, to augment locally depleted aquifers, and where hydraulic conductivity can facilitate recharge. Such approaches may be key to recovering groundwater-dependent streams and wetlands in arid and semiarid regions (Lacher et al. 2014). For example, much of the riparian vegetation along the Upper San Pedro River basin in Arizona (US) relies on groundwater. To offset water pumping and diversion, a network of recharge sites is being designed to return treated effluent or stormwater runoff to the aquifer to sustain riparian vegetation and associated wildlife (Lacher et al. 2014).

Restoration is increasingly focusing on reversing the hydrological and ecological impacts of dams. Typically built to retain water for agriculture or hydropower, dams homogenize downstream flow regimes by modifying the magnitude and timing of ecologically critical extreme flows (high and low) and sediment fluxes (Poff et al. 2007). River flows below dams are usually very different than they were historically (fig. 14-4), often being driven by reservoir releases to meet daily power needs. When dam removal is not an option, efforts to restore downstream riverine ecosystems including sandbars for habitat have involved planned releases from the reservoir (Grams et al. 2015). Deliberate flows can be planned to mimic historical flow and thermal regimes (Warner et al. 2014). High flows during parts of the year can inundate floodplains (“making room for the river”; Overton et al. 2014).

Ecological flow releases in the dry season that are necessary to support fish are also a restoration option (e.g., as in plans for the Dahewan Reach of the Yalongjiang River in southwestern China; Chen et al. 2014b). Additionally, temperature control devices (TCD) on dams can allow for variable water withdrawals from the reservoir to control temperatures in water released downriver (e.g., Shasta dam TCD on the Sacramento River; Caldwell et al. 2015). Some of the most high-profile restoration projects have removed dams to restore anadromous fisheries. For example, along coastal Maine (US) dam removals have restored the density and biomass of Atlantic salmon, alewife, and sea lamprey in previously inaccessible upstream reaches (Hogg et al. 2015). As we describe later, scientists have made good use of these projects to advance their understanding of hydrogeomorphological processes.

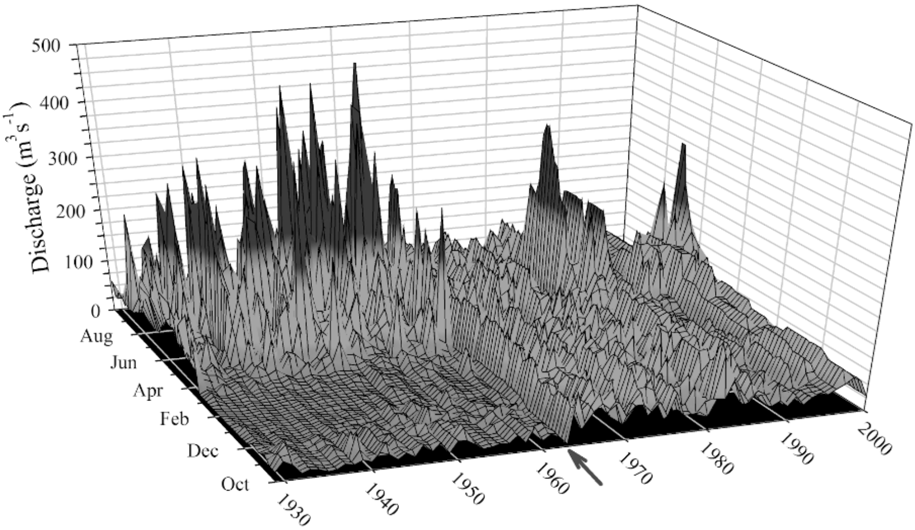

Figure 14-4. The construction of dams fundamentally alters the timing and magnitude of river flows below reservoirs (Lytle and Poff 2004). Here, the Green River in Utah, US, historically had extremely low flows throughout the winter and fall and high, somewhat flashy flows starting in the spring when snowmelt runoff began. Once the dam was built (arrow), variability in flows was dramatically reduced so there were fewer droughts and floods. To fully restore river biota and ecosystem processes under such conditions, some or all of the historic flow regime will need to be restored. Modified from Lytle and Poff (2004).

Geomorphological Processes

Among the multiple geomorphological processes shaping Earth's surface (e.g., glacial, volcanic, tectonic, eolian processes), a few can be framed in a generalizable watershed context. Some of the most relevant are fluvial processes, including erosion and sediment deposition, and hillslope processes, including landslides or rock-falls. Land erosion is a natural process that drives important geomorphological processes, like meandering, scouring, or sediment accumulation in streams, rivers, and estuaries. Erosion is accelerated by the loss of plant cover derived from human and natural disturbances, and extreme rainfall events can enhance erosion, particularly where bare soil is exposed.

Four erosion processes affect bare soils: (i) splash erosion caused by the force of water hitting the soil and releasing fine particles, (ii) sheet erosion caused by laminar water flowing over land, (iii) rill erosion caused by water that concentrates in small rivulets, and (iv) gully erosion caused by large, rapid flows. As flowing water accumulates the released sediments, its viscosity increases, thus increasing its energy to transport more sediments until the energy dissipates in flatter areas (Julien 2010). Erosion increases the steepness of hillslopes, washes nutrients and organic matter from soils, and reduces soil cohesion. Sediments are transported downstream and deposited in stream valleys, pools within streams and in nearby wetlands, eventually filling them in.

Sediment accumulation negatively affects the structure and functioning of wetlands and streams. Coarse stream sediments can clog with excessive fine-grain deposits, which affects invertebrate and fish communities (Rehg et al. 2005). Sedimentation also complicates the restoration of vegetation. Restoration to reduce the impacts of excessive erosion and downhill/stream sedimentation typically occurs through native plantings. Restoring dense plant cover in the headwaters has proven effective in reducing soil erosion (Zhang et al. 2015). In southeast China, forest restoration on former agricultural areas reduced soil loss from 53 to 256 tons ha^{-1} to no loss after eight years (Zhang et al. 2004), and except in very high rainfall years, soil loss has continued to remain low (Zhang et al. 2015). Similarly, in Mediterranean watersheds, plant cover was restored and sediment yields were reduced by three orders of magnitude after eighty years, compared with the prerestoration state ($>10^5$ mg L^{-1}) (Navarro Hevia et al. 2014).

It is not always excessive sediment that degrades streams and rivers; deficits of sediment can be just as damaging. Restoration in such cases involves inputs of sediment or gravel, which is often done below a dam or other permanent flow-reducing structures. This can benefit aquatic food webs and fish that depend on specific particle sizes for spawning. However, the gravel is rarely retained over the long term, so repeated efforts are needed (Pander et al. 2015). Alternatively, sediment might be passed through or around reservoirs an action that comes closer to restoring a natural sediment regime (Wohl et al. 2015). In salt marshes sedimentation must keep up with rising sea level to sustain current ecosystems. Additionally, urbanization, dikes, and levees have reduced sediment flux down rivers resulting in subsidence of marshes (Wigand et al. 2014).

In coastal Louisiana, US, where wetland loss has been and continues to be extreme (estimated at 5,000 km^2 since 1932; average rate >40 km^2 per year between 1985 and 2010) restoration measures could include large sediment diversions to the marshes to increase accretion rates (Wang et al. 2014). Restorationists need to anticipate negative impacts of sea level rise and treat sediment as a resource; for example, dredge spoils from maintenance of boat channels can be used to elevate marsh plains that have subsided behind dikes in coastal wetlands (e.g., San Francisco Baylands; Callaway and Parker 2012).

Other biogeomorphological processes are being restored in a variety of ecosystem types. Inputs of wood from fallen trees and associated log-jams can increase aquatic habitat heterogeneity and reduce flow speed, positively affecting the diversity of aquatic macroinvertebrates, purifying water, controlling erosion, and enhancing fish populations (Beechie et al. 2010; Acuña et al. 2013). Indeed, one of the most common and simple restoration actions for streams is to add large woody debris. For example, adding large wood and boulders to northwest streams of the US increased coho salmon-rearing capacity by 32% in about six years (Jones et al. 2014) and increased juvenile coho salmon density from 0.19 to 2.32 individual m^{-1} (Beechie et al. 2010). At larger scales, adding wood and log jams helps trap sediment, organic matter, and plant propagules. Over the long term, these processes help recover degraded rivers (Osei et al. 2015). The presence of woody debris may be particularly important in mid to lower watershed areas that lack steep slopes (about 6%). Beaver dams strongly affect sedimentation, morphology, and stream species diversity (Burchsted et al. 2010). They can also help recover the hydrology and biogeochemical processes of highly incised stream channels (Pollock et al. 2014). In such cases, reintroducing beaver populations where they have been extirpated may be an essential management tool integrated in watershed restoration programs, including those targeting wetland and stream restoration (Gibson and Olden 2014).

Watershed Perspective on Restoration of Aquatic Ecosystems

The relative importance of various hydrologic processes to ecological recovery varies regionally and among ecosystem types, and restoration of water dynamics largely defines recovery of aquatic ecosystems. We provide brief overviews of the role of hydrology in the recovery of two types of aquatic systems; more in-depth treatments of riverine and wetland restoration appear in general texts (e.g., Moreno-Mateos et al. 2012); and new findings are continually emerging on the link between watershed processes and restoration of ecological structure and function in these systems (Meli et al. 2014; Palmer et al. 2014).

Running Water Ecosystems

Hydrologic regime has long been considered a master variable in riverine ecosystems because it, along with sediment dynamics, directly affects channel form and consequently the biota and ecological processes within the channel. Aside from dams and diversions, one of the most significant impacts on streams is a reduction in watershed infiltration capacity due to land use changes. In such cases, there is disagreement over whether manipulating various aspects of the flow regime (e.g., restoring or reducing peak flows) is sufficient for full recovery of stream ecosystems. This controversy has arisen because the dominant restoration practices for streams have been focused on direct manipulation of the stream channel in order to alter in-channel flow velocity (Palmer et al. 2014); restoration focused on entire watersheds is far less common (Smucker and Detenbeck 2014).

Most stream restoration has centered on channel morphology: how to design a channel given the water discharge and sediment regime in the context of a particular watershed and landscape (Smith et al. 2011). Restoration designs typically use a "reference reach" (section of a nondegraded or less degraded nearby stream channel) to identify the channel patterns and processes that need to be achieved. The assumption is that once a channel is manipulated to handle the prevailing flow and sediment fluxes and habitat heterogeneity is enhanced, then species assemblages, primary production, decomposition, nutrient processing, and other ecological processes will be restored (i.e., the "field of dream hypothesis"; Palmer et al. 1997). However, this assumption is rarely valid (Palmer et al. 2014; Kitto et al. 2015). Similarly, while habitat influences ecosystem processes and species interactions (chaps. 3 and 10), if the water is polluted, restoration of processes and species will be very difficult. The source of ecological degradation for most streams and rivers is at the watershed scale and is most often associated with poor land use management that leads to polluted water or highly eroded stream channels; this is why landscape scale restoration approaches (chap. 4) must be taken.

Manipulating channel shape to convey flow does not necessarily restore the hydrological and geomorphological processes necessary to support healthy ecological communities. Restoration of several processes is critical for recovery of stream and river ecosystems (Wohl et al. 2005). Examples of such processes extend well beyond water infiltration to include the subsequent biogeochemical transformations as water is routed from the soils to streams, the dynamic water exchanges between the groundwater, hyporheic zone, and surface water, and the overbank flows into vegetated floodplains.

Restoration ecologists are now working actively with practitioners to apply hydrologic, geomorphologic, and ecological principles to advance our understanding of how the complex interactions between vegetation, groundwater, river flows, channel morphology, and water quality determine restoration outcome (Booth and Loheide 2010; Hall et al. 2014). There is an increasing emphasis on defining "process-based watershed restoration" and the best way to undertake it (Beechie et al. 2010; see case study box 14-1). Many of the watershed actions involve stormwater management, wastewater treatment, wetland restoration, revegetation, and other forms of land management, such as no-till agriculture that have not previously been considered as "restoration," but in fact may be necessary for restoration of streams and rivers impacted by major changes in land use (Richardson et al. 2011; Palmer et al. 2014; Smucker and Detenbeck 2014). Stormwater management

Case Study Box 14-1

Hydrologic Restoration to Facilitate Native Prairie Grasses and Water Quality Improvements

Walnut Creek watershed, IA: Beginning in 1992, the Walnut Creek watershed restoration project was initiated by the US Fish and Wildlife Service (USFWS) at the Neal Smith National Wildlife Refuge in Jasper County, Iowa, to restore native prairie and improve water quality in the watershed's streams.

Test of theory: Importance of restoring key hydrological processes

Took parcels of land out of row agriculture and planted native grasses. A paired watershed study, led by Dr. Keith Schilling (University of Iowa) and colleagues, accompanied the project. The result is based on watershed data minus the contribution of row crop flow; thus, this result represents the contribution of prairie restoration to hydrology.

Progress: By 2005, 23.5% of the watershed had been planted in native prairie. Full recovery of hydrologic processes at watershed scales takes a long time, particularly because parts of Walnut Creek are still in agriculture and tiled land use. Despite this, progress is being made as summarized below, where Q = discharge, ET = evapotranspiration, [NO_3] = nitrate concentration; [P] = phosphate concentration, and W:D = width:depth.

Progress toward hydrologic restoration →

None	**Some**	**Measurable**
Discharge (watershed scale) • no decrease in stormflow Q • no decrease in contribution of stormflows to annual Q	**Discharge** (scale) • increased baseflow Q in lower watershed • increased baseflow contribution to annual Q	**Discharge** (plot scale) • decreased stormflow Q • decreased infiltration
Channel • W:D not same as historic • channel & floodplain disconnected	**Channel** • some channel widening	**Channel** • none
Groundwater (riparian zone) • depth not changed	**Groundwater** • increased ET suggests potential groundwater change (plot scale)	**Groundwater** (uplands) • increased groundwater recharge
Water quality (watershed scale) • [P] not reduced • sediment export not reduced	**Water quality**	**Water quality** • lower [P] (plot scale) • less sediment export (plot scale) • lower [NO_3] (watershed scale)

Case Study Box 14-1 continued

Long-term outcomes: Through this project, a series of key restoration lessons were learned:

- Restoring the hydrology is key to restoring the land.
- Monitoring hydrologic restoration is best suited at the plot or subcatchment scale, but results from the plot scale do not necessarily scale up to the watershed level.
- Uplands offer a much greater opportunity for restoring hydrologic processes than lower in the watershed, because the former are primary sites of groundwater recharge, while lowland areas integrate hydrologic inputs from all upslope areas and often contain a legacy of historical alterations.
- Headwater areas must be restored before hydrologic conditions in downstream areas.
- Restoring the stream channel is a long-term project.
- The timeframe for hydrologic restoration should be realistic.

References: Schilling et al. 2006; Schilling and Drobney 2014.

and revegetation at watershed scales can contribute significantly to the restoration of urban stream water quantity, quality, and habitat (Rios-Touma et al. 2014).

Slow Water Ecosystems

Restoration of lakes can require recovering the hydrologic dynamics of their tributaries. Changes in lake water depth are usually related to seasonal changes in tributary inputs but can also result from changes in the groundwater, the water table, and from losses through evaporation and infiltration. These changes can be heavily influenced by water management in agricultural or highly developed watersheds. Recovering lake water quality is also a challenge. With their high water residence times and slow turnover, lakes accumulate pollutants which are most commonly derived from fertilizer application. This can render lakes eutrophic, completely changing their biology. For example, eutrophication can increase phytoplankton production and water turbidity, decreasing subsurface oxygen and phytoplankton grazers, creating a feedback loop where clean water and predators mostly disappear (chap. 11) leaving bottom feeders that maintain turbid water (Carpenter et al. 2001).

When planned at a watershed scale, wetland restoration can help retain nitrogen and phosphorus in agricultural subwatersheds (Moreno-Mateos et al. 2010), although the extent to which this leads to lake recovery varies. When phosphorus, a highly conservative element, is the dominant pollutant, it may be necessary to excavate the lake sediments that store it, because once phosphorus precipitates and binds to mineral soil components the biological system cannot readily remove it (Kadlec and Wallace 2009).

Wetlands may accumulate pollutants and become eutrophic, fostering regime shifts to alternative states with different species composition (chap. 2). For example, along a gradient of phosphorus concentration in inflowing water, the Everglades marsh shifted from dominance by *Cladium* to *Typha* when it crossed a first threshold, and from *Typha* to *Nymphaea* after a second threshold of phosphorus concentration (Hagerthey et al. 2008). The removal of the phosphorus that has already infiltrated in groundwater flows or reached wetlands and lakes may be impossible with present technology although extensive studies and restoration modeling projects are still under way (Long et al. 2015). Invasive species dominate wetlands in many other regions because they are highly efficient at taking up nutrients. In Wisconsin, >200,000 ha are now invaded by the exotic, clonal, invasive grass *Phalaris arundinacea* due to its ability to uptake nitrogen from water eutrophicated by agriculture (Hatch and Bernthal 2008).

Overall, restoring historical hydroperiods increases wetland functionality although not necessarily to levels similar to those in reference wetlands (Moreno-Mateos et al. 2012; Meli et al. 2014). Restored hydroperiods have been reported to increase biogeochemical processes, such as denitrification and carbon mineralization (Roley et al. 2012; Hunt et al. 2014), organic matter accumulation (Ballantine and Schneider 2009), and nitrogen and phosphorus removal from water (Ardón et al. 2010). Restored hydroperiods can also help recover ecological processes, such as propagule dispersion via hydrochory (Nilsson et al. 2010) and macroinvertebrate colonization (Paillex et al. 2009). Beyond these few examples on the effects of restoring hydrological function to wetlands, there is a vast literature that cannot be fairly addressed in this chapter.

Coupling Hydrological and Ecological Theory for Restoration

Ecology and hydrology are tightly linked, and there are a variety of theoretical frameworks that are common to both, including a central focus on spatial structure, connectivity and boundary fluxes, and cross-scale interactions. Here, we provide examples in which hydrological dynamics are major determinants of an ecological process that in turn influences ecological theory or in which ecological theory guides hydrological restoration and also is advanced by restoration.

Ecosystem Subsidies and Hydrological Dynamics

Ecological theory on the importance of cross-system subsidies has been developed and refined for many years (Polis et al. 1997). Loreau et al. (2003) extended this to the concept of metaecosystems outlining a theoretical framework on the ecological role of spatial flows of materials and organisms across ecosystem boundaries.

Recognizing these flows helps ecologists and restoration practitioners understand unexpected emergent properties that come from the spatial coupling of ecosystems. Many of these subsidies are tightly linked to hydrological dynamics.

The abundance and diversity of aquatic insects emerging from streams toward terrestrial habitats are affected by multiple watershed factors. For example, the amount and diversity of mayflies, stoneflies, and caddisflies in alpine watersheds may increase with watershed area and may be higher in central streams at mid-elevations (Altermatt et al. 2013). Thus, steeper alpine streams with less water flow in secondary tributaries could host smaller and less diverse insect communities and produce fewer emerging insects that serve as prey for terrestrial predators. Changes in aquatic insect communities caused by hydrological alterations associated with restoration actions can also influence prey abundance (Heinrich et al. 2014). The abundance of riparian fishing spiders feeding on aquatic insects can be lower in streams that are less flood prone due to flow management than in more dynamic streams because the management action has led to changes in the in-stream habitat of the insects (Greenwood and McIntosh 2008). Similarly, the abundance and richness of riparian arthropod communities, including spiders, ground beetles, and rove beetles, inhabiting regulated steams was lower than in unregulated streams, again caused by changes to the stream substrate (Paetzold et al. 2007).

In aquatic ecosystems, the duration of the hydroperiod can affect emergence. For example, Schriever et al. (2014) found that insect emergence from ponds to forests is highest with intermediate hydroperiods while for amphibians emergence is highest with short hydroperiods. In some systems, if the hydroperiod is shortened by anthropogenic activities, a species might survive but have reduced activity or change its emergence timing (Leberfinger et al. 2010). For all these reasons, restoring hydroperiods will improve aquatic vertebrate and invertebrate communities as well as those in the surrounding terrestrial landscapes. In some places, the effects of emerging aquatic invertebrates can be detected beyond 0.5 km from the stream (Muehlbauer et al. 2014).

We emphasize the phenomenon of insect emergence as a resource “subsidy” for terrestrial species because it is far less well known than its reciprocal. Terrestrial subsidies to waterways are extremely important and for freshwaters, are strongly influenced by hydrological regime including periodic floodplain inundation. Decades of work demonstrating the importance of riparian litter inputs to aquatic systems can be found in numerous texts. Certainly, loss of riparian vegetation and even deforestation in a watershed’s headwaters can reduce in-stream food web dependence on terrestrial subsidies (Wallace et al. 2015). Extended periods of low flows or droughts can influence the accumulation and decomposition of terrestrial litter inputs, which, in turn, advantages certain stream species over others (Wallace et al. 2015). Similarly, floodplain inundation results in significant inputs of nutrients to streams—a healthy process unless the system is under intense agriculture or there are other sources of pollution.

Metapopulation Theory, Restoration of Populations, and Restoration of River Networks

Seasonal or drought-induced drying of some aquatic systems is normal but spatially variable and is especially common in small streams and many wetlands. Large rivers in arid regions may have sections that dry every year. There are diverse life history strategies that help aquatic species persist in such systems and many rely on nearby refuges that retain surface water even during dry periods. Ponds, streams, or wetlands in low-lying areas may retain water during summer months, and these can provide colonists to other sites that become rewetted after rains. In such cases, one of the most important bodies of theory in ecology may be useful: metapopulation theory (chaps. 3 and 7). This body of theory views landscapes as networks of idealized habitat patches in which species occur as discrete local populations connected by migration (chap. 4). The theory is broadly recognized as useful in guiding restoration of species that are dependent on some degree of movement between spatially separated habitat patches. Decisions such as how many individuals to reintroduce, how many habitat patches to restore, what their degree of connectivity should be, and where on the landscape restoration efforts should be targeted all benefit from metapopulation models (chap. 7).

While metapopulation theory can provide guidance on the restoration of systems with variable hydrological dynamics, these same systems can provide fertile ground for testing and advancing metapopulation theory (case study box 14-2). For example, isolated ponds distributed across the landscape that support breeding populations of frogs have been used experimentally to show that predators or invasive species may respond to patch structure in ways that increase the risk to species that are of restoration or conservation interest (Atobe et al. 2014). Plans to restore and conserve "metapopulations species" that disperse in stream or river networks must take a different approach from linear or two-dimensional descriptions of dispersal across landscapes (Fagan 2002). In addition to the fact that regions of river networks may experience different levels of connectivity due to hydrologic conditions, their hierarchical, branching geometries directly influence ecological processes and patterns (Perkin et al. 2015). Patch geometry alone does not determine persistence; instead, it is the combination of network geometry, hydrology, and dispersal mechanisms (Mari et al. 2014). Species that are confined to water

Case Study Box 14-2
Restoring Hydrological Dynamics in Doñana (Guadalquivir Estuary, Spain)

Doñana wetlands, Spain: Doñana is Spain's largest wetland complex and provides one of the most important wintering sites for waterfowl in Europe. Despite the site's protected status, the marshes are threatened by eutrophication due to pollution and severely altered hydrological conditions that promote toxic cyanobacterial blooms and dominance by invasive floating plants that cause anoxia in subsurface waters. The loss of Doñana wetland area dates to the eighteenth century, when people began to drain marshes for agriculture. This practice continued until the 1970s. The drainage and isolation of marshes from their main water courses and tidal waters altered virtually every ecological process and caused drastic reductions of fish, mammal, amphibian, and bird populations.

Supporting theory: Restoring hydrological connectivity will increase biodiversity by reducing sedimentation and increasing ground-water recharge.

Expected outcomes and progress: In the early 1990s, initial attempts were made to recover lost biodiversity and ecological functions by reconnecting marshes with old inflowing streams. However, expected benefits to fish and bird populations were not achieved due to inadequate understanding of marsh hydrodynamics. In 1998, a major spill of toxic mine wastes (millions of cubic meters of pyrite sludge) catalyzed major restoration efforts. The efforts, based on numerical hydrodynamic models, focused on restoring the complex hydrology of most of the watersheds feeding the marsh, as well as reducing pollution from agricultural and developed areas. The models convinced decision makers to reconnect the marsh to the old streams that provided water inflows, to reduce sedimentation from agricultural watersheds, to permeabilize water barriers (road walls) within the marsh, to reduce groundwater extraction, and allow groundwater recharge. Additionally, actions were taken to reduce pollution from urban areas in and around the marsh.

Long-term outcomes: Fourteen years after the larger projects began, most plans have been implemented and long-term monitoring shows rewards. Watershed restoration catalyzed the recovery of bird communities in one of the streams affected by the spill. In fact, the bird richness, abundance, and diversity matched those of reference areas within five years. Similarly, zooplankton communities in temporary ponds recovered about 80% of their diversity of cladocera, copepods, and rotifers within two years.

Case Study 14-2: Restoration of the Caracoles farmland within the Doñana 2005 restoration project. Multiple circular ponds of different sizes were created to mimic natural temporary ponds and to study the effects of pond size, distance, and connectivity on the long-term recovery of invertebrate communities.

References: Bayán-Jardín 2006; García Novo and Marín Cabrera 2006; Badosa et al. 2010; Ontiveros et al. 2013; Scheffer et al. 2015.

and subject to unidirectional flows will respond differently to network patch structure than aquatic species capable of overland dispersal.

Closing Remarks

Restoration of degraded ecosystems, regardless of the type or position, involves a reestablishment or rebalancing of water processes, that is, hydrological restoration. Among others, four theories and concepts are essential to understanding how to accomplish this, and why some ecosystems recover while others do not. First, hydrological restoration requires a holistic approach that considers watersheds as geomorphological units in which water flows connect vegetation, soils, groundwater, and surface waters. Restoration of any of these—plant communities, forests, aquifers, lakes, wetlands, streams—requires a focus on the interaction among these four components. Second, movement of water among these four components via surface flows occurs directionally downslope while subsurface flows occur in more dimensions: upward from soils and plants as evaporation, vertically downward into soils toward groundwater storage, and laterally as flows in subsurface layers. This means that, for a given climate, position on the landscape with respect to topographic relief, geology, and connectivity to water (across all dimensions) will determine an ecosystem's restoration potential, particularly if water is a limiting factor in the region.

Third, restoration of soil conditions—its ability to absorb, hold, and transport water—is critical to the restoration of degraded terrestrial and aquatic ecosystems. If soil infiltration capacity or hydraulic conductivity is low, access to water may limit plant growth; too much water along with eroded soils may continue to degrade wetlands, lakes, and streams. Fourth, the frequency, timing, and magnitude of hydrologic fluxes can influence restoration trajectory. Many wetlands require distinct hydroperiods in which water elevation changes; streams and rivers have flow regimes that are characteristic of their region; and that aquatic organisms have evolved in response to, and many lakes are fed by groundwater fluxes that vary seasonally in a predictable way.

Restorationists need to couple hydrological and ecological theory because water fluxes play an essential role in many key processes ecologists have come to understand and predict. These include, for example, dispersal dynamics, seasonal variation in growth and reproduction, metapopulation dynamics, and ecosystem subsidies. Restoring hydrological dynamics, and thus populations, communities, and ecosystems, often involves actions at different scales, on different elements, and at different locations within degraded watersheds. To restore aquatic ecosystems that have been degraded by mining, agriculture, or other activities that have dramatically altered the landscape, actions may involve influencing infiltration capacity at the scale of the entire watershed. Restoring water flows in areas with massive deforestation may take decades to centuries if the aquifers have been depleted; they will only slowly recharge and, in fact, water yield may initially or permanently decrease after planting. Thus, one of the main challenges in applying and growing what is now being called “ecohydrology” is the mismatch between the time-scale of ecological studies (<20 years), the real time for ecosystem recovery (up to centuries), and the social pressure to see results quickly. However, we will meet these challenges as we continue to learn more through careful studies of how water fluxes change during restoration, and the reciprocal effects they have on ecological processes.

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PART IV

The Spatial and Temporal Dimensions of Restoration

Chapter 15

Evolutionary Restoration Ecology

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Theory and Application

- Evolutionary restoration ecology: recognizes how restoration outcomes can be altered or even driven by contemporary evolution which occurs on ecological time scales (less than a few hundred generations).
- Restoration genomics: the application of next generation technologies to identify neutral and adaptive genetic variation important to identifying genetically appropriate sources in restorations, monitoring genetic diversity, and characterizing the genetic basis of adaptive trait variation.
- Eco-evolutionary dynamics: the reciprocal interactions and feedbacks between contemporary evolution and ecological processes. For example, contemporary evolution of body size can alter trophic cascades as well as nutrient cycling.

Although restoration biology is commonly depicted as an ecological field, it is in many ways an evolutionary science. When we manage habitats to enhance or impair the performance of target species we are implicitly managing adaptation. In the past, restoration practitioners have emphasized preserving genetic diversity as a resource for future evolution (Lesica and Allendorf 1999; Broadhurst et al. 2008). Here, we discuss ways in which evolution on contemporary time scales (within a few hundred generations) might also be important to restoration outcomes. Such *contemporary evolution* is relatively common in nature and commonly associated with colonization and anthropogenic disturbances, situations that often prevail in restoration contexts (Hendry and Kinnison 1999; Stockwell and Weeks 1999; Bone and Farres 2001; Reznick and Ghalambor 2001; Stockwell et al. 2003; Hendry et al. 2008; Merilä and Hendry 2014). Contemporary evolu-

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tion not only results from natural and anthropogenic changes, but it reciprocally influences population, community, and ecosystem processes that are central to restoration success (Fussmann et al. 2007; Kinnison and Hairston 2007; Carlson et al. 2014). Thus, conservation and restoration will benefit from considering evolution in not only the *past*, but also the *present*, and *future*.

Restoration efforts often involve dramatic and rapid shifts in habitat that can even lead to alternative ecological states (Suding et al. 2003; chap. 2). Thus, genotypes that evolved within historically different evolutionary contexts (the past) may be pitted against novel or mismatched current conditions (the present). The degree of mismatch should then determine the pattern and strength of selection acting on trait variation (box 15-1; fig. 15-1). If trait variation is heritable and selection is sufficiently persistent, contemporary evolution is expected to occur. Adaptation to current conditions (the present) may in turn influence the ability of such populations to persist and evolve over short or long periods (the future). However, evolution by natural selection can come with appreciable demographic costs. Strong selection often equates with reduced survival or reproductive success for the population as a whole, such that population persistence becomes a race between the demographic costs of selection and its adaptive benefits (Maynard Smith 1989; Gomulkiewicz and Holt 1995; Kinnison and Hairston 2007; Carlson et al. 2014). In addition, contemporary evolution may alter the interactions of species with their environments and each other. Thus, restoration ecologists may be faced with an ecological theater filled with a cast of evolutionarily changing players (*sensu* Hutchinson 1965), even if many of the same nominal species are restored (Post and Palkovacs 2009).

We have argued that evolutionary thinking can influence restoration ecology, but it is equally true that restoration ecology can influence evolutionary thinking (e.g., Bailey and Kinnison 2010; Kulpa and Leger 2013). For instance, the tempo and mode of contemporary evolution is still not well understood (Hendry and Kinnison 1999; Kinnison and Hendry 2001; Hendry et al. 2008; Haller and Hendry 2014), and restoration ecology offers many opportunities to study these dynamics for diverse taxa under a variety of circumstances. In this chapter, we consider the roles of evolutionary processes in both population persistence and ecological restoration. Because our actions as practitioners of restoration are largely limited to the present, much of our discussion will surround interactions with contemporary evolution. First, we describe the conditions under which contemporary evolution occurs and the factors by which it may be facilitated or constrained. Second, we discuss approaches and tools available for assessing evolutionary dynamics acting in populations of restoration concern. We consider evolutionary dynamics in a landscape context because restoration schemes will generally involve contributions from, and interactions with, the larger environment, metapopulation, and

Box 15-1
Evolutionary Change in Quantitative Traits

Two key equations are useful in understanding and predicting evolution of quantitative traits in theory. The first of these is the deceptively simple,

$$\Delta z = G\beta$$

where Δz is the change in mean trait value from one generation to the next, G is the additive genetic variance for the trait and β is the selection gradient acting on the trait (slope of the relationship between the trait and fitness). When considering a single trait, this equation is analogous to the traditional ‘breeder’s equation’ (evolutionary response = heritability × selection; $R = h^2S$) When considering multiple traits, Δz becomes a vector of changes in mean trait values, G becomes a matrix of additive genetic variances/covariances, and β becomes a vector of selection gradients. That is: $\Delta z = G\beta$, which for two traits becomes

$$\begin{bmatrix} \Delta z_1 \\ \Delta z_2 \end{bmatrix} = \begin{bmatrix} G_{11} G_{12} \\ G_{21} G_{22} \end{bmatrix} \begin{bmatrix} \beta_1 \\ \beta_2 \end{bmatrix}$$

where G_{11} and G_{22} are the additive genetic variances for the two traits z_1 and $z_{2,}$ respectively, and G_{12} and G_{21} are identical and are the additive genetic covariance between the two traits. These genetic variances and covariances are statistically estimated trait values of individuals of varying degrees of relatedness (e.g., parents and offspring, half-sibs, etc.). Selection gradients are commonly estimated as partial regression coefficients from a multiple regression of both traits on fitness, and thus represent the effect of each trait on fitness after controlling for the direct effects of selection on the other trait.

This equation shows how the evolutionary response for each trait will be a function of (i) selection acting directly on that trait, (ii) the additive genetic variance for that trait, (iii) selection acting on the other trait, and (iv) the additive genetic covariance between the traits. It also illustrates how apparently paradoxical evolutionary changes can be observed in some situations due to genetic covariances. For example, a trait might evolve to be smaller even if it is under direct selection to be larger, provided opposing indirect effects of selection on another genetically covarying trait are stronger.

The second equation provides us with some insight into factors determining the strength of selection. In a restoration context, a disturbance to the environment may create a mismatch between the phenotypic optimum and the current phenotype distribution of a population (Figure 15-1). Under a number of assumptions, the strength of this selection can be represented as

$$\beta = \frac{-(z - \theta)}{\omega^2 + P}$$

where z is the mean trait value, θ is the optimal trait value, P is the phenotypic variance, and ω^2 is the strength of stabilizing selection around the optimum (for simplicity, we assume ω^2 is the same around the optimum before and after the disturbance). Smaller values of ω^2 correspond to steeper fitness functions and therefore stronger stabilizing

Box 15-1 continued

selection around the optimum. When a disturbance shifts the optimum away from the current phenotypes, directional selection on the population increases (larger $|\beta|$), causing evolution toward the new optimum. All else equal, evolutionary responses will increase as the strength of stabilizing selection increases (ω decreases). In turn, the rate of evolutionary change is best measured as *Haldanes* which are standard deviations of change per generation.

These equations can be used to predict the evolutionary responses of traits following a disturbance, and have proven effective in predicting evolutionary responses in natural populations, although several factors can lead to discrepancies. However, it is worth noting that these models are best suited to large populations where the effects of genetic drift are negligible.

References: Lande and Arnold 1983; Hendry and Kinnison 1999; Grant and Grant 1995; Arnold et al. 2001; Etterson and Shaw 2001; Kingsolver et al. 2001; Merilä et al. 2001; Grant and Grant 2002; Frankham and Kingsolver 2004.

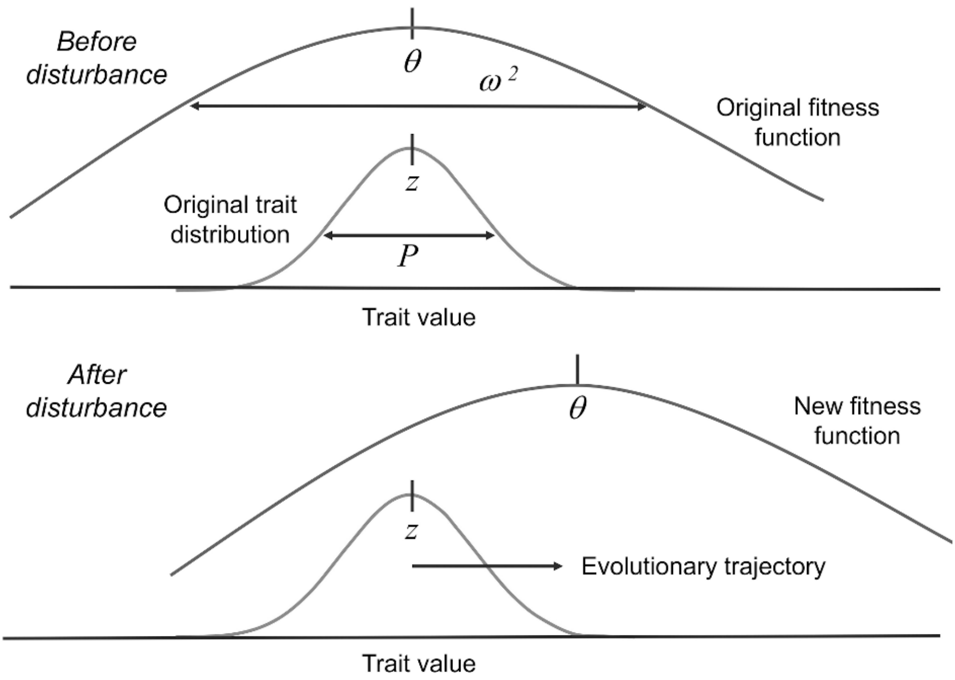

Figure 15-1. The distribution of trait values is shown in relation to the fitness function before and after a disturbance (native habitat versus restoration habitat). The width of the fitness function reflects the strength of stabilizing selection which is denoted by ω^2.

metacommunity (chap. 7). We conclude by considering traditional restoration ecology topics that are ripe for evaluation in the context of evolutionary restoration ecology.

Contemporary Evolution

In a post-disturbance but pre-restoration context, we might expect a mismatch between the optimal trait values for the environment (the values yielding highest fitness in the disturbed environment) and the actual trait distribution for the population. This mismatch causes directional selection, which favors evolution of the mean trait value toward the fitness optimum (fig. 15-1). This evolutionary response is the product of selection and additive genetic variances-covariances for the given trait(s) (box 15-1). Thus, genetic variation within populations is important because it mediates adaptive evolution in response to changing conditions associated with restoration (Houle 1992; Pitchers et al. 2014). The strength of selection, as well as its potential demographic costs, will be determined by the degree of mismatch. In cases with gradual or modest change, "adaptive tracking" may allow a population to persist without a reduction in population size (Vander Wal et al. 2013), particularly if a population is more limited by its carrying capacity than by its recruitment potential (Kinnison and Hairston 2007). In fact, Turcotte et al. (2011) showed that contemporary evolution could accelerate population growth of experimental aphid populations compared to nonevolving treatments.

In some restoration contexts, the demographic costs of selection might be large enough to cause the population to decline. However, if there is sufficient genetic variation for the trait, the population mean should begin evolving toward the fitness optimum in the next generation, which should then slow or reverse population decline over time (Gomulkiewicz and Holt 1995), a phenomenon referred to as "evolutionary rescue" (Bell and Gonzalez 2009; Carlson et al. 2014; Vander Wal et al. 2013; case study box 15-1).

Contemporary evolution should occur in the above situations in general, but it can be hampered by many factors. First, *small populations* may have less genetic variation, thus slowing and/or limiting their response to selection (Lande 1995; Lynch 1996). Further, small populations have less demographic capacity to persist through the initial reduction in population size caused by selection (Gomulkiewicz and Holt 1995; also fig. 15-3). Second, *gene flow* may either increase genetic variation and facilitate evolution, or impede adaptation by introducing maladapted genes and further selective costs (genetic load) (Garant et al. 2007; Bell and Gonzalez 2011; Carlson et al. 2014). Third, *antagonistic pleiotropy* may impede adaptation when genetically correlated traits (e.g., partly influenced by same underlying genes) are under different patterns of selection (Etterson and

Case Study Box 15-1
Evolutionary Rescue from Microbes to Mammals

Supporting theory: A population may experience negative population growth following an abrupt change in environmental conditions. Evolutionary rescue occurs when rapid adaptation to that new environment results in positive population growth allowing the population to persist. In theory, success or failure of this process can be important in both restoring species of conservation concern and in controlling pest species.

Expected outcome: Theory predicts that three major factors will determine the likelihood that a population will experience evolutionary rescue: (1) the severity of maladaptation created by the change in environment, (2) the initial population size, and (3) the amount of genetic variation available in the trait(s) determining fitness. Genetic variation to promote recovery may come from within a population, but may also come from natural or human-introduced migrants (a form of "genetic rescue").

Progress: Evolutionary rescue is not commonly prioritized in many species restoration programs, likely because practitioners have low confidence in the adaptive capacity of populations already showing sharp declines, and empirical support in applied contexts is still mounting. Although genetic rescue has been successfully applied with a number of high-profile species, it has been implemented primarily to reduce inbreeding depression rather than to facilitate adaptation.

Long-term outcomes: Support for the long-term relevance of evolutionary rescue comes primarily from two sources, lab studies of microbe populations, and demography in wild pests. For example, highly replicated studies of yeast populations experiencing salt stress clearly demonstrate evolutionary rescue and suggest that previous selection at low levels of a stressor may improve odds of rescue (fig. 15-2a). Pest populations of wild rabbits and rats show repeated recovery of population abundances following initial population declines due to strong selection imposed by poisoning programs or pathogen outbreaks.

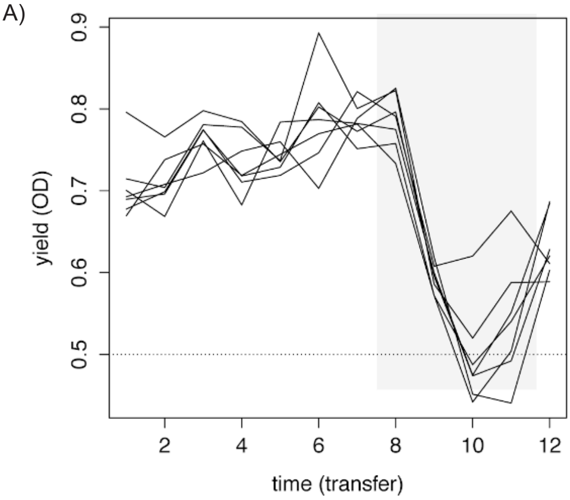

Figure 15-2. Examples of evolutionary rescue in microbe and mammals. (A) Replicate yeast populations experience recovery (measured by optical yield) following an abrupt increase in salt stress (from Gonzalez and Bell 2013).

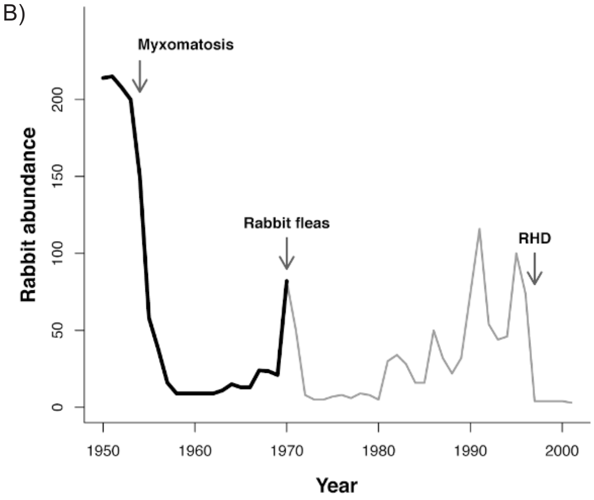

Figure 15-2. (B) Likewise, mammalian pests, like rabbits, show repeated patterns of decline and recovery following exposure to pathogens used as control measures (from Vander Wal et al. 2013).

What was learned: Much work remains to broadly incorporate evolutionary rescue in species management and restoration. However, the conditions that favor evolutionary rescue, and the time frames involved, provide a strong argument for earlier restoration interventions to preserve species.

References: Gomulkiewicz and Holt 1995; Stockwell et al. 2003; Kinnison and Hairston 2007; Gonzalez and Bell 2013; Vander Wal et al. 2013; Whiteley et al. 2015.

Shaw 2001; Hansen and Houle 2008; but see Kopp and Matuszewski 2014). Finally, species- and population-specific life-history characteristics (e.g., mating system, growth rate) can hinder demographic recovery and the potential for evolutionary rescue (Reznick et al. 2004; Baskett and Gomulkiewicz 2011). For example, guppy populations from environments with fish predators adapt readily to sites without predators, but the opposite pattern of adaptation appears to be strongly constrained by the demographic costs of selection (Reznick et al. 2004; Weese et al. 2011).

Quantitative Traits

The vast majority of examples of contemporary evolution in wild populations are for "quantitative" traits, such as morphological and life history characters (Hendry and Kinnison 1999; Reznick and Ghalambor 2001; Stockwell et al. 2003). These characters are influenced by numerous interacting loci and environmental variation and can display a near-continuous range of trait values, as opposed to discrete

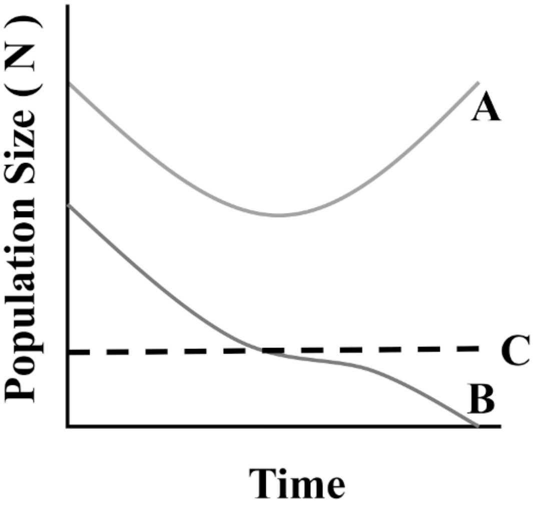

Figure 15-3. For large populations, (A) novel selection is expected to cause an initial decline in population size (N) until the population adapts and population size increases (A). However, small populations (B) are more vulnerable to extinction because they are more likely to reach sizes where demographic stochasticity becomes overwhelming (C).

phenotypes expected under simple Mendelian inheritance. The proportion of such trait variation, and covariation among traits, that is attributed to the additive effects of parental genotypes are referred to as the additive genetic variance and covariance, respectively (box 15-1). Additive genetic variance is often expressed as a proportion of the total phenotypic variation, called the "narrow-sense heritability." Thus, the simplest model predicting an evolutionary response for a single quantitative trait is the breeder's equation:

$$R = h^2 S$$

where R is the evolutionary response, h^2 is the narrow sense heritability for the given trait, and S is selection on that trait (see box 15-1). Frankham and Kingsolver (2004) expanded this model to include N_e, as a way to consider the effects of genetic drift.

It is worth noting that quantitative trait variation can be remarkably hard to deplete in populations in contemporary time (Dudley and Lambert 2004). This is likely due to the combined effects of recombination and mutation at many loci (Bürger and Lynch 1995). Low heritabilities do not necessarily mean depleted additive genetic variation. A trait can possess a substantial amount of additive genetic variation and still have low heritability if that trait happens to be subject to a relatively large amount of environmental and nonadditive genetic influences

(Houle 1992). Given this, it is questionable whether there are simple rules for predicting which types of quantitative traits will be more or less likely to evolve in a restoration context. Furthermore, it is not clear whether rapid losses of additive genetic variation in quantitative traits is common or nearly as much of a concern for restoration as the inherent environmental, nonadditive, and covariance effects that muddle responses to selection.

Environmental and nonadditive effects on trait expression can be very important for restoration success. In fact, natural selection has shaped the environmental component of expression of many traits into reaction norms of adaptive phenotypic plasticity (Franks et al. 2013). Phenotypic plasticity enables the same genotype to produce different phenotypes in response to different environmental conditions (Chevin and Lande 2011). Such plasticity can represent a large part of the initial trait change in response to natural selection, and subsequent fitness consequences may facilitate adaptive trait evolution (Waddington 1953; Hendry et al. 2008; Anderson et al. 2012). However, plasticity might also hasten population extinction where increased environmental stochasiticy leads to unreliable cues causing greater mismatch between fitness optimum and environmental cues (Reed et al. 2010). Indeed, cues might not only become unreliable, they can become wrong, leading to *evolutionary traps* in cases where native species respond inappropriately to invasive species. For instance, Tewksbury et al. (2002) reported that monarch butterflies (*Danaus plexippus*) may lay up to 25% of their eggs on black swallowwort (*Vincetoxicum nigrum*) even though their larvae are unable to develop on this nonnative species. However, even where similar trait values are favored across environments, with environmental effects on trait expression not particularly adaptive, selection can give rise to substantial genetic differences among populations that override environmental heterogeneity (e.g., countergradient variation; Conover and Schlutz 1995).

The above examples also illustrate how inferences about heritable variation may be tenuous when based solely on phenotypic variation among wild individuals. We have already mentioned narrow-sense heritability and genetic correlations for quantifying within-population additive genetic variation in particular traits. With this information, one can predict the evolutionary response of a trait, or fitness, to a given intensity of selection (box 15-1). A related metric is the so-called evolvability of a trait (the coefficient of variation of additive genetic variance) (Houle 1992; Hansen et al. 2011).

Heritabilities and evolvabilities are often estimated with animal model analyses in natural populations (Kruuk 2004) or controlled breeding designs (Roff 1997). At the among-population scale, the most direct, robust, and informative way to infer heritable adaptive divergence is through the use of reciprocal transplants (O'Hara Hines et al. 2004; Kawecki and Ebert 2004; Agren and Schemske 2012;

Bennington et al. 2012). Differences in trait expression and fitness components (e.g., survival, growth, reproductive success) between individuals in "home" versus "foreign" environments can be used to infer adaptive genetic differences (Rehfeldt et al. 1999; McKay et al. 2005; Mitchell-Olds and Schmitt 2006; Fournier-Level et al. 2011), although the optimal design of reciprocal transplant experiments has many important nuances (O'Hara Hines et al. 2004; Kawecki and Ebert 2004; Blanquart et al. 2013). These nuances will include (i) the locations of transplant sites and source populations; (ii) degree of replication across both space and time; and (iii) assessment of fitness, particularly where assessment of a subset of life stages overlooks life history stages most critical to establishment (Hargreaves et al. 2014).

Where reciprocal transplants are logistically difficult, a more tractable approach is to rear/grow individuals from different populations in controlled environments, such as a greenhouse, where conditions can be set to mimic environmental features at natural sites. Such laboratory "common-garden" experiments can reveal whether phenotypic variation within or among populations is heritable and can be incorporated into breeding designs that reveal the quantitative genetic architecture (e.g., additive, dominance, epistasis) underlying that variation (Savolainen et al. 2007; Hendry 2013). The dissection of complex traits, such as growth, yield, resistance, or tolerance to abiotic and biotic stresses into additive and nonadditive variance components remains a staple component of breeding programs; including maize, wheat, and other crop species where potential genetic gains have been evaluated in response to different breeding strategies (Lynch and Walsh 1998; Neale and Kremer 2011).

Although common garden experiments are useful, they have important limitations. A seemingly obvious point, yet one that is often forgotten or ignored, is that genetic variation *within* populations (e.g., high heritability) does not mean that phenotypic differences *among* populations necessarily share the same genetic basis. Designs that include hybrids (population crosses) can provide insights on this potential problem (see Collyer et al. 2011). In addition, the phenotypic expression of genetic variation will depend on the specific rearing/growing conditions due to genotype-by-environment (G×E) interactions and controlling for maternal environment may require rearing individuals in common conditions for more than one generation (Roff 1997; Hoffmann and Merilä 1999; Turner et al. 2014; chap. 5). Accordingly, differences observed in a specific common environment may not reflect important differences under rearing environments, or in nature, but rather the influence of the maternal environment. Finally, common-garden experiments do not directly demonstrate the adaptive significance of phenotypic variation, because they do not expose organisms to the full suite of challenges they would encounter in nature.

Armed with data from reciprocal transplants or common garden experiments, some investigators attempt to infer the traits under selection by comparing *genetic* divergence in those traits to the divergence that would be expected in the absence of natural selection (i.e., based on mutation and genetic drift alone; e.g., Collyer et al. 2011). When additive genetic differences *exceed* these "neutral" expectations, selection is inferred as the basis of phenotypic divergence (review Turelli et al. 1988; Merilä and Crnokrak 2001).

An explicit approach to such inference is to compare metrics of divergence in putatively adaptive traits to metrics based on neutral characters. The most commonly assayed "neutral" characters are genetic makers (e.g., microsatellites, Single Nucleotide Polymorphisms = SNPs) where divergence is quantified using various metrics of genetic differentiation (F_{ST}), comparing the amount of genetic variation among populations (v_a) to the total variation among and within populations ($v_a + v_w$):

$$F_{ST} = \frac{v_a}{v_a + v_w}.$$

For a single locus with two alleles, F_{ST} will equal zero when none of the genetic variation is found among populations (i.e., they have the same allele frequencies), but will equal unity when all of the genetic variation is found among populations (i.e., they are fixed for alternative alleles) (Wright 1969; for microsatellites, also see Hedrick 1999). Thus F_{ST} can be used as a "null" expectation of divergence in the absence of selection. By contrast, adaptive divergence/convergence can be measured by a quantitative-trait analog of F_{ST}, termed Q_{ST} by Spitze (1993):

$$Q_{ST} = \frac{s_a^2}{s_a^2 + 2s_w},$$

where s_a^2 is the additive genetic variance among populations and s_w^2 is the additive genetic variance within populations.

When phenotypic traits are not under selection, Q_{ST} is hypothesized to be approximately equal to F_{ST} (Lande 1992; Spitze 1993; Whitlock 1999; Leinonen et al. 2008). Q_{ST} values greater than F_{ST} imply that phenotypic differences are driven by divergent selection and are adaptive, whereas Q_{ST} values less than F_{ST} may imply range-wide stabilizing selection (i.e., countergradient selection). However, while Q_{ST} (and its phenotypic equivalent P_{ST}) is a useful metric of trait differentiation, F_{ST}-Q_{ST} comparisons have a number of biases that limit the conclusions that may be drawn from them (Hendry 2002; Whitlock 2008; Edelaar et al. 2011). Comparison of Q_{ST} for a single trait with mean F_{ST} across a number of neutral genetic markers is incorrect. Rather, to evaluate whether a trait is under selection, a simulated distribution of neutral Q_{ST} values should be generated from the neutral F_{ST} distribution to evaluate whether observed Q_{ST} values fall within that neutral distribution or not (Leinonen et al. 2013). Nevertheless, in a restoration context, F_{ST}-Q_{ST} comparisons may be useful as part of a broader assessment, by looking for greatest phenotypic match for traits with the largest F_{ST}-Q_{ST} disparities. For instance, restoration efforts might benefit from choosing source populations that have phenotypes similar to those at the restoration site (lower pairwise Q_{ST} or P_{ST}) and thus might be "preadapted" to the restoration environment (see Weeks et al. 2011; Jones 2013; Hamilton et al. 2015a). If populations are locally adapted, climate matching between native and introduced environments may predict those genotypes that will be successful in the introduced environment. Evidence of preadaptation is reflected for many invasive species through signatures of climate matching between native and invasive ranges. For instance, greater fitness was reported for *Arabidopsis thaliana* (native to Eurasia) accessions in environments whose origins were climatically similar to the introduced North American range (Hamilton et al. 2015a). These types of findings suggest similar screening will be useful for identifying well-matched source populations to be used during restoration.

Spatially Explicit Restoration

The spatial context of restoration is important for considering source populations as well as considering how a restored population will interact with nearby populations. *Landscape genetics* provides a very useful framework for understanding patterns of neutral and adaptive genetic variation in a landscape context (Manel et al. 2010; chap. 5). Genetic structure has historically been evaluated using genetic distance metrics such as F_{ST}; however, genetic data combined with spatially implicit statistical tools provide a means to link spatial and environmental heterogeneity with population genetic structure (Schoville et al. 2012). These models provide new perspectives in forecasting population genetic changes and gene flow on the landscape that will impact decisions regarding selection of restoration sources and design of restoration programs (Jay et al. 2012). Furthermore, these tools are useful for inferring contemporary levels of gene flow by estimating "current" immigration with genetic assignment methods (Pritchard et al. 2000; Paetkau et al. 2004; Jay et al. 2012). Jay et al. (2012) applied this approach to twenty alpine species in the European Alps, combining estimates of genetic ancestry with climate forecasts to predict shifts in genetic ancestry associated with global warming scenarios. These types of data provide additional layers of information to complement species distribution modeling for predicting within species level responses to changing environments.

Estimates of gene flow are important for restoration scenarios because gene flow affects adaptive divergence. Low gene flow facilitates the independent evolution of different populations, whereas high gene flow creates a *migrational load* that constrains adaptive divergence (Storfer et al. 1999; Hendry et al. 2001; Savolainen et al. 2007; Yeaman and Guillaume 2009). Estimates of gene flow interpreted using neutral markers reflect the "effective" number of migrants between populations. However, the effective number of migrants may be partly determined by selection, and contribute to adaptive divergence. Thus, even in the face of moderate gene flow, selection can contribute to adaptive differentiation (Hendry et al. 2001; Petit and Hampe 2006). Thus while estimates on the extent and direction of gene flow can provide useful tools in restoration contexts, these estimates are best interpreted with an understanding of selection acting on traits in the populations of concern.

If high migrational load is expected, restoration practitioners can consider restricting gene flow, limiting the potential introduction of maladapted variation. However, the negative effects of gene flow need to be weighed against potential positive effects, such as reduced inbreeding depression, increased genetic variation, and increased evolutionary potential (e.g., Hedrick 1995; Newman and Tallmon 2001; Weeks et al. 2011). Indeed, precedent already exists for providing artificial gene flow for the purpose of "genetic rescue" of inbred populations (Hedrick 1995; Whiteley et al. 2015). In either case, information on the extent and distribution of neutral and adaptive genetic variation, associated environmental and habitat data, and species-specific biological data will be required to inform the management of gene flow.

Restoration Genomics

Emerging next generation sequencing and analytical tools offer promise for teasing apart the distribution of neutral and adaptive genetic variation in a spatial context (Schoville et al. 2012; chap. 5). As these advances become more affordable, next-generation sequencing technologies will have broad impacts to restoration, particularly as genomic resources become available for a wider spectrum of species of conservation concern (Mijangos et al. 2015; Ouborg et al. 2010; Williams et al. 2015). These genomic tools extend our ability to address traditional questions important to conservation; including evaluation of population structure, relatedness metrics and genetic connectivity, as well as identifying potential consequences of demographic shifts, and inbreeding coefficients (Shafer et al. 2015). The real advantage of genome-wide technologies, however, is their burgeoning ability to (i) identify regions of the genome that may be important to adaptation, or even (ii) identify particular genes/proteins that underlay these adaptations (Allendorf et al. 2010; Hoffmann et al. 2015). Ultimately, these genomic tools will transform our ability to tease apart the amount, distribution, and functional variation observed within and among natural populations that may be important to restoration (Allendorf et al. 2010).

Whole genome scans offer the opportunity to survey within and among population variation, informing the amount and structure of neutral and adaptive genetic variation (Storz 2005; Nosil et al. 2009; Barrett and Hoekstra 2011). These scans provide increased resolution of genetic variation underlying traits that may be under direct selection or are physically linked to loci under selection (Cao et al. 2011; Evans et al. 2014). Further, genomic regions that differ between populations can be identified allowing one to test for genomic associations with adaptive trait variation across the landscape (Cao et al. 2011; Evans et al. 2014; Lamichhaney et al. 2015). Evans et al. (2014) combined whole genome sequencing of accessions spanning the geographic range of *Populus trichocarpa* with phenotypic trait measurements. This approach allowed them to detect signatures of selection across the *Populus* genome and identify regions of the genome enriched for associations with the adaptive phenotypic traits themselves. Although presently prohibitively expensive and computationally intensive, these types of approaches may be useful for informing the amount and distribution of adaptive genetic diversity across a species' distribution and provide powerful tools to inform seed-transfer guidelines in restoration programs (Evans et al. 2014).

Short of whole genome sequencing, targeted sequencing through generation of reduced-representation libraries has opened the door to screening thousands of genetic polymorphisms. These polymorphisms include neutral and potentially adaptive genetic variants in nonmodel organisms with little to no genomic information (Namroud et al. 2008; Narum et al. 2013). Emerging statistical tools, such as outlier detection methods and allele-environment associations, will improve our understanding of the amount and distribution of adaptive genetic variation (Schoville et al. 2012). However, links between individual SNPs and traits or fitness often remain weak, and sampling strategy can bias detection of adaptive variants (Rockman 2012).

An alternative to genomic scans is the study of "candidate" genetic polymorphisms with known gene functions that might be targets for selection in a particular restoration context (Nachman et al. 2003; Hoffmann and Willi 2008). For example, Holliday et al. (2010) associated candidate gene SNP polymorphisms with phenotypic variation in cold hardiness development and bud set timing across Sitka spruce populations spanning a latitudinal gradient. This approach relies on extensive knowledge of the genetic architecture underlying trait variation most often inferred from model organisms with distant relationships to species of conservation interest. Because of this constraint, unknown genes or traits can be overlooked (Hoffmann and Willi 2008). Furthermore, although "large effect" genes clearly have important consequences to phenotypic variation, these major gene/trait associations are likely the exception rather than the rule as many genes of "small effect" likely underlay most quantitative traits (Rockman 2012). However, even given these limitations, the approach can be successful in identifying candidate genes under selection in wild populations (Hamilton et al. 2013; Jaramillo-Correa et al. 2015), and in turn this information may be relevant to closely related species, broadening the conservation value of initial investments (Hamilton et al. 2015b).

Yet another approach is the examination of gene expression through microarrays or next-generation sequencing (Ouborg et al. 2010; Alvarez et al. 2015). These technologies examine genome-wide patterns of differential gene expression, as well as novel transcript responses to particular environmental cues that may be important to adaptation to changing conditions (Alvarez et al. 2015). This approach extends our ability to associate ecological triggers with transcriptomic responses that may be critical to restoration efforts (Narum and Campbell 2015). For example, Narum and Campbell (2015) examined gene expression following exposure to heat stress conditions in both desert and montane populations of redband trout (*Oncorhynchus mykiss gairdneri*). The desert population exhibited a large number of differentially expressed genes under similar thermal exposure, pointing toward a distinct genetic basis for adaptation to heat stress conditions that may have evolved independently in the desert environment. Thus, variation in gene expression patterns may be associated with mechanisms of adaptation important to persistence under varying environmental conditions. However, while these approaches may be promising for restoration in the near future, their current applicability remains challenging due to expense and limited user-friendly methodological and analytical pipelines (Shafer et al. 2015).

Ecological Consequences of Contemporary Evolution

Since we wrote the first edition of this chapter the field of "eco-evolutionary dynamics" has blossomed, examining the reciprocal interactions and feedbacks of contemporary evolution and ecology (e.g., Fussman et al. 2007; Kinnison and Hairston 2007; Schoener 2011). Theory and empirical studies now provide evidence of many ways in which evolution might promote not only evolutionary rescue, but can also influence community structure and ecosystem function (Palkovacs et al 2009; Schoener 2011), and thus affect restoration outcomes beyond the scale of the focal species. For example, studies of alewife (*Alosa pseudoharengus*) provided evidence that trophic evolution resulting from landlocking populations due to dams can reshape size structure and grazing capacity of zooplankton communities (Post and Palkovacs 2009), with potential cascading effects to primary producers.

Species interactions and coevolution (Thompson 1998) should be very common in restoration settings where important species are often lost or gained in communities. This creates the potential for contemporary coevolution (e.g., herbivory/defense) (Thompson 1998) that may itself reshape community and ecosystem properties (Palkovacs et al. 2009; 2011). For example, predator losses and introductions are major challenges and tools of restoration. Further, evolutionary changes of top predator body size can have cascading impacts across trophic levels (Palkovacs et al. 2011). Eco-evolutionary dynamics are likely to affect restoration outcomes, but at the same time, restoration programs offer invaluable systems to better understand these dynamics.

Application of Contemporary Evolution to Restoration Ecology

We spent the bulk of this chapter describing potential contributions of contemporary evolution to restoration. However, restoration activities also provide excellent opportunities for evolutionary biologists to study population genetics, natural selection, and contemporary evolution. From an evolutionary biology perspective, exciting opportunities may be afforded by manipulative experiments posed by restoration activities. Here we identify a few topics that we think are ripe for collaborative attention.

Selection of Restoration Sources

The restoration of populations to environments from which they have been extirpated requires the selection of suitable source populations (e.g., seed sources). Geographically proximate sources are often chosen under the assumption that the traits those individuals carry are likely to have similar structure and function to that required at the restoration site (Jones 2003, 2013). However, optimal source populations may be geographically distant from the target restoration site. Indeed, Wang et al. (2006) predicted a 10% to 35% increase in lodgepole pine (*Pinus contorta var. latifolia*) productivity when comparing the most productive seed sources identified using future climate projections compared to using local sources. The dramatic difference between local seed sources and optimized seed sources suggest that the "local is best" rule may no longer be valid, particularly given a rapidly changing climate. Thus, alternative restoration strategies should be considered, such as matching source populations to the *general* ecological condition of the restoration site, while also using a mixture of subpopulations from representative microclimates (Rice and Emery 2003). The idea here is that the general population is sufficiently matched to manage genetic load, but mixture from various microclimates maximizes evolutionary potential. Consequently, selection on a diversity of seed sources through composite provenancing may provide a bet-hedging mechanism to both increase diversity and resilience while reducing the risk of restoration failure (Aitken and Bemmels 2015). In cases when the restoration site is a novel environment and local adaptation is strong, a genetically diverse group of source populations may increase the probability of success as selection at the restoration site can then weed through the relative fitness of various recombinant genotypes (Lesica and Allendorf 1999).

The various strategies for reintroduction have different implications depending on the local conditions. If adaptation is limiting at the introduction site, increasing the number of sources might increase the proportion of individuals that are maladapted and hence the genetic load. In such cases, a better strategy might be to select seed sources based on insights into patterns of selection, genetic variation, and local adaptation (with the above-described methods). In the absence of such information, small-scale releases or test gardens might be used to empirically assess best performing sources or crosses before implementing larger introductions. Alternatively, if adaptation is not thought to be limiting at the new site, and the goal is to preserve genetic variation that might be at risk elsewhere (e.g., habitat loss), one might introduce a single source or mixture depending on diversity goals. However, even in these cases, some sources will almost certainly do better than others, as has been shown in lodgepole pine (Wang et al. 2006), providing potentially useful insights into aspects of adaptation that could be relevant to future restorations. Aitken and Bemmels (2015) advocate tracking the health and resilience of local and nonlocal seeds included in restored populations to facilitate adaptive management strategies under climate change (see chap. 17 for more on restoration under climate change).

Managed and Unmanaged Evolution of Captive and "Refuge" Population

Although captive populations are commonly used in restoration efforts and may retain the traits best suited to a restoration site, they could pose some severe drawbacks. In particular, captive populations may have limited genetic variation, suffer from inbreeding, and might have adapted to captive conditions at the expense of performance in the wild ("domestication," see Frankham et al. 2000; Gilligan and Frankham 2003). Some studies suggest a near 40% reduction in fitness in the wild per generation of captive rearing (Araki et al. 2007). Such maladaptation can arise through relaxed selection (e.g., Heath et al. 2003) or interactions between environmental effects of captivity and natural selection when captive-reared individuals are released back into the wild (Bailey et al. 2010). One way to reduce these concerns is to manage captive populations so as to prevent unwanted evolutionary changes. Common prescriptions include (1) maintaining inputs from wild source to slow adaptation to captivity, (2) monitoring release of captive-reared offspring to ensure their fitness in response to natural selection in the wild, and (3) management of captive environments to better match the wild environment (Frankham 2008; Williams and Hoffman 2009). We suggest practitioners consider a hybrid approach that favors propagation of individuals with phenotypes/genotypes that are well matched to the restoration site and avoid undue inbreeding (i.e., not mating with close relatives).

In addition to captivity, protected species are often managed by creating ex situ "refuge populations" under natural or seminatural conditions as a hedge against extinction (Minckley 1995; Falk et al. 1996; Maschinski and Haskins 2011). This management tool poses some of the same challenges previously mentioned for captive populations. For instance, even when refuge populations are established using a large number of individuals (Guerrant et al. 2015), bottlenecks and founder effects during early phases of establishment may result in a limited and nonrepresentative colonizing pool of genetic variation (Stockwell et al. 1996). Further, refuge populations may adapt to the refuge environment and simultaneously become maladapted to their native habitat (Stockwell and Weeks 1999; Collyer et al. 2011). In these cases, captive-centric management actions designed to limit local adaptation might reduce sustainability of the refuge population. Thus, we contend that refuge populations not be managed for evolutionary stasis, but as reserves of the future evolutionary legacy of species (Collyer et al. 2011; Smith et al. 2014), an objective perhaps more consistent with the realities of global climate change.

A question of critical importance for both captive and refuge populations, as well as other contexts, is whether or how rapidly they might evolve back toward their original condition if needed. Restoration ecologists may have unique opportunities to evaluate the reversibility of contemporary evolution by studying cases where, for example, exploitation is ceased (Conover et al. 2009), captive lineages are reintroduced to the wild, or where refuge populations are reintroduced to native habitats. A related question pertains to how "resurrection biology" may be used in a restoration context. The response of archived genotypes to the restoration environment provides important information regarding temporal shifts in local optima that may impact fitness and, consequently, selection of seed sources for restoration (Franks et al. 2008; Wilczek et al. 2014).

Inoculation, Stocking, and Natural Colonization

One philosophy of restoration is "if you build it, they will come." That is, restoration sites that exhibit suitable environments will be naturally recolonized by appropriate species/genotypes. However, natural colonization can be slow or vary as a function of species vagility and habitat fragmentation. In such cases, human-mediated introductions or colonization efforts may have important implications for genetic variation. Restoration efforts that proceed by introduction often result in reduced neutral genetic variation (Stockwell et al. 1996). These founder effects suggest such programs either drew from a small portion of the source pool or that selection and/or genetic drift reduced the pool of effective colonists. In contrast, natural colonization may reflect repeated immigration mediating the consequences of random founder events. Unlike introductions by humans, nonrandom processes may be very important to founder effects in the wild, where colonizers must first pass through selective filters in the landscape that bias the traits of colonists (Kinnison and Hairston 2007; Shine et al. 2011). Hence, it may be that natural colonization is preferable, when possible, but more research should be conducted to confirm these conclusions and to evaluate alternative introduction approaches.

Managed Releases

The traditional approach for reintroduction efforts is to use large numbers of individuals to maintain genetic variation. An alternative is to not only introduce suitable sources, but to select phenotypes within those sources that are best matched to the new environment or are preadapted to restoration environments (Stockwell et al. 2003; Hamilton et al. 2015a; chap. 5). This alternative may result in lower initial genetic variation but may speed contemporary adaptation, akin to the nonrandom filtering of landscapes. After all, adaptation and population productivity are the product of natural selection associated with reduction of maladaptive variation from the population. Again, the best phenotypes may be gleaned empirically by monitoring preliminary releases and colonization success, or eventually with genomic tools. These and other approaches for source selection could be compared in experiments in which multiple sites are targeted for restoration with comparable species and sources. The rich history of provenance trials in forest trees provide an excellent model for explicitly examining population-level responses across a wide range of environmental conditions (Rehfeldt et al. 1999; Alberto et al. 2013).

Closing Remarks

We have argued throughout this chapter that an evolutionary approach to restoration ecology will provide novel insights and solutions that have the potential to enhance the success of restoration programs. Our arguments are based on the emerging recognition that significant evolution occurs on ecological time scales (years to decades). Further, contemporary evolution is often driven by the rapid environmental changes that occur during restoration. Thus, populations used in restoration may well evolve during the early stages of restoration efforts. These evolutionary changes may in turn influence community-level responses, impacting ecological processes such as trophic cascades that influence predator-prey cycles. To date studies of contemporary evolution have focused on key phenotypic traits, but increasingly genomic tools offer additional scales of information important for the fields of conservation and restoration genomics. We hope that this chapter facilitates collaborations among evolutionary biologists and restoration ecologists in the emerging research area of evolutionary restoration ecology.

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Chapter 16

Macroecology and the Theory of Island Biogeography: Abundant Utility for Applications in Restoration Ecology

Andrew J. Dennhardt, Margaret E. K. Evans, Andrea Dechner, Lindsay E. F. Hunt, and Brian A. Maurer

Theory and Application

- Ecological systems are dynamic, which poses a number of challenges to restoration efforts because ecosystems can change at multiple spatiotemporal scales.
- With respect to practical application, an ecological restoration project must take into account issues regarding the size, macrogeographic composition, and connectedness of the system being restored.
- When restoring biota to locations in degraded landscapes, the ecosystem may depend on both the quality and quantity of colonists it receives from beyond its borders.
- Through explicit assessment of species' assemblages on broad scales, macroecology promotes insight into the structure of biodiversity and influences the success or failure of restoration efforts.

Restoration ecologists are tasked with the challenge of returning an ecological system to a configuration that approximates its natural state (Hobbs and Norton 1996, 2001). Restoring any altered ecosystem comprises a sizeable challenge in that it is critical to determine the appropriate target for restoration (chap. 1), especially prior to disturbances such as novel anthropogenic impacts as well as the relevant scales thereof. Determining the target for restoration involves four main considerations: (1) the "natural" state of the system might include pre-European human influences (e.g., widespread colonialism); (2) change is normal in ecological systems (i.e., systems exhibit a historical range of variation in disturbance regimes and species composition); (3) some system changes are completely irreversible (e.g., legacy effects), or nearly so (e.g., ecological tipping points); and (4) stochasticity plays a crucial role in shaping ecosystem state (Jackson and Hobbs

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2009). Moreover, some historically important steady states may not be attainable because of legacy effects such as the emergence of novel configurations and the spread of invasive species (e.g., establishing new biotic interactions and ecosystems; Hobbs et al. 2014), prevalence of historical contingencies (e.g., immigration of despotic breeders to isolated populations; Hedrick et al. 2014), or altered boundary constraints (e.g., climatic thresholds such as critical thermal maxima; Lee and Rinne 1980). Nevertheless, historical knowledge of ecosystems may still play a critical role in the success of future restoration efforts in the face of modern-day ecological novelties (Higgs et al. 2014).

Ecosystems are dynamic and constantly in flux, which poses a number of difficulties to restoration efforts because ecosystems can change at a variety of spatiotemporal scales (Jackson and Hobbs 2009; Jackson 2012). Multiscale ecosystem dynamics (chap. 2) make it challenging to define the natural conditions that existed prior to novel disturbance of the system. Furthermore, various biotic processes within ecological systems may change at different rates in space and time. For instance, some population-level processes (e.g., immigration) operate at very different scales than processes associated with the geophysical template of the ecosystem (Heffernan et al. 2014). At the root of the aforementioned difficulties is the realization that multiple biotic components (e.g., species with respect to composition) and abiotic processes (e.g., fire, with respect to disturbance) of the original ecosystem may be significantly altered or even entirely absent at present, and thus unavailable to the restored system. Counter to this is the notion that some abiotic and biotic processes may, in fact, be restored to the degraded system; however, to what degree can such processes be restored? It is likely that some impaired processes may never be fully restored. As a consequence of imperfect restoration, the resultant configuration and functional organization of "restored" systems is often attenuated and inadequate to sustain basic ecosystem functions and biodiversity over time (Hooper et al. 2012).

Another difficulty in defining natural system states is that many ecological communities (e.g., tallgrass prairie in central North America) likely occupied larger spatial extents than are presently available to the system designated for restoration. This implies that the current abiotic and biotic context within which the restored system must function may be very different from that of the historic context—which largely depended on ecosystem size and other relevant scales. Although there are many challenges to ecological restoration, the approaches to meet those challenges are also abundant. However, this only begs the question: are the scales and perspectives employed in restoration ecology adequate to meet the challenges of system restoration within complex, evolving contexts?

To answer this question, we begin by considering how ecosystem size affects ecological processes—considerations informed by advancements in ecological theory. Building upon reflections on system size and intrinsic processes, we then discuss the importance of scale in restoring ecological systems and ultimately propose a macroscale perspective for restoration efforts. We then outline four areas of rapid development in macroecology that offer important tools and insights to restoration ecologists: species distribution models, species-area relationships, metapopulation models, and neutral theory. Finally, we conclude this chapter with a discussion of its central themes—considerations of which may lead to improved ecological restoration efforts in the future.

System Size, Ecological Processes, and Theoretical Foundations

Biological systems of all kinds vary functionally with size (Brown and West 2000). It is fairly straightforward to understand the consequences of size variation when examining the properties of individual organisms or groups thereof. As biotic systems grow in size, physiological processes often change in a nonlinear fashion as a consequence of the fractal nature of organismal structure (West et al. 1999). These changes can have a number of profound implications for the structure of communities and ecosystems (Enquist et al. 1999a, b). For example, although much is known about organismal scaling, less is known about the way that populations, communities, and ecosystem functions change with system size (Enquist et al. 2003). The first model to address this problem was the equilibrium theory of island biogeography (MacArthur and Wilson 1963, 1967). In subsequent decades, the field of macroecology emerged as a paradigm for evaluating how spatial and temporal processes on macroscales affect the maintenance of species diversity and organization (Brown and Maurer 1987, 1989; Brown 1995; Gaston and Blackburn 2000).

Macroecology began as an attempt to explain patterns in geographical distribution, abundance, and body size among species inhabiting continents (Brown and Maurer 1987, 1989). However, it became evident that mechanistic explanations for such patterns required an expansion of perspective from focus on local ecological processes at smaller scales (e.g., individuals, populations, and ecosystems) to larger continental-scale processes (e.g., species' range distributions; Brown 1995; Maurer 2012; Gaston and Blackburn 2000). These insights were reinforced by advances in other fields, including studies of species diversity (Rosenzweig 1995), community ecology (Ricklefs and Schluter 1993), biogeochemistry (Schlesinger 1997), global ecology (Kareiva et al. 1993), and biogeography (Brown and Lomolino 1998; Hubbell 2001). Essentially, ecologists found that it was necessary to expand the spatiotemporal scales at which they viewed ecological systems in order to understand what processes were important in determining patterns in distribution, abundance, ecosystem function, and species diversity. Today, macroecology continues to enhance the present understanding of biodiversity conservation and management as well as ecological restoration, as we explore below.

By examining the properties of continental-scale species assemblages, macroecology provides the empirical basis for developing insights into the structure of biodiversity and how that organization influences the success or failure of ecological restoration efforts. Because of its focus on large-scale processes, macroecology explicitly assumes that the spatiotemporal scales of ecological systems extend far beyond political, geographical, and functional boundaries within which these systems are often managed. In this chapter, we examine the implications of a macroscale perspective for biodiversity conservation and management based on tools for ecological restoration.

Macroecology provides a benchmark for understanding the context within which ecological restoration efforts must operate as well as the limitations that are imposed by restricting the extent of restoration efforts because of mechanisms operating across scales. For example, macroecological systems (i.e., called *macrosystems*) consist of complexly interacting biological, geophysical, and sociocultural mechanisms that exhibit variation on spatiotemporal scales relevant to regions and continents such that system-wide restoration efforts now require much broader considerations than ever before (Heffernan et al. 2014; Soranno et al. 2014). Recent conceptual advances of direct relevance to ecological restoration include cross-scale interactions (i.e., how processes at one scale interact with processes at another scale; Soranno et al. 2014) and cross-scale emergence (i.e., how components at local scales interact and accumulate across scales; Peters et al. 2007). Although the importance of scale across general ecological studies is duly noted historically, one of the major questions currently confronting macroecology is the functional extent(s) to which various macroscale patterns exert controls on species' distributions (see also chap. 4 on spatial context). This knowledge gap is a central consideration in restoration ecology, and cumulative results from recent work in macroecology may shed light on how macrogeographic characteristics shape species' distributions.

Focal Areas of Current Research in Macroecology

We now outline four areas of active research in macroecology that may offer valuable insights to ecological restoration efforts.

Species Distribution Models: Macrogeographic Controls and Realized Distributions

Macroecology integrates macrogeographic patterns and processes into explanations of local and continental dynamics that control species' distributions (Kerr et al. 2007; Mokany et al. 2012). For restoration ecology, there are numerous distribution-shaping processes that warrant greater consideration in the development and improvement of new and ongoing restoration efforts. First, understanding how conditions and resources (e.g., the multidimensional niche; Hutchinson 1957, 1965) shape species' distributions is crucial to the success of ecological restoration projects, for they represent boundary constraints for species—constraints mediated via macroevolutionary adaptations (Parnell and Streelman 2010). Examples of distributional constraints include species-specific climatic thresholds (e.g., critical temperatures; Lee and Rinne 1980), changing landscape pattern (e.g., patch/matrix composition and configuration; Koh and Ghazoul 2010; Kennedy et al. 2011), and density-mediated processes (e.g., availability and quality of breeding habitat as well as intra- and interspecific competition for space, mates, and resources). Here, we describe these distribution-shaping factors both in theory and in practice for modeling geographic distributions.

Hutchinson's concept of the niche as an "*n*-dimensional hypervolume" of conditions and resources rests at the foundation of niche-distribution theory (chap. 3), and the concept has shaped how ecologists have viewed species' distributions for decades (Hutchinson 1957, 1965; Blonder et al. 2014; Swanson et al. 2015). In terms of organismal distribution, the *fundamental niche* comprises the complete range of resources and environmental conditions a species can use and occupy. Recent decades have witnessed an explosion of efforts aimed at modeling species' distributions with what are termed *bioclimatic envelope models*, or species distribution models, wherein species' occurrence data are predicted solely as a function of climatic variables (Hampe 2004; Araújo and Peterson 2012; chap. 17). While there is no reason, in theory, that other factors could not be included as covariates (e.g., density of competitors or mutualists, time since disturbance, land use classes, etc.), in practice, climate data are the most readily available sources of information for prediction. This contributes to the impression that bioclimatic envelope models estimate climatic boundary constraints for species' ranges on geographic scales. However, models fit to occurrence data are likely to confound climatic boundary constraints with other distribution-limiting factors (e.g., interspecific competition, dispersal limitation, etc.). In fact, to the degree that species distribution models are fit tightly to occurrence data, they model the *realized niche* and not the fundamental niche, where the former is the subset of geographic space a species is actually observed to occupy (i.e., in the presence of competitors, predators, mutualists, facilitators, etc.; fig. 16-1). This has raised concern that such approaches (1) simply model the environmental conditions associated with the presence or abundance of a particular species (Kearney 2006; Morin and Lechowicz 2008); (2) fail to provide any mechanistic understanding of what limits species' ranges (e.g., dispersal constraints; Colwell and Rangel 2009); and (3) may not produce reliable forecasts of how species' distributions might change under future climates.

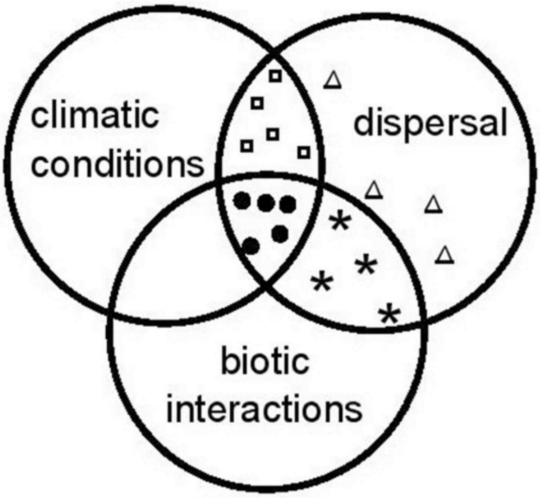

Figure 16-1. Species' niches and geographical distributions are shaped by many factors, of which, three important categories are illustrated here: climatic conditions, biotic interactions, and dispersal. The *upper left* circle indicates the geographical area in which climatic conditions support an intrinsic population growth rate at or above population replacement level. The *bottom* circle designates the geographical area in which the species can persist in the presence of interfering species (e.g., competitors or predators) or beneficial species (e.g., mutualists or facilitators). The *top right* circle signifies the geographical area within the species' capacity to disperse (i.e., over a specified time frame). The open triangles represent sink populations wherein both the climatic and biotic components of the environment are (collectively) insufficient for the population to replace itself, on average. The asterisks and open squares denote sink populations in which the climatic and biotic components of the environment, respectively, are (separately) insufficient for the population to replace itself, on average. Finally, the filled circles specify source populations wherein the climatic and biotic components are sufficient for the population to replace itself on average. This diagram is modeled after the conceptual foundations laid by Soberón (2007).

Factors other than climate that limit species' presence at a given site demand additional attention in restoration efforts. This includes biotic interactions, from competition to mutualism to facilitation; from predation to parasitism to disease, and more; as well as the diversity of spatiotemporal scales at which such interactions operate—from fine to broad. Specifically, intra- and interspecific levels of competition may often be important for explaining species composition and configuration at both localized and geographic scales (e.g., *sensu* emergent or interactive ecological processes that operate across scales in a macrosystem; Heffernan et al. 2014). Species' realized geographic distributions are the result of all of the above processes acting at once, including abiotic conditions, biotic interactions, and landscape-scale ecological processes such as dispersal, succession, disturbance, irruptions of competitors, and outbreaks of disease (fig. 16-1; Soberón 2007).

Given these considerations, the frontier of distribution-modeling research aims to better represent these processes in models of species' distributions. One avenue for doing so is the integration of macrogeographic (occurrence) data into process-based or mechanistic models of species' distributions. Examples of process-based or mechanistic distribution models include those based on phenology (Chuine and Beaubien 2001; Morin et al. 2008), physiology (Kearney and Porter 2009), and demography (Vanderwel et al. 2013; Lynch et al. 2014; Merow et al. 2014). A second avenue is to model distributions in terms of landscape-scale processes using metapopulation models, stochastic patch-occupancy models, integrated population models, or other formulations that treat dispersal explicitly (Pagel and Schurr 2012; García-Valdés et al. 2013; Chandler and Clark 2014; Newman et al. 2014; Yackulic et al. 2015).

Another example of this landscape-scale approach is the use of a spatially explicit dynamic macroecological model. Mokany et al. (2012) projected the future geographic distributions of the native plants in Tasmania (2,051 species) under climate and land use scenarios using dynamic, climate-driven models of α- and β-diversity. Addition or loss of species in each 250 m grid cell was governed by a species' proximity to a focal cell in geographic and environmental space. Though the number of species modeled and spatial scope are impressive, the explanatory power (i.e., R^2) of the underlying diversity models was poor, and all species were assigned an identical dispersal capacity. The next step would be to account for nonclimatic drivers of species diversity (e.g., biotic interactions or disturbance)—that is, incorporate additional processes into these models along with their relevant data.

Hierarchical and inverse models are promising tools to integrate occurrence data into process-based range models, or add more processes into coarse landscape-scale models. These integrated models have the capacity to fuse data across natural hierarchies of both biological organization and spatiotemporal scales, reflecting the multitude of processes, from fine to broad scales, which shape species' distributions (Marion et al. 2012; Pagel and Schurr 2012; Schurr et al. 2012). Models that more explicitly treat the underlying processes that shape species' distributions should improve understanding of which ecological processes ensure local persistence of species in space and time—which, in turn, should help increase the success of restoration efforts.

Species-Area Relationships: Ecosystem Size and Species Diversity

Ecologists have long sought to understand how ecosystem size determines the number of species inhabiting it (Rosenzweig 1995; chap. 4). MacArthur and Wilson (1963, 1967) first proposed that the number of species in an ecosystem of a given size reflects a dynamic balance between immigration of new species into the system and local extinction of species already residing in the system. Although capable of predicting some aspects of a *species-area relationship* (SAR), the island biogeographic model proved too simplistic to completely explain how species richness varies with ecosystem size (Lomolino 2000a, b, c; Lomolino et al. 1995). Clearly, mechanisms underlying SARs on continents and island archipelagos must incorporate both dispersal and population viability, as MacArthur and Wilson (1967) envisioned. However, ecological processes that regulate population rates and determine population viability, as well as individual dispersal, depend on a large number of complexly interacting mechanisms. These components include, among other things, the ecological attributes of individual organisms, abundance and variety of resources, spatiotemporal patterns of those resources, and the context in which the ecosystem exists (McGill et al. 2007; Morlon et al. 2009).

A macroscale perspective on the processes that generate SARs provides a different viewpoint that, in some ways, simplifies the problem and may take the place of mechanistic-based explanations. The basic idea is that SARs are generated as a consequence of overlapping distributions of species in geographic space (Maurer 1999; McGill and Collins 2003). However, explaining why each species has a unique geographic distribution is difficult if the focus is solely on the particular mechanisms bounding each species in space and time. If the patterns in demography of species across their ranges are examined, the myriad components underlying SARs may be condensed into simpler models describing population-level mechanisms responsible for SARs (Hubbell 2001; Maurer 1999; McGill and Collins 2003). Consider the following simple model for distributions of species in space (Maurer 1999; McGill and Collins 2003). Suppose species are distributed across space in a unimodal manner (fig. 16-2). Each species has a different-sized geographic range, some with larger ranges and others with smaller ones. At any given point in space, this results in a skewed distribution of abundance. The SAR resulting from this pattern is similar to empirical patterns seen in many collections of species at the level of metacommunities (fig. 16-3). This approach can thus be expanded to examine SARs at different geographic scales, leading to the prediction that SAR exponents will vary with the scale at which they are measured (Rosenzweig 1995).

Of particular relevance to ecological restoration is the observation that the smallest islands often depart from a SAR for an archipelago (MacArthur and Wilson 1967; Brown and Lomolino 1998; Rybicki and Hanski 2013). Many such islands are too small to maintain viable populations of any species, and must therefore be maintained by immigration alone. This observation has important implications for ecological restoration projects. Island biogeographic theory predicts that small or isolated areas may require closer proximity to a source of colonists, or greater connectivity to such source pools if the objective of restoration is to

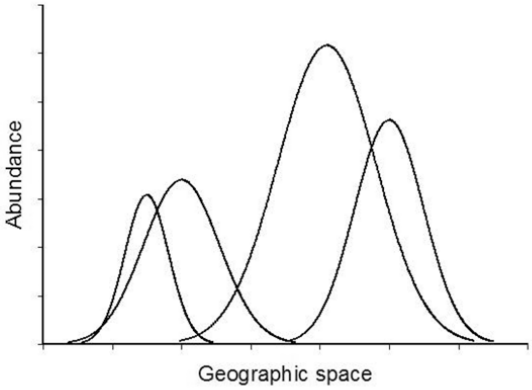

Figure 16-2. Graphical representation of the distribution of species in geographic space hypothesized to be responsible for species-area relationships.

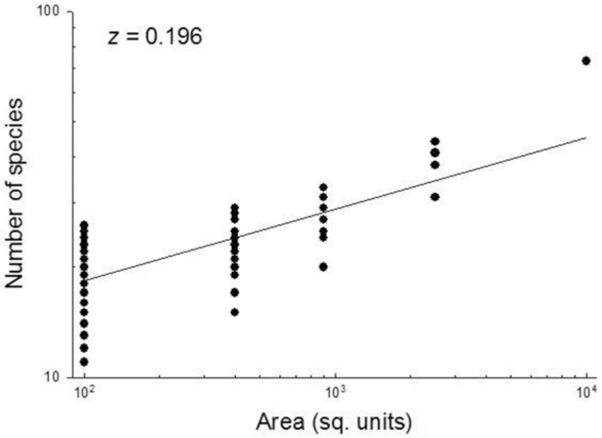

Figure 16-3. An example species-area relationship derived from a simulation of a two-dimensional version of the model represented in figure 16-2.

maintain the species diversity of a larger ecosystem. Many local populations persist as parts of larger metapopulations (Hanski 1998a, b, 1999); therefore, if the size of the area to be restored is too small, or too isolated from colonist source pools, then the likelihood of maintaining the original species richness and diversity of the restored ecosystem may be relatively small (Haddad et al. 2015; Jarzyna et al. 2015; but see also Sabatino et al. 2010).

Such consequences regarding species diversity have been debated for many years (Brown and Lomolino 1998; Whittaker 1998). What is less clear is whether there are additional properties of ecosystems that are affected by ecosystem size, patch composition, and configuration. Some unknown properties might involve ecosystem stability, functional redundancy (or equivalence) between species, and spatiotemporally autocorrelated system states. One system property that is likely to be important is the unique characteristics of the landscape matrix in which habitat islands are embedded and the degree to which the matrix is inhospitable to dispersers (Debinski 2006; Nowicki et al. 2014). In some situations, altered portions of the matrix may even facilitate connections between habitat islands. For example, Barnes et al. (2014) demonstrated that restored matrix habitat mediated responses of dung beetle (i.e., family Scarabaeidae and subfamily Scarabaeinae) communities to edge effects in Nigerian tropical rainforests. Beetle community responses were so striking, in fact, that formerly extirpated species reestablished themselves in the restored matrix habitat, which led to improved capture rates of individual beetles in the matrix as well as more abundant populations in areas adjacent to it (Barnes et al. 2014). In similar cases where the landscape is manipulated and restored in some functional manner, the once hostile matrix may act as a networked conduit for colonists, helping to sustain crucial ecological processes at the level of populations and communities.

Metapopulation Models: The Matrix and Connectivity between Habitat Islands

Metapopulation dynamics comprise a fundamental ecological process that operates across scales and is relevant to the long-term success of any restoration project (Hanski 1998a, b, 1999; see also chaps. 4 and 7). How metapopulations operate emphasizes the importance of external transport processes in maintaining a viable ecological system. A *metapopulation* is simply an aggregate of local populations connected via dispersal. The metapopulation can only persist if there is sufficient exchange of individuals among local populations to offset extinctions with colonization of new local populations—a type of ecological restoration that is organism-driven (Zhang et al. 2012). Although local populations may experience negative growth rates (e.g., “sink” populations), a metapopulation may persist indefinitely as a consequence of the external transport of colonists between subpopulations (chap. 7). Metapopulation dynamics are essential to buffering population size against demographic and environmental stochasticity as well as maintaining gene flow across populations.

For ecological restoration, this means that the species diversity of a restored ecosystem may depend heavily on the quality and quantity of colonists the ecosystem receives from beyond its borders. In the face of degraded and fragmented landscapes, subpopulations are coerced into colonizing remaining areas of suitable habitat, which often have complex shapes, greater amounts of edge habitat, and reduced connectivity between disparate and isolated fragments. Such patch fragments have been termed *habitat islands*—ecological units readily conducive to island biogeographic theory and its applications (Fernández-Juricic and Jokimäki 2001; Kennedy et al. 2011; Szlavecz et al. 2011). Moreover, the concept of habitat islands allows for direct integration with ideas about ecosystem size and species diversity as well as restoration efforts that help recover connectivity between species-specific habitat patches in a frequently inhospitable matrix on landscape-scales.

Facilitation of colonist dispersal through the landscape matrix is a relatively new idea. For decades, the landscape matrix was assumed in practice to be wholly inhospitable to species moving between disparate patches of habitat, and to some extent, the matrix does affect several species in this manner (Debinski 2006; Nowicki et al. 2014). For example, Nowicki et al. (2014) found that forest-dominated matrix was an inhospitable environment to focal grassland butterflies such that dispersal mortality was highest in forested matrix compared to other areas of open matrix, which suggested that forests impose strong selection against colonist dispersal in their study system. Though examples such as these exist, recent data suggest that for some systems the landscape matrix may, in fact, aid colonist dispersal to new population patches when the matrix is managed and improved for dispersers (Barnes et al. 2014; Kang et al. 2015). Such findings are clearly relevant to ecological restoration efforts in that managing landscape matrices to produce gradients of hospitability for various species may facilitate colonist dispersal by connecting isolated habitat islands (fig. 16-4; Blaum and Wichmann 2007; Szlavecz et al. 2011; Kang et al. 2015). These conceptual advancements may thus allow for improved mitigation of the effects of fragmentation by ensuring demographic and genetic exchange between separated subpopulations via landscape connectivity (Fernández-Juricic and Jokimäki 2001; Blaum and Wichmann 2007; Storfer et al. 2007; Hedrick et al. 2014; Wang et al. 2014) as well as in the context of connected stream networks (Dunham et al. 1997; Neville et al. 2006).

Macroecology contributes to this conceptual understanding by promoting management of population connectivity across the landscape matrix. Findings from fragmentation experiments worldwide indicate that landscapes deficient in connectivity between habitat islands lead to more broad and accelerated extinctions on localized scales over time and may exacerbate ecosystem changes (Hooper et al. 2012) on broad scales via biodiversity loss in the face of increased landscape fragmentation (Haddad et al. 2015; Jarzyna et al. 2015). Properties of metacommunities (e.g., the size, shape, composition, configuration, and connectivity between like communities) are also of great interest to restoration projects that intend to alter characteristics of the matrix to improve landscape connectivity and dispersal conditions (Kang et al. 2015).

Consider the following example, which highlights the importance of avian

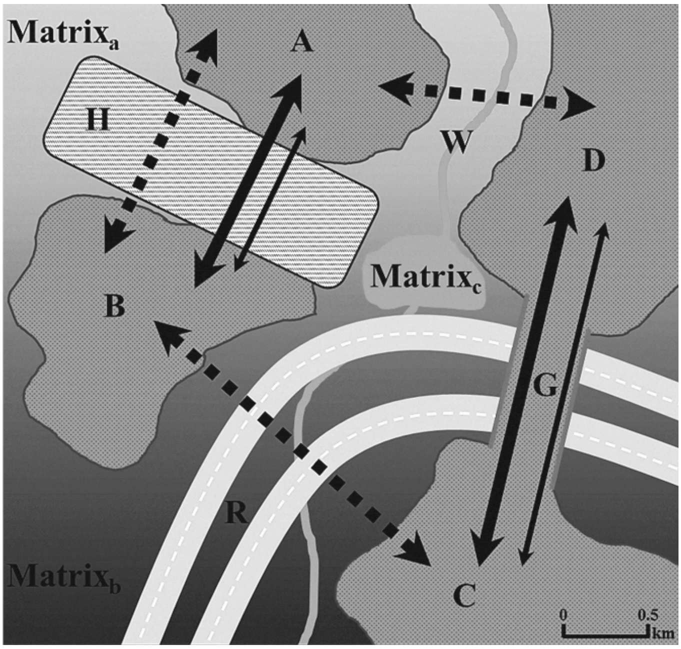

Figure 16-4. Schematic of a hypothetical landscape where habitat islands (A–D; i.e., supporting disparate local populations) are separated by a gradient of matrix. This gradient represents changing matrix habitat that is either (a) conducive, (b) semiconducive (e.g., an agricultural field), or (c) unconducive (e.g., a lake) to dispersal between patches for two hypothetical organisms, a mammal (i.e., high vagility; thick black arrows) and an insect (i.e., low vagility; thin black arrows). Dispersal events are assumed low risk (e.g., to mortality (solid lines), high risk (dashed lines), or impossible (e.g., for the insect between B and C; no lines) between habitat islands for each organism across the matrix. Obstacles to dispersal include an open agricultural hayfield (H), a fast-moving waterway (W), and a highly trafficked roadway (R); while one corridor is a green-way (G) bridge constructed for wildlife. In all cases, local population persistence across the landscape is mediated by immigration and colonization, influenced by the dispersal limitations of the organism and connectedness of patches as well as subsets of a connected and permeable matrix.

metacommunity properties on a broad spatial scale. Maurer et al. (2013) developed methods for describing spatial properties of metacommunities based on avian species' sampled during 1996–2000 from the North American Breeding Bird Survey (Pardieck et al. 2014). Maurer et al. (2013) used information on species' abundances, local environmental variation, and avian phylogenetic relationships to estimate the extent of metacommunities for breeding bird assemblages across 1,393 survey routes (fig. 16-5). Metacommunity extent (i.e., distance, in km) was estimated as a function of ecological similarity between survey sites. By plotting the similarity among sites as a function of the distance between them, Maurer et

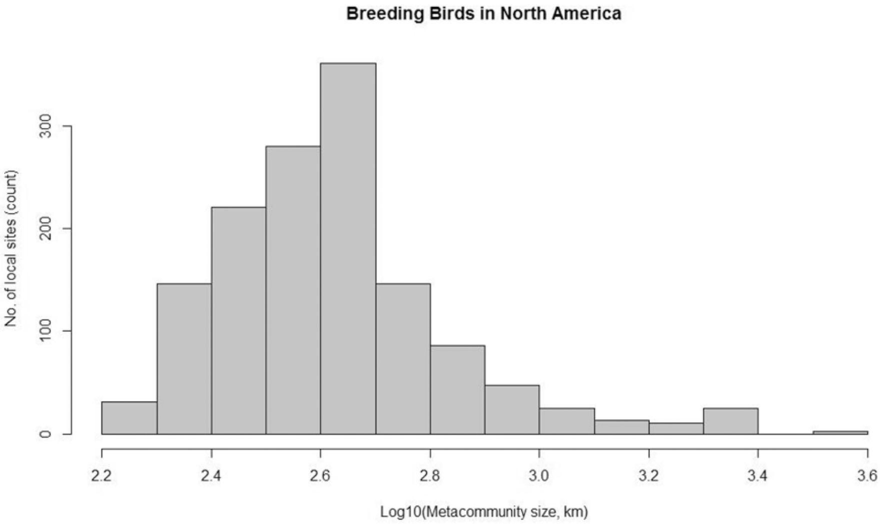

Figure 16-5. Distribution of metacommunity size (i.e., distance, units of $\log_{10}$ km) for 1,393 avian assemblages sampled by the North American Breeding Bird Survey (Maurer et al. 2013).

al. (2013) were able to estimate a maximum distance beyond which the similarity decreased as more sites were added to the pool of metacommunity-eligible sites. Interpreting this maximum distance as a measure of metacommunity extent thus facilitates understanding of spatial patterns of metacommunity size.

Applying this method to data on North American terrestrial birds during the breeding season, the size of metacommunities (in terms of geographic distance) reveals that breeding bird assemblages are diverse in the spatial extent from which local communities draw colonists from other communities. Interestingly, patterns of metacommunity size reflect the underlying structure of important ecoregions in North America. For instance, metacommunity sizes tend to be much smaller in the eastern temperate forests than in the northwestern forested mountains and southwestern deserts (fig. 16-6). In contrast, metacommunity size tends to be larger in the Great Plains and northern boreal forests.

These patterns imply that the region from which a restoration project might draw colonists will likely be smaller in the eastern temperate forests than in the Great Plains, for example. Metacommunity extents illustrate the importance of macroecological context in restoring ecological systems. Analyses such as these demonstrate that no ecological community is entirely isolated, and sites vary in the degree to which they are able to draw upon colonists. This suggests that spatial connectivity *among* habitat patches must play an important role in local community persistence over time. Furthermore, connectivity between ecologically simi-

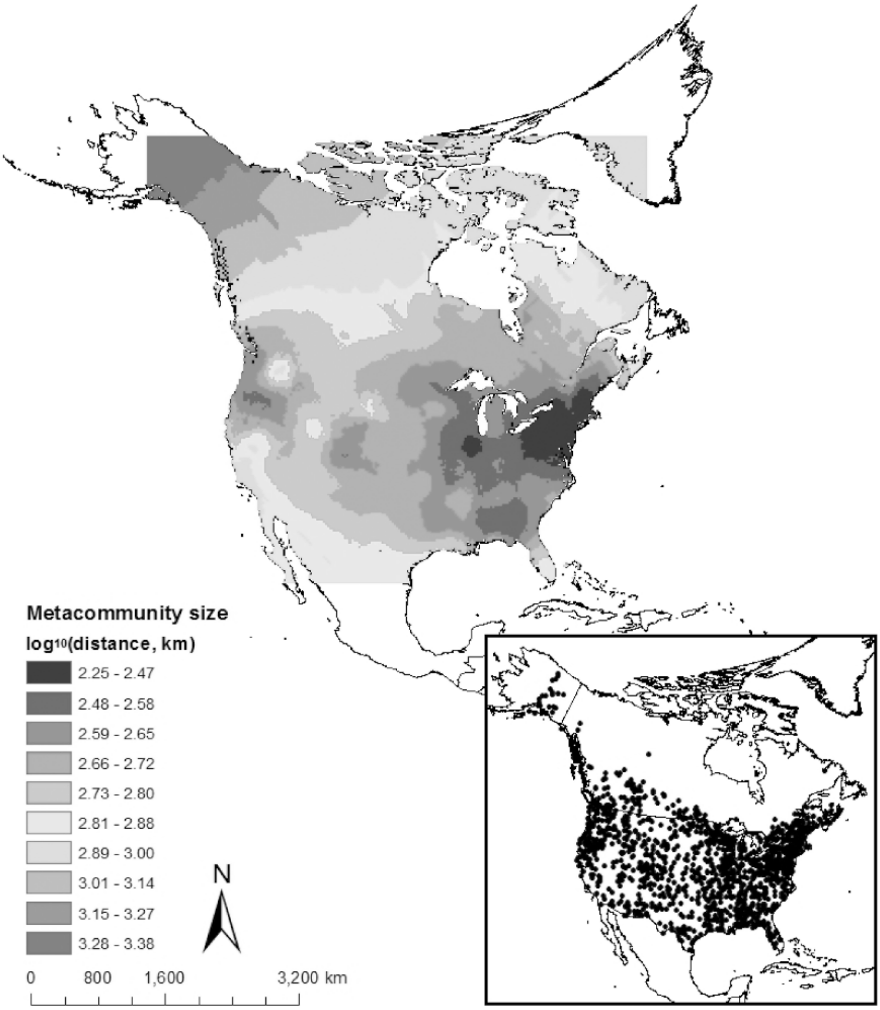

Figure 16-6. Geographic variation in metacommunity size (i.e., distance) for avian assemblages across 1,393 Breeding Bird Survey routes in North America—produced via an ordinary kriged interpolation. Metacommunity distances are measured as a function of site similarity based on species relative abundance, local environmental variation, and phylogenetic relationships between species (Maurer et al. 2013). The inset displays the spatial distribution of routes (*n* = 1,393) sampled during 1996–2000. The geographic patterns in metacommunity size suggest the immediate significance of spatial context in system restoration efforts—settings which likely depend on ecoregion type, connectivity between ecological communities, and relative anthropogenic influences, among other potential factors.

lar communities likely relies upon the unique ecoregion to which a community belongs as well as influences from human populations and other disturbances.

Neutral Theory: Species Equivalence and the Maintenance of Biodiversity

In attempting to understand the underlying causes for patterns such as SARs, the neutral theory of biodiversity (Hubbell 2001) posits a specific population mechanism responsible for macroscale diversity patterns is based on the assumption of functional equivalence among species. From the perspective of restoration ecology, neutral theory implies that a complete, functional ecosystem can be constituted from an arbitrary set of species from the pool of available organisms that could occupy a given site. Because one species is substitutable for another in this model, the relative abundances and identities of species in a community should have little impact on the final structure and function of the ecosystem (fig. 16-7). Contrast this with an ecosystem where species differences were important and where an "optimal" set of species best adapted to local conditions existed. In such a context, maximal ecosystem functioning would only exist for a few (or even just one) set of species best adapted for the local conditions. As such, restoration would require identification of the best set of species necessary to meet functional goals of the restoration endeavor.

To what degree are the assumptions of the neutral theory met in nature? The initial response to this question by many ecologists would be that differences among species are ecologically important. However, demonstrating that differences among species have a cumulative impact on the structure and function of ecosystems has not been straightforward (Loreau et al. 2001). Furthermore, successful ecological restoration may often depend on bringing together the right combination of species to generate and maintain a functional ecosystem. If this is generally true, then restoration projects can be viewed as experiments that can provide tests for the assumption of functional equivalence among species. If functional equivalence is true, then there may be a relatively large number of species combinations that might produce a persistent, functional ecosystem. If functional equivalence is false, then there would only be a few appropriate combinations of species that will produce an ecosystem that can persist and function appropriately over time (fig. 16-7). There are a number of ways that these hypotheses might be tested. In fact, a survey of restoration activities that were evaluated based on whether or not they led to an appropriately functioning ecosystem might provide a test of functional equivalence if it was found that species composition was an important factor in determining the success of the restoration attempt.

Adaptive management of restored ecosystems might also provide opportunities to design experiments to test the degree to which degraded habitats and eco-

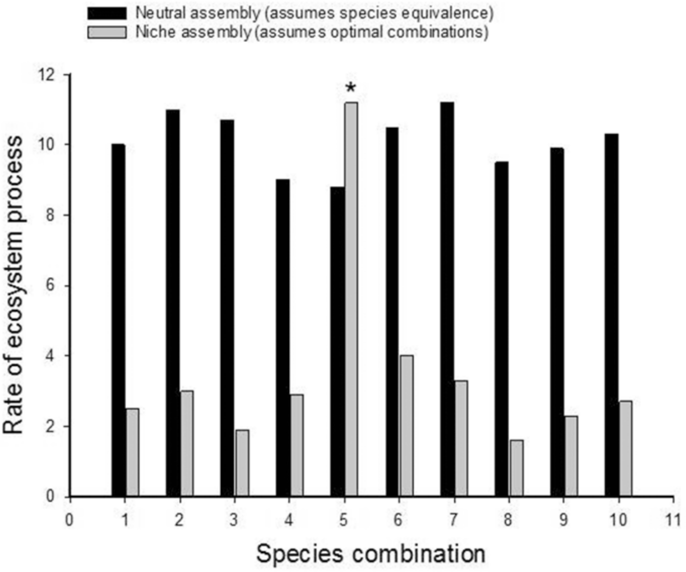

Figure 16-7. Graphical representation of the differences between the neutral assembly and niche assembly hypotheses. The vertical axis is the rate of some ecosystem process of interest to restoration efforts. Suppose that there are ten different combinations of species that could occupy the local ecosystem. In this hypothetical system, the neutral theory would predict that all ten species combinations would generate roughly the same rate of the process because each species was composed of the same kind of ecologically equivalent individuals. Under the niche assembly hypothesis, there is a combination of species ($x = 5$, asterisked) that maximizes the rate of the ecosystem process. This combination contains the species that are best adapted to the local conditions in the ecosystem. As illustrated, it is apparent that restoration efforts for a particular system would necessitate different goals, given these two hypotheses of community assembly.

systems are restored (Millar et al. 2007; Theiling et al. 2015). Because of the importance of understanding how species composition of an ecosystem affects its structure and function, it is imperative that restoration projects be monitored carefully and thoroughly after they are completed (Heer et al. 2013; Theiling et al. 2015). Such monitoring will serve the dual purpose of establishing criteria to judge the degree to which restoration objectives are met via decision support tools (e.g., Optimal Restoration of Altered Habitats; Lethbridge et al. 2010) and provide data to test models of community assembly that make assumptions about the functional equivalence of species (chap. 9). In this way, ecological restoration can become not only a practical field that deals with the *what* of restoring ecosystems, but it can also provide a fertile field to test scientific theories that provide answers to *why* and *how* degraded ecosystems should be restored in order to maintain their integrity in space and time. Macroscale concepts thus provide restoration ecology with a conceptual framework for long-term management on landscape scales with the goal of maintaining biodiversity and the functional integrity of restored ecosystems (Hooper et al. 2012).

Thematic Considerations for Applied Developments in Restoration Ecology

A comprehensive discussion of how large and connected specific restored ecosystems must be in order to preserve target species and ecosystem functions is beyond the scope of this chapter. For the present purpose, we can say confidently, as a basic principle, that any restoration project needs to take into account practical issues regarding the size, macrogeographic composition, and connectedness of the ecosystem being restored (Aronson and Le Floc'h 1996; White and Walker 1997). Since ecosystem functions often require input from processes not physically contained within the boundary of the ecosystem, a fundamental principle of ecosystem restoration should be to ensure that the restored ecosystem resides within a comprehensive landscape context (Weinstein et al. 2014). Such a setting must be conducive to providing adequate flux of individual organisms, energy, and resources between populations inhabiting patch islands in order to maintain ecosystem viability over long-term temporal scales. To understand the importance of the aforementioned concepts to restoration ecology, we briefly consider management challenges that the planet faces today.

Although global societies foster a well-connected landscape for human populations, the same cannot be said for numerous floral and faunal populations. While landscape fragmentation is an important issue today, increasing trends in land use change that are detrimental to wildlife are likely to continue (Sala et al. 2000). Moreover, landscape changes in composition and configuration will likely produce harmful synergistic effects with future climate scenarios as species begin to track their climatic constraints. The emergence of species' range shifts poses a great challenge to biodiversity management and conservation (Morin and Lechowicz 2008; Chambert et al. 2015). However, analytical tools exist now that can help managers address multiscaled environmental drivers of range shifts. For example, once again, species distribution models may provide valuable capacity for anticipating conservation concerns such as forecasting species' range shifts (Pagel and Schurr 2012; Schurr et al. 2012).

One of the emerging challenges to restoration ecology is managing ecological systems in the face of nonstationary climate regimes (chap. 17). Such climatic shifts suggest that the targets for restoration are moving targets, including the composition and functionality of ecological communities (García-Valdés et al. 2013).

Case Study Box 16-1
Hypothetical Restoration of Wild Populations Facing Demographic Consequences Mediated by Landscape Structure on Broad Spatiotemporal Scales

Marys River watershed, Great Basin Desert, US: The Marys River (41°33′ N, 115°18′ W) is a 500 km^2 watershed located in the Lahontan Basin of the Great Basin Desert, US, and the area supports federally threatened populations of the Lahontan cutthroat trout (*Oncorhynchus clarkii henshawi*). These trout are endemic to the region and often restricted to small isolated streams. This makes investigation of demographic consequences from landscape structure on their populations a model case for restoration considerations on broad scales. In this stream network system, Neville et al. (2006), hereafter *researchers*, assessed the genetic characteristics of trout populations with respect to attributes of the local landscape, research that we now summarize and discuss with respect to macroecological considerations for ecological restoration.

Expectations informed by island biogeographic and metapopulation theory: Given the long-standing recognition that landscape patterns have important influences on ecological processes that shape and constrain populations, researchers sought to investigate the influence of dispersal barriers on genetic population structure in this stream network.

Results of the population-level assessment: Trout populations facing low spatial connectivity exhibited sedentism and also occupied habitats of poor quality, which contributed to lower genetic diversity than subpopulations inhabiting connected, higher quality habitats. Concomitant increases in genetic differentiation were also associated with isolated populations in response to decreased gene flow across one-way dispersal barriers in contrast to more connected populations, which were able to move to and from the river main stem or were able to traverse more passable barriers throughout the stream network. Researchers found no evidence that genetic differences arose solely based on the type of dispersal barrier present (e.g., man-made dams or natural waterfall features); however, the response of trout to such barriers depended markedly on the habitat that isolated populations occupied. For example, one subpopulation inhabited broad, high quality habitats above a waterfall yet was also subject to asymmetrical gene flow across that same barrier. Despite deficiencies in gene flow, over time, these areas still supported larger and more stable populations than did areas with fine, poor quality habitats in the face of similar constraints with respect to gene flow. Finally, researchers found that spatial structure, rather than temporal structure, was more important for shaping population genetic diversity in the system.

Research implications: Spatial aspects such as habitat connectivity and quality, as well as concomitant genetic effects on dispersal behavior or individual fitness, may be important factors for limiting population productivity, recruitment, and persistence over time. Researchers concluded that population persistence concurrently depends on the life history strategy (i.e., sedentary versus migratory behavior), the connectedness of habitat patches (i.e., whether symmetric or asymmetric gene flow across barriers), and general habitat complexity (i.e., in both quantity and quality) in order to sustain the greater metapopulation of cutthroat trout.

Considerations for ecological restoration and management objectives: If we imagine that this region was of interest to restoration ecologists, then what solutions might we offer to managers of this region with respect to conservation of Lahontan cutthroat trout? Our discussion suggests that we should consider several criteria for restoration: (1) the size of the system (e.g., a 500 km^2 freshwater catchment); (2) the macrogeographic constraints on the system (e.g., multiple subpopulations of migratory trout capable of moving >50 km annually and also constrained by the distribution of quality habitats); (3) the connectedness of the system (e.g., the variable flux of genes, energy, and resources throughout the stream network); and (4) the broader context of the system's landscape (e.g., the proximate influences of genes, energy, and resources beyond the stream network). Management solutions relevant to each of these considerations might include regular long-term assessments of individual trout (e.g., via genetic methods), macroscale enhancement of key habitat resources and movement corridors (e.g., via in-stream manipulations of habitat or via facilitation across dispersal barriers, whether by permanent removal or retrofitting thereof), and recurrent monitoring surveys beyond the stream network in order to improve conditions for the species' metapopulation to persist across the system (fig. 16-8).

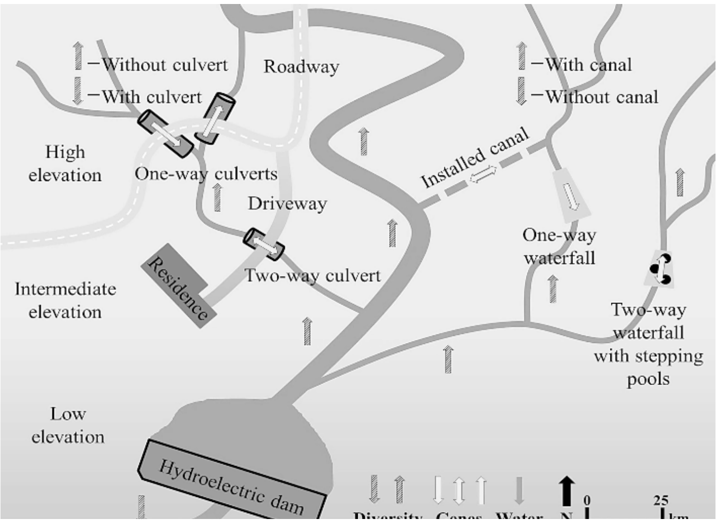

Figure 16-8. Schematic of a hypothetical riverscape where water predominantly flows southward and fish populations are either connected or isolated across tributary waters that contain both natural (i.e., waterfalls) and man-made barriers (i.e., dams and culverts) to individual dispersal. If this area were unmanaged for fish, then we might imagine that movement barriers would remain in place and meet their intended purposes. However, these barriers might also produce various unintended consequences (e.g., changes in gene flow [white arrows] and genetic diversity [gray arrows]). For example, inhibited dispersal could lead to decreased genetic diversity in isolated fish populations, and thus produce increased probabilities of local extinction. Despite these conditions and their associated demographic consequences (e.g., hindered productivity, recruitment, and persistence), restoration efforts could provide solutions through management intervention (e.g., barrier removal, retrofitting, or facilitation measures, such as installing movement corridors) intended to promote spatial (genetic) connectivity throughout the watershed and ensure greater probability of metapopulation persistence for the target species over time.

References: MacArthur and Wilson 1967; Slatkin 1985; Dunham et al. 1997; Davies et al. 1999; Manel et al. 2003; Neville et al. 2006.

Distribution models or bioclimatic envelope models have been used extensively to project future species' distributions (Thuiller et al. 2005; Jetz et al. 2007; chap. 17), and these projections may offer key guidance to restoration ecologists in terms of anticipating appropriate targets of species composition and associated ecosystem function at a given location. For example, adaptive strategies aimed at managing forests in the face of climate change include mixed species plantings, neonative translocations (e.g., assisted migration), and enhancing genetic diversity in managed populations (Millar et al. 2007; Storfer et al. 2007), which can be informed by forecasts of the distributions of species, subspecies, varieties, or haplotypes.

Management actions such as assisted migration and the use of future climate-adapted genotypes have thus far been discussed more in theory than attempted in practice (McLachlan et al. 2007; Vitt et al. 2010; Maschinski and Haskins 2012). Nonetheless, it seems likely that restoration ecology is poised to use macroecological distribution models in such ways. Reconstructions of species' past distributions, as well as past ecological communities, indicate consistently that organismal distributions can change dramatically over time and often lead to the realization that some local communities in the past have no analogues in the present (Jackson and Hobbs 2009). Furthermore, individualistic trajectories of species' past distributions (*sensu* Gleason 1926) suggest that species-level prediction, as opposed to community-level forecasting, is most appropriate for coordinated conservation and management. Pairing species distribution models and other conservation tools with innovative ideas, such as efficient theories (Marquet et al. 2014), may also provide unique insights into ecological patterns and processes on macroscales—insights useful to applied management and restoration efforts.

Moreover, species distribution models and similar tools may provide guidance for establishing new, and managing existing, set-aside areas for conservation (e.g., national reserves, parks, and local easements). What is certain from our review of current literature is that connectivity between habitat islands is an *essential* component for dispersing organisms, genetic flow, and persistent metapopulations (Cushman et al. 2011). Additionally, macroscale management of wild populations across landscapes is also important for the maintenance of such crucial ecosystem properties (i.e., populations that are connected, genetically diverse, and stable; McKinney et al. 2010; Hobbs et al. 2014). In addition, set-aside areas and reserves should incorporate management procedures that enhance landscape connectivity between habitat islands, especially those areas confronted with increased isolation as well as shifting rates of local population growth and genetic diversity (Rybicki and Hanski 2013; Wang et al. 2014). Such management practices will enable ecological restoration to advance beyond efforts at localized scales (e.g., individuals, populations, and ecosystems) to conservation of the properties of single ecosystems and their connections to other systems at broader scales, such as those of continents, biomes, and the biosphere—coarse scales that structure and interact with ecological patterns and processes at finer scales (Cattarino et al. 2014).

Closing Remarks

Ecological systems are dynamic and constantly in flux, and systems in need of restoration are certainly no exception to such fundamental characteristics. Restoration of degraded ecosystems thus requires special consideration of features such as the target system's former natural state, its alternative steady states, inherent legacy effects and ecological tipping points, and the role of stochasticity in shaping the target system's state. These requirements underscore the numerous difficulties facing ecological restoration efforts. Such complications include issues with (1) identifying ecosystem size and restoration scales; (2) analyzing macrogeographic controls and selecting tools to forecast or hindcast species' distributions based on those controls; and (3) applying mechanistic or process-based (e.g., metapopulation) tools versus species-area or neutral system relationships to inform restoration objectives. Despite these challenges, macroecological perspectives may provide guidance to restoration efforts moving forward, especially with respect to accounting for historic and current ecosystem factors, both abiotic and biotic, in space and time.

The macroscale perspective we have described strongly suggests that ecosystem restoration cannot be successfully carried out without thoughtful consideration of the spatiotemporal context within which the restored system will exist. Ecosystems are composed of numerous collections of species, each of which are shaped by unique macrogeographic controls (e.g., abiotic and biotic factors) on their distributions and abundance in space and time. Consequently, ecological restoration should not lose sight of these species-specific controls that partly assemble ecological systems. An ecosystem is not only defined by the species composition, edaphic conditions, and interaction networks that exist within its boundaries, but also by the ebbs and flows across its boundaries that connect its internal processes with broader external systems and their processes, for example, nutrient, energy, and hydrological (chaps. 12–14). Accordingly, restoration efforts must acknowledge the emergent novel dynamics of habitat islands for populations that exist in modified landscapes. This also necessitates focused recognition and management of landscape-scale factors, such as habitat matrices for increased hospitability, to connect and facilitate flows of colonists between distinct habitat islands and ecological communities—factors well-grounded in island biogeographic and metapopulation theory.

Through explicit incorporation of established theory to assess the properties of species assemblages and distributions on broad spatiotemporal scales, macroecology provides an empirical basis that can generate insight into the structure of biodiversity and how that organization influences the success or failure of ecological restoration efforts. Because of its focus on regional- and continental-scale processes, macroecology readily identifies the importance of landscape connectivity between, as well as the relative isolation of, ecological communities, because ecosystems extend far beyond political, geographical, and functional boundaries —even though such systems are frequently managed at these scales. Therefore, a restoration project that fails to consider external transport processes (e.g., species dispersal across project boundaries) over managed landscapes may be unable to meet crucial project objectives, because the restored system may be governed (e.g., limited or enhanced) by flows across its borders such as from neighboring landscapes (chaps. 4, 7). One important way to maintain the integrity of a restored ecosystem is to replace external transport processes with intensive management activities that serve or enhance the same function, but such approaches represent a more or less permanent commitment that may not be logistically or fiscally viable.

Furthermore, data on the relationship between species composition and the success of restoration activities can be used to test the functional equivalence of species, an assumption that underlies neutral models of macroecological patterns. In particular, carefully planned restoration projects can be used as active experiments in adaptive management to test this (and other) important assumption(s) about the assembly, functionality, and persistence of disparate ecological communities and systems, especially on landscape-level scales. Restoration ecology must become increasingly able to anticipate and address species' range shifts, novel system configurations, and accelerated extinction rates in response to complex synergies amidst changing land use practices, expanding human populations, and future climate dynamics (chap. 17). In the face of these substantial interacting processes, macroecology thus provides a foundational framework to enhance endeavors in restoration ecology on vast spatiotemporal scales as well as aid the future of biodiversity conservation and management in a nonstationary and ever-challenged world.

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Chapter 17

The Influence of Climate Variability and Change on the Science and Practice of Restoration Ecology

Donald A. Falk and Constance I. Millar

Theory and Application

- Species, ecological communities, and ecosystems have been exposed to climate variation over ecological and evolutionary time scales, but future climate change may exceed past variability, making some reference conditions potentially less relevant to guide future restoration efforts.
- Ecological responses to climate change may include altered species ranges, disassembly of contemporary multispecies communities, and biome shifts driven by elevated mortality.
- Restoration ecology may need to focus on adaptive capacity and resilience by anticipating future species distributions, assisting migration into new areas, and conducting experiments to identify persistent assemblages under future conditions.

Variation in Earth's climate system has always been a primary driver of ecosystem processes and biological evolution. In recent decades, however, the prospect of anthropogenically driven change to the climate system has become an increasingly dominant concern for scientists and conservation biologists. Understanding how ecosystems may adapt to rapid contemporary and future change benefits from our knowledge of how they have responded to natural climatic variation across prehistoric time, especially during periods when Earth system conditions and ecosystems correspond to those of the modern era (e.g., Quaternary, the past 2.5 million years). Despite the dominant and pervasive influence of both climate variability and climate change, the restoration field is still learning how to accommodate these emerging influences. In this chapter we explore the consequences of climate

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variability and change for the science of restoration ecology and the practice of ecological restoration.

Earth's Climate System: A Paleoclimatology Primer

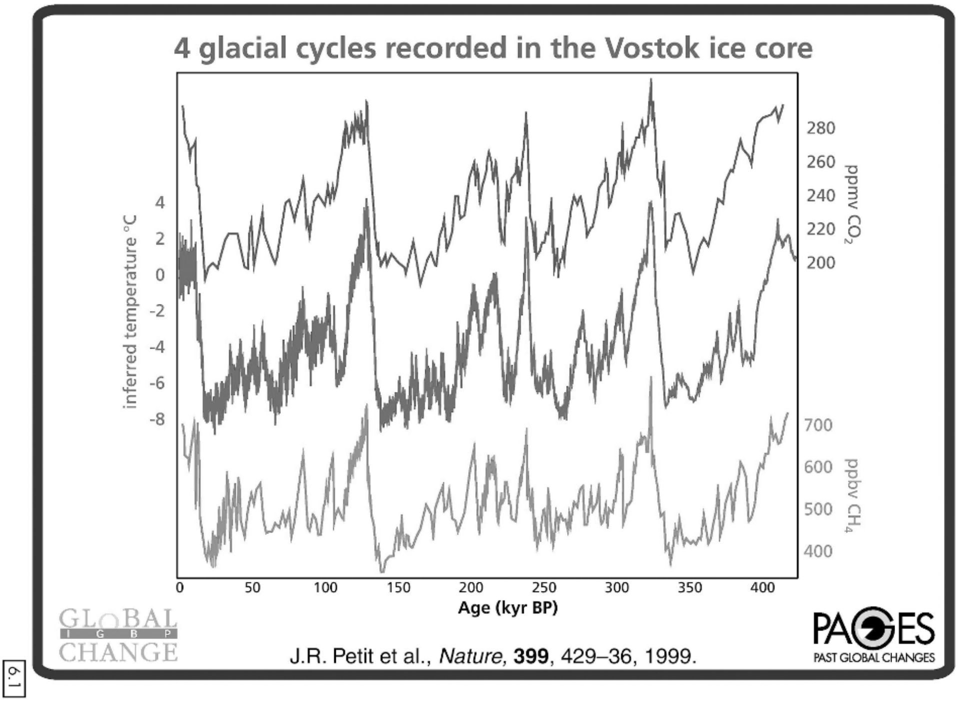
Climate variability in space and time has been a characteristic of the evolutionary and biogeographic context for life on Earth since its inception. All forms of life are influenced by this variability in where and how they live, including how they tolerate episodes of adverse weather effects through conditioned responses and evolved adaptations. The climate envelope of each species at various life stages is a fundamental property of its evolved ecological niche (Colwell and Rangel 2009). The species, communities, and systems that we attempt to conserve and restore are all thus preadapted through evolutionary experience to varying degrees of climate variation, from gradual and directional to abrupt and chaotic.

In recent decades, new tools with high precision and resolution, new models reliant on high-speed computing capacity, and a critical mass of empirical research have revolutionized understanding of Quaternary climate.

The deepest time proxies are derived from deep ocean sediment cores and ice cores retrieved in polar ice caps (Andersen et al. 2004; Barker et al. 2011; Bradley 2015). Cores drilled to the bottom of continental ice sheets (e.g., Greenland and Antarctica) have yielded highly resolved information on more than forty climate variables over the past 800,000 years (Jouzel et al. 2007; Bazin et al. 2013). Analysis of these and other climate-related isotopes are now extracted routinely from other environmental contexts where undisturbed deposition occurs, such as varved lake beds, coral reefs, and sea floor sediments. Other climatologically important indicators retrievable from ice and sediment cores that include greenhouse gas (CO_2, CH_4) concentrations, deuterium, atmospheric aerosols that indicate dust and volcanic ash, and species composition of past marine plankton rain.

Multimillennial Climate Cycles

These long, highly resolved records collectively document the repeating, cyclic nature of climate over the past 2.5 million years (fig. 17-1) (Bradley 1999; Wright 1989; Raymo and Ruddiman 1992). Oxygen-isotope records show a repeating pattern of more than forty glacial/interglacial cycles. A primary mechanism for these periodic climatic oscillations was proposed by Serbian mathematician Milatun Milankovitch (1941) long before detailed paleoclimate variability had been documented. From the many oxygen-isotope curves now available around the world, it is clear that major warm-cold oscillations of glacial/interglacial phases have been



J.R. Petit et al., *Nature*, **399**, 429–36, 1999.

Figure 17-1. Primary fluctuations in temperature, CO_2, and CH_4 between glacial and interglacial periods for the past 400,000 years, derived from oxygen-isotope analysis of ice cores from the Vostok station in Antarctica. Our current interglacial period (Holocene) is at the *far left*, from 0 to 10,000 years ago. Pages International Project Office—modified from Petit et al. 1999.

expressed more or less synchronously on global scales (Mayewski et al. 2004). Global temperature differences between glacial and interglacial periods averaged 12°C–17°C (Petit et al. 1999; Bintanja et al. 2005).

Century- To Millennial-Scale Climate Variation

Analyses of oxygen-isotope variation, tree rings, and other proxies reveal that century- to millennial-scale variability has been common through the Quaternary. Multimillennial climate variation is driven by oscillations in solar input to Earth's atmosphere, greenhouse gas (GHG) concentrations, thermohaline ocean circulation, and other forcing factors that operate on scales of 1,000–2,000 years, within the life span of some long-lived organisms such as temperate trees (fig. 17-2) (Mann et al. 2008). Climate intervals exemplifying multicentury to millennial cycles during the recent Holocene include the Little Ice Age (LIA), a minor ice advance and global cold period from AD 1450 to 1920 (Grove 1988; Overpeck et

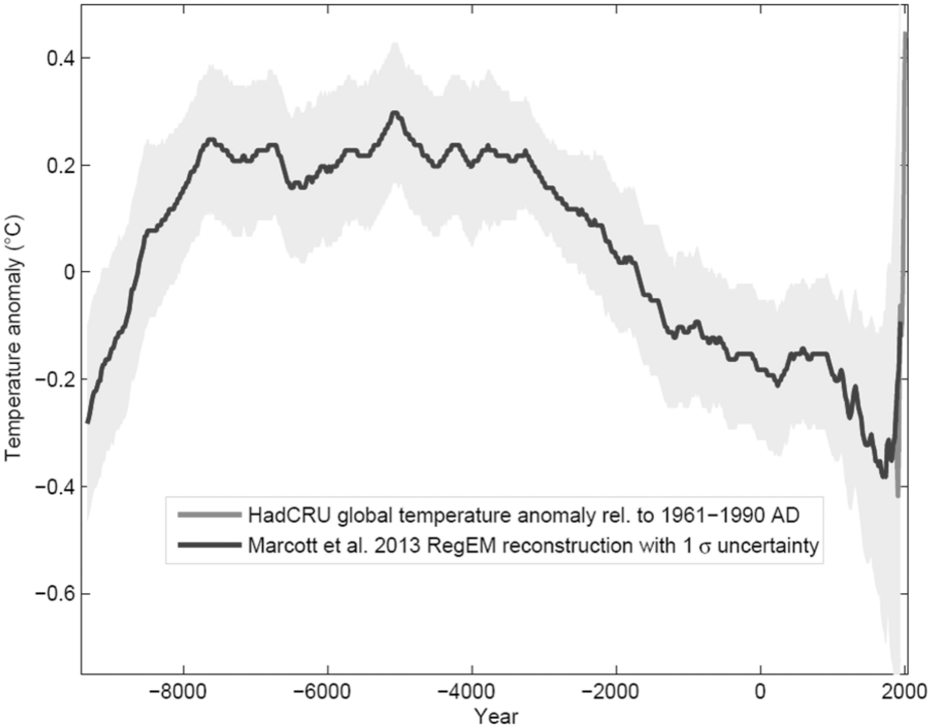
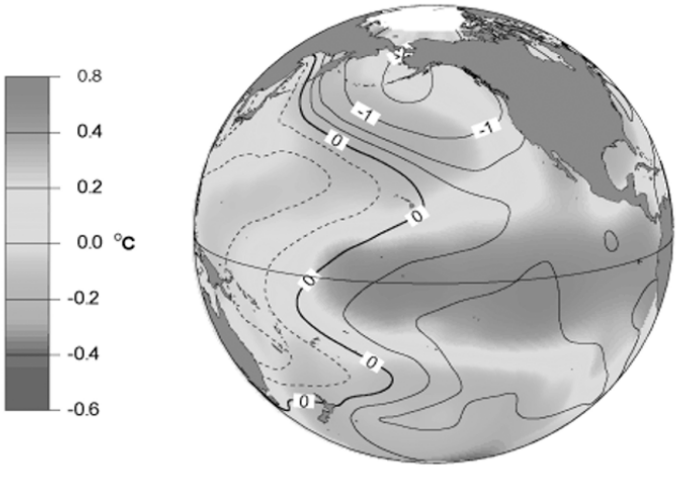


Figure 17-2. Holocene (past 10,000 years) mean global temperature variation. The rapid rise in global temperatures at the end of the last Ice Age was followed by a ~5,000 year period of relative stability with variation on centennial to millennial scales. Temperatures declined ~0.5°C over the following 5,000 years until the recent abrupt rise due to anthropogenic warming. Graphic from www.realclimate.org , modified from Marcott et al. 2013.

al. 1997; Mann 2002) and the Medieval Climate Anomaly, a warm, dry interval in some regions from AD 900 to 1350.

Interannual to Decadal-Scale Climate Variation

Climatologists have identified many climate modes operating on scales from a few years to several decades, using proxy information derived from tree rings, corals, layered ocean sediments, and other sources, as well as instrumental data for the past century. The best known of these is the El Niño pattern, called the El Niño-Southern Oscillation (ENSO) for its interhemispheric, atmospheric, and oceanographic expression and concentration in the tropical and subtropical Pacific Ocean (Sarachik and Cane 2010; fig. 17-3). ENSO brings opposing seasonal weather conditions to different parts of the world, referred to as *teleconnections* from oceans to terrestrial weather. For instance, El Niño events portend unusu-



Warm Phase ENSO

Source: Climate Impacts Group, University of Washington

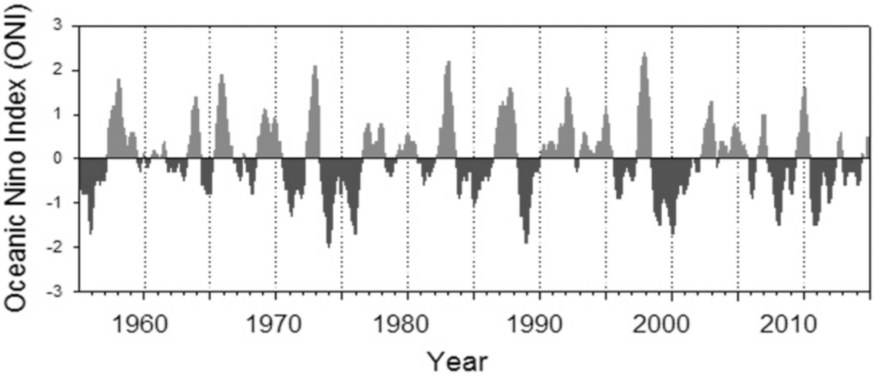


Figure 17-3. The El Niño/Southern Oscillation is an internally regulated, ocean-atmospheric dynamic process that affects global climate on interannual and decadal scales. Warm phase ENSO figure from Mantua et al. 1997; (©American Meteorological Society. Used with permission). Ocean Niño index from: NOAA Fisheries (*lower* panel).

ally warm and wet autumns and winters in the southwestern United States, and unusually cool and dry weather in the Pacific Northwest, with reversed expression during La Niña events.

Multidecadal (twenty-year to sixty-year) periodicities in the climate system have also been identified but remain poorly understood mechanistically in part because the instrumental record captures at most a few complete cycles. The Pacific Decadal Oscillation (PDO) is a multidecadal cycle of northern Pacific sea surface temperatures (SSTs) that affects the climate of northwestern North America. The

PDO reflects decadal changes in ocean circulation patterns in the high-latitude Pacific Ocean (as opposed to ENSO's tropical locus) and yields climate effects and regional patterns similar to ENSO (Mantua et al. 1997; Zhang et al. 1997).

Climate Variability as an Ecosystem Architect

Abundant evidence worldwide shows that life on Earth has responded to climate variability at all of these scales of space and time documented by pollen and plant remains deposited in sediment cores extracted from meadows, bogs, lakes, and ocean bottoms. In dry environments, packrat middens preserve macrofossils, while in temperate forests, tree-ring records archive annual tree growth.

Changes in Species and Communities over Millennial to Multimillennial Time

At multimillennial scales, paleoecological records document changes in regional floristic composition multiple times in correspondence with major climate phases. For instance, in the northeastern United States, eastern Canada, parts of Scandinavia, and northern Asia, species shifted latitudinally hundreds of kilometers in the late Pleistocene and early Holocene as regional climate warmed (fig. 17-4) (Davis 1981; Jackson et al. 1987). In more mountainous regions, species responded primarily by changes in elevation and aspect, illustrated by conifers of the Great Basin and southwestern desert region, which shifted as much as 1,500 m (Thompson 1988, 1990; Grayson 2011). Where habitats were highly patchy, such as areas with steep and discontinuous gradients, species responded by fluctuations in population size and smaller geographic shifts, as exemplified by oaks in California (Adam and Robinson 1988; Heusser 1995). Areas occupied by continental ice caps were often revegetated via rapid colonizations from refugia (Brubaker and McLachlan 1996).

Paleorecords in areas where abundant information exists can be used as a test of ecosystem stability or flux over time (case study box 17-1). Millar and Woolfenden (2016) found that at subregional scales within the Sierra Nevada, individual species ranges and population abundances shifted, often substantially. Vegetation assemblages have also changed over time and/or shifted locations as individual species followed separate climate envelopes (Woolfenden 1996). In the Great Basin of North America, major changes in population size and extent of singleleaf piñon (*Pinus monophylla*), and changes in floristic diversity, correspond to century-long climate fluctuations (Tausch et al. 2004). Most species responses are individualistic, time lags are common, and nonanalog patterns frequent, so that population geographic shifts may appear to lag behind climate variation, es-

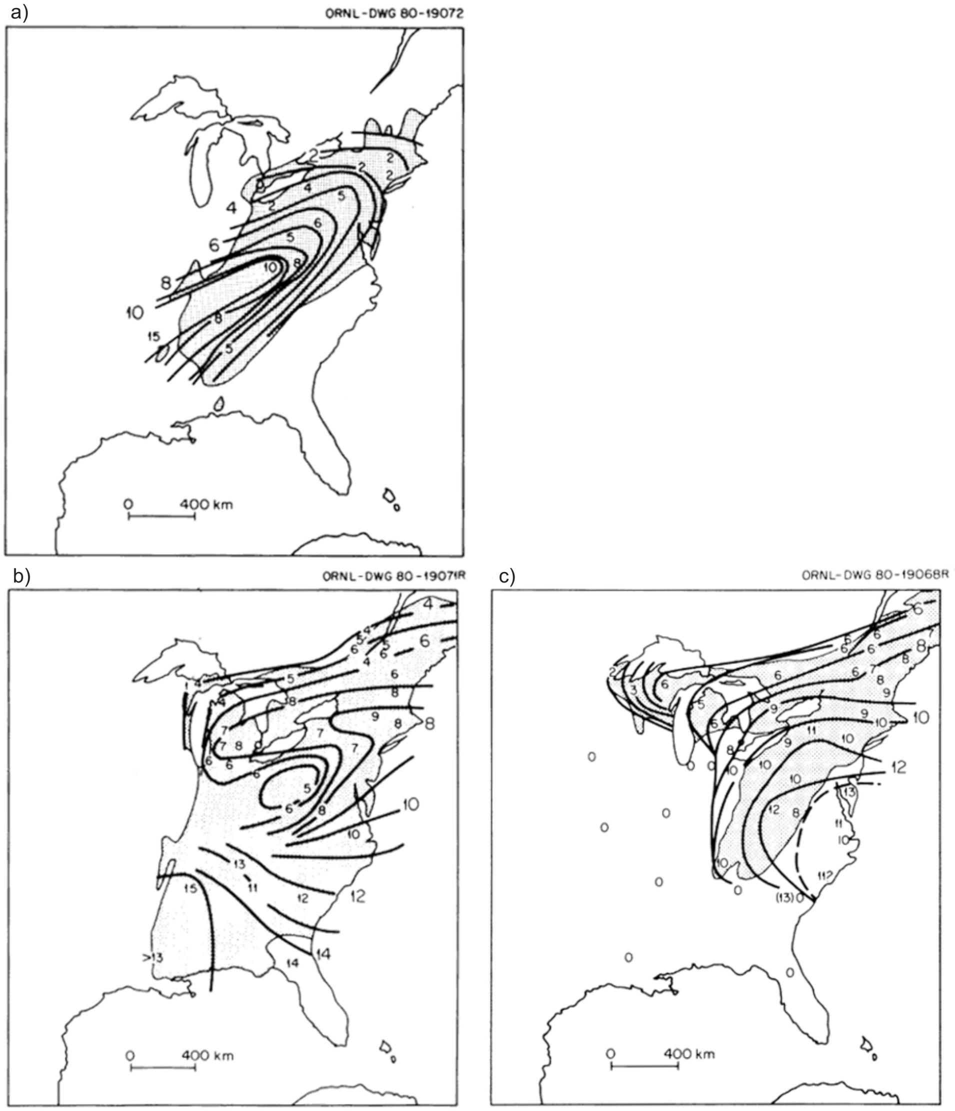


Figure 17-4. Shifts in ranges of (a) American chestnut (*Castanea dentata*), (b) American beech (*Fagus grandifolia*) and (c) eastern hemlock (*Tsuga canadensis*) in eastern North America as they tracked changing temperatures following the Last Glacial Maximum. Modified from Davis 1981.

pecially when changes are extreme and abrupt (Davis 1986; Webb 1986; Jackson and Overpeck 2000).

In addition to species ranges, ecosystem processes are also influenced profoundly by the prevailing climate regime. Fire regimes reconstructed from paleorecords in lake and bog sediment charcoal (Power et al. 2008; Marlon et al. 2009) and tree rings (Falk et al. 2011) reveal evidence of significant change in fire

Case Study Box 17-1
Species Range Shifts in Response to Past Climate Variation

Studies of paleoclimate and paleoecology allow us to put current species distributions in a longer-term context. Using records derived from tree rings, pollen analysis, packrat middens, and other sources, changes in space and time of many species distributions can be mapped in considerable detail.

Giant sequoia (*Sequoiadendron giganteum*) is one of the most iconic trees of North America. Currently limited to small and disjunct groves between 1,500 and 2,100 m in the southwestern Sierra Nevada, giant sequoia's range over the past 10,000 to 26,000 years included the eastern Sierra Nevada (Mono Lake), and locations in the western Sierra Nevada that are both well above (2,863 m) and below (1,000 m in current chaparral shrubland; and 54 m at Tulare Lake in the California Central Valley) its current range. Giant sequoia did not appear in its current range until 4,500 years ago and did not reach modern abundance there until about 2,000 ago, that is, the age of the oldest living individuals.

In the American Great Basin, singleleaf piñon (*Pinus monophylla*) radiated latitudinally following the last glacial cycle. Pollen and woodrat-midden records document that singleleaf piñon distribution was widespread in the late Pleistocene at the southern end of its current range, in the distribution of the current Mojave and Sonoran Deserts. As climates warmed during the early Holocene, the species migrated gradually northward and upslope in the Great Basin, reaching western Nevada 300 years ago (fig. 17-9). A similar well-documented example of species range shifts in response to century-scale climate variation is two-needle piñon (*Pinus edulis* Engelm.) in the western US. *P. edulis* is primarily a species of the Colorado Plateau, but new populations in northern Utah near the Wyoming border became established in the 1200s, as shown by pollen, tree ring, and packrat midden analyses. Piñon largely replaced Utah juniper (*Juniperus osteosperma*) as the dominant species in the 1300s. In the southern portion of its range, piñon has been experiencing significant dieback, especially at lower elevations. These coupled processes of mortality and recruitment lead to the emergent property of species range shifts.

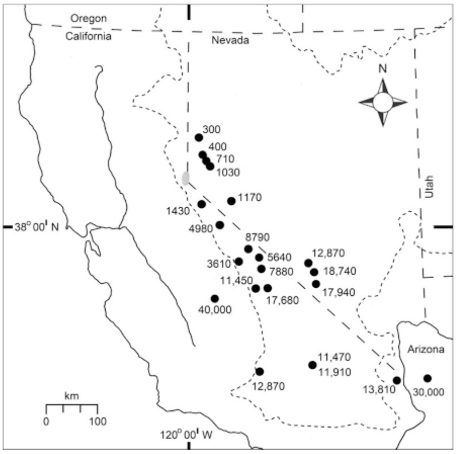


Figure 17-9. Arrival (years before present) of single-leaf piñon (*Pinus monophylla*) along the western Great Basin and in southern California and western Arizona from refugial regions in the current Mojave and Sonoran Desert regions as temperatures warmed from the last glacial maximum, to its current distribution limit north of Reno near Pyramid Lake. Dotted line shows the boundary of the hydrologic Great Basin. Sites from the central and eastern Great Basin are not shown. Note the arrival of the species in west central Nevada just 300 years ago. Modified, with permission, from DK Grayson (2011), *The Great Basin: A Natural Prehistory*.

References: Anderson and Smith 1994; Heusser 1995; Heusser and Sirocko 1997; Davis and Shaw 2001; Gray et al. 2006; Grayson 2011; Macalady and Bugmann 2014.

frequency and extent over time at multiple spatial scales. At mid elevations of the western Sierra Nevada beginning about 4,000 years ago, charcoal records indicate increased local fires and effect on regional vegetation (Anderson 1990; Anderson and Smith 1994). In giant sequoia forests, fire regimes shifted from frequent, light, and localized fires to infrequent, intense, and widespread fires in the last 1,000 years, tracking climate variation (Swetnam 1993). Fire frequency (as detected by sediment charcoal) in what is now Yellowstone National Park increased significantly 11,000 years BP as the region warmed and less flammable tundra gave way to forest, as reflected in the pollen record (Millspaugh et al. 2000).

Ecological Responses to Interannual, Decadal, and Centennial Variability

Decadal and centennial climate and vegetation fluctuations are well documented in the tree ring record, such as recurring variation in precipitation over the past 2,000 years in New Mexico (fig. 17-5) (Grissino-Mayer 1996), persistent droughts in the Colorado River Basin (Meko et al. 2007), and episodes of widespread and persistent drought in the western United States, especially the period AD 900–1300 (Cook et al. 2004). Recurring patterns of tree growth in big-cone Douglas fir (*Pseudotsuga macrocarpa*) (Biondi et al. 2001), mountain hemlock (*Tsuga mertensiana*) (Peterson and Peterson 2001), and subalpine fir (*Abies lasiocarpa*) (Peterson et al. 2002) are correlated with the PDO for up to 400 years. Vegetation type conversions from meadow to forest, changes in species growth rates and crown morphology, and changes in forest density have been associated with PDO cycles in conifer forests of the Sierra Nevada, California (Millar et al. 2004).

Climate variability drives interannual to multicentury changes in fire regimes by regulating plant productivity and fuel conditions in areas where teleconnections are strongest. Fire occurrence in western North America was higher during some periods of extended drought, and lower in some areas during the LIA (Pierce et al. 2004; Whitlock et al. 2010). These oscillations also govern fire regimes in regions where El Niño and La Niña influences on winter precipitation regulate fuel loads and snowpack development and persistence, which govern the length of fire season (Westerling et al. 2006). ENSO and other ocean-atmosphere processes force fire regimes at interannual to decadal time scales (Swetnam and Betancourt 1998; Kitzberger et al. 2001; Littell et al. 2009).

Current and Impending Changes to Earth’s Climate System

This brief review of past variation in Earth’s climate, and some of the processes that drive natural variability, establishes the principle that species and ecosystems have been exposed to variation in climate throughout their histories. If so, then

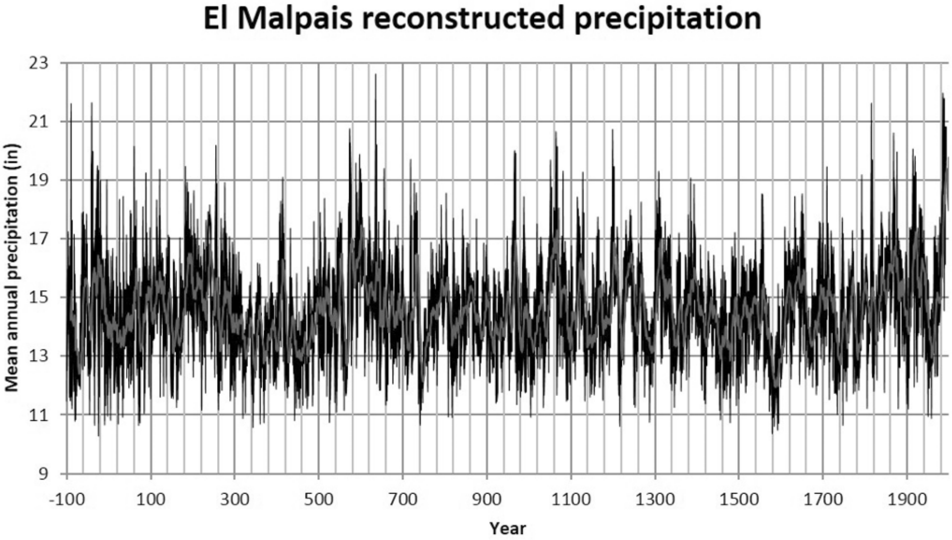


Figure 17-5. Decadal and centennial precipitation variability for the past 2,115 years based on tree-ring reconstruction of annual rainfall from western New Mexico, US. Gray line is a ten-year moving average. From this perspective a major recent drought in the 1950s was not exceptional in magnitude or duration compared to the historical record. Data from Grissino-Mayer (1996).

how is our current period different, and what implications do these differences have for sustainable ecological restoration and management?

An Overview of Global Change

Significant warming of the Earth's surface in the past century is now established unequivocally (Mann et al. 2002). Warming since the late 1800s has been ca. 0.85°C globally with much of the increase occurring due to increases in minimum temperature (Hansen et al. 2010; IPCC 2014b). Similar changes have affected other properties of the Earth's climate system, including spatial and temporal patterns of precipitation, sea ice extent, mean sea level, frequency of extreme events (droughts, severe storms), and others.

Most of the continued warming since mid-twentieth century can be explained only by the effects of recent anthropogenic-induced greenhouse gases (GHGs; Meehl et al. 2004; fig. 1.10 in IPCC 2014b), many of which are now at their highest level in 650,000 years (Karl et al. 2009; Montzka et al. 2011). In contrast, natural forcing factors that might contribute to global warming (solar irradiance, volcanic emissions) contribute essentially 0% of changes in surface temperature since 1950, compared to GHGs, which account for nearly all of the 0.85°C global mean increase. Roughly half of all GHG emissions since 1750 have occurred since 1970, of which ~40% of these emissions remain in the atmosphere; the remainder is taken up by vegetation, soils, oceans, and other "sinks." Effects on the global climate system from just the GHGs that are already in the atmosphere are projected to persist for centuries, due to their long residence time in the atmosphere (O'Neill et al. 2010).

The future trajectory of Earth's climate system depends primarily on how much, and how soon, human societies reduce CO_2 and other GHG emissions to the atmosphere. IPCC quantifies these using "representative concentration pathways" (RCPs), which estimate the total change in Earth land-surface temperature as a function of future emissions. Current RCPs range from 2.6 to 8.5, reflecting potential global mean temperature increases of 1.5°C–4.5°C by the end of the current century (Karl et al. 2009). These increases will likely not be uniform: under RCP 8.5, some parts of the globe (particularly boreal and polar regions) could experience temperature increases of up to 11°C, and mean temperature in many regions of the northern hemisphere could increase 5°C–9°C (IPCC 2014b).

Ecological Manifestations of Global Change

The ecological consequences of these changes to Earth's climate are already unfolding (table 17-1) (Walther et al. 2002). Short-term ecological responses to climate change can be difficult to separate from the inherent noise in ecological data, such as population sizes, reproductive and mortality rates, local species distributions, disease outbreaks, and disturbance events. Over decadal time, however, certain ecological properties are projected to have the clearest ecological signal, based on both empirical and modeling studies.

Shifts in Species Ranges and Phenology

Among the most immediate and visible expressions of ecological response to changing climate are shifts in species ranges (Parmesan 2006; Thomas 2010; Chen et al. 2011). For example, Hill et al. (2011) found that the ranges of many insect species have shifted to higher elevations and latitudes, with population loss at lower elevation species boundaries, during the twentieth century warming. Root et al. (2003) surveyed 143 studies globally and found consistent temperature-driven changes in 82% of species surveyed: invertebrates, amphibians, birds, and many plant taxa.

Range shifts are often predicted using bioclimatic envelope (BCE) models that project the future geography of suitable climate for a species, given where it occurs presently or in the recent past (Pearson and Dawson 2003; Rehfeldt et al.

Table 17-1.

Summary of primary ecological effects of climate change with relevance to the science and practice of restoration ecology. Adapted from IPCC 2014a (table 2.3) and other sources.

Reduction in terrestrial carbon sinks	Carbon stored in terrestrial ecosystems is vulnerable to loss back into the atmosphere, resulting from increased fire frequency due to climate change and the sensitivity of ecosystem respiration to rising temperatures.
Increased tree dieback and mortality	Persistent seasonal drought and elevated temperatures lead to reduced soil moisture and increased vapor pressure deficit. Larger trees in moisture-limited forests are already showing signs of increased mortality and replacement by drought-tolerant trees and shrubs.
Boreal tipping point	Arctic ecosystems are vulnerable to abrupt change related to the thawing of permafrost, spread of shrubs in tundra, and increase in pests and fires in boreal forests.
Amazon tipping point	Moist Amazon forests could change abruptly to less-carbon-dense, drought-and fire-adapted ecosystems.
Increased risk of species extinction	Species with an intrinsically low dispersal rates, especially those occupying flat landscapes where the projected climate velocity is high, and species in isolated habitats such as mountaintops, islands, or small protected areas are especially at risk.
Displacement of species populations from current range and habitat	Species populations may not persist in their current locations due to geographic shifts in suitable climate. Dispersal barriers and the rate of climate movement will prevent some species from migrating or being able to reach suitable habitat.
Altered disturbance regimes compound the direct effects of climate change	Major ecological disturbances, such as wildland fire, insect and disease outbreaks, and other processes are regulated directly and indirectly by climate and are likely to cause additional stresses to terrestrial ecosystems and species populations.
Increased abundance and competitiveness of nonnative invasive species	Warmer temperatures and altered rainfall patterns may favor invasive nonnative species at the expense of native species. Once established, nonnative species can displace native populations, contribute to altered fire regimes, and cause cascading ecological effects such as reductions in native pollinators.
Changes to hydrologic regimes and biogeochemical processes	Streamflow regimes, stream chemistry and water temperature, groundwater and aquifer replenishment, and cycling of essential nutrients (N, P, K) are altered by local and regional patterns of precipitation and temperature, influencing terrestrial and aquatic communities.

2006). While BCEs have limitations, especially at finer spatial scales, they suggest a likely null model for how species may respond to climate change over multiple decades. For example, Notaro and colleagues (2012) projected current and future ranges of trees and shrubs from the southwestern United States under current and potential future climate in the late twenty-first century. While there are both winners and losers, more species were reduced in range and displaced from their current locations, with especially large losses of area in species characteristic of cooler and high elevation forests (fig. 17-6).

Climate also influences the *phenology* (seasonal timing and progression) of species life cycles (Cleland et al. 2007; Schwartz et al. 2012). When phenology is altered (e.g., earlier flowering due to warmer spring temperatures), species interactions can be affected adversely by "phenological decoupling" (Walther 2010). For example, if insects arrive early to forage on host plants that have not yet flowered, the temporal mismatch may lead to pollination failure (Inouye 2008; Rafferty et al. 2015).

Elevated Tree Mortality

Persistent drought stress, especially when accompanied by elevated temperatures, is likely to lead to widespread forest dieback in many regions (Allen et al. 2010; Allen et al. 2015); indeed, this is likely occurring already. While the mechanisms of tree mortality are complex, combinations of reduced soil moisture and higher temperatures (leading to increased evaporative demand in the canopy) can initiate tree death more quickly than either factor acting in isolation (Adams et al. 2009). Mortality can be induced either by hydraulic failure (insufficient water in the xylem to maintain water transport from roots to canopy), or by "carbon starvation," which occurs when leaves close stomata to reduce transpiration water loss, which also closes off their essential source of carbon for metabolism (McDowell et al. 2011). Expressed over large geographic regions, these physiological responses to persistently warmer and drier climate are projected to lead to reduced tree growth and, ultimately, widespread tree mortality and replacement of current forests by more drought tolerant life forms (Williams et al. 2010; Williams et al. 2013).

The Emergence of Megadisturbances

Altered climate will inevitably produce disturbance regimes that are novel in some respects. In some cases, the properties of these new regimes may exceed the life history adaptation of species to cope with conditions outside of their evolutionary envelope. While disturbance processes such as fire, insect outbreaks, drought, and nonnative species, can be studied individually, it is their interactions that are

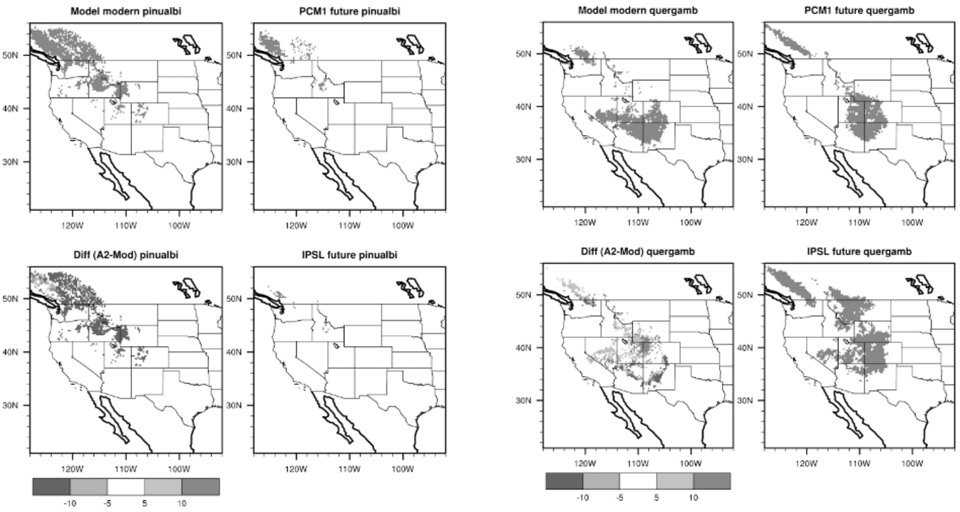


Figure 17-6. Current and projected (2100) ranges of (*left*) whitebark pine (*Pinus albicaulis*) and (*right*) Gambel oak (*Quercus gambellii*) under a consensus of 17 CMIP3 GCM projections based on IPCC A2 and B1 emissions scenarios, modeled contemporary distribution (*upper left*), future distribution under moderate climate (*upper right*) and more extreme change scenarios (*lower right*), and the percent change in each pixel (*lower left*). Full details in Notaro et al. (2012); figure courtesy of MA Notaro, University of Wisconsin (http://faculty.nelson.wisc.edu/notaro/maxent.html).

likely to lead to *megadisturbance* regimes and trigger rapid ecosystem degradation (Zedler 2009; Millar and Stephenson 2015).

Wildland fire regimes respond both directly (through direct climatic influences on combustion, such as short-term fuel moisture, air temperature and humidity, lightning ignition, and other factors) and indirectly (through influences on live vegetation mass and distribution, seasonal soil moisture, and snowpack) (Crimmins 2011; Hostetler et al. 2006). As a consequence, climate change is likely to be expressed strongly in changes to wildland fire regimes (Flannigan et al. 2009; Krawchuk et al. 2009; Littell et al. 2010; Moritz et al. 2012).

Evidence suggests that fire behavior, area burned, and fire severity (effects of fire on ecosystem attributes such as tree survivorship and soil integrity) are already increasing due to the combined effects of accumulated fuels, more extreme fire weather, and longer fire seasons. For example, Westerling and colleagues (2011) found that warming temperatures through the twenty-first century could increase the rate at which the landscape experiences fire by a factor of 3x–10x in the Greater Yellowstone Ecosystem. Fires that occur during extreme or anomalous climate episodes (for example, unusually warm droughts) can have persistent ecological effects and lead to *tipping point* abrupt change into new ecosystem states (Falk

2013). Wildfires are also a significant source of interannual variability in terrestrial emissions of carbon to the atmosphere, creating a feedback to the climate system (van der Werf et al. 2006).

Increased Abundance and Distribution of Invasive Nonnative Species

Nonnative species have been increasing in abundance and distribution worldwide in recent decades (chap. 8). Nonnative species can outcompete native species and drive them to local extirpation; alter nutrient pools and carbon dynamics; change ground cover and surface erosional processes; and alter fire regimes by increasing the mass, spatial distribution, and continuity of fine fuels (Brooks et al. 2004; Didham et al. 2005; Stevens and Falk 2009). As a consequence, many nonnative species, once established, create or reinforce conditions favorable to their continued dominance, thus creating a positive feedback or tipping point response in the local ecosystem (Ehrenfeld 2010).

Rapid increases in nonnative species are also associated with climate change and are thus predicted to become even more widespread in coming decades (Hellmann et al. 2008). Rahel and Olden (2008) found that nonnative species would expand in aquatic communities due to altered thermal and streamflow regimes, altered water chemistry, dispersal into currently nonsuitable habitat, and decline of competing native species. Thus, the progression of climate change may alter the relative competitive abilities of native and nonnative species in site- and species-specific ways (Bradley et al. 2009; Bradley et al. 2010).

Implications for Restoration Ecology

The role of the climate system as a pervasive driver of ecological change and species evolution is a fundamental element in any meaningful theory of restoration ecology. The resulting awareness of the dominant effect of climate variation in space and time in driving ecological change, and of the dynamic relationship of climate, vegetation, and disturbance, prompts us to evaluate assumptions about future species ranges, ecosystem processes, and restoration objectives.

Ecological Responses to Climate Change

Advances in environmental sciences during the mid- to late-twentieth century on ecological succession, disturbance, and spatial and temporal variability motivated a shift from viewing nature as static and typological to dynamic and process driven (Botkin 1990; Millar and Stephenson 2015). In turn, restoration ecology and practice have also matured from emphasis on nature preservation to maintaining variability and natural function (Falk et al. 2006; Choi 2007; Perring et al. 2015). As a result, dynamic processes such as prescribed fires and managed floods have become important restoration tools, and recovery of ecosystem function, composition, and structure has been added to restoration goals.

Important as these changes have been, static views of nature still sometimes implicitly constrain restoration objectives (Harris et al. 2006). As we have shown, the climate system is a central physical force on Earth and significant agent of physical, ecological, and cultural change at micro- to macroscales. From this perspective, climate is a cross-scale disturbance element, the background stage of change on which evolutionary and successional dynamics play out (Jackson 1997). Such dynamism has been incorporated into evolutionary and ecological theory, but remains largely untranslated into conservation and restoration ecology. As a result, resource analyses and prescriptions, such as evaluation and diagnoses of ecological change, determination of baselines and evaluation of change in monitoring, and development of targets for restoration, need to become more fully informed by a more dynamic understanding of Earth systems. If there is one lesson from the study of paleoclimate and paleoecology, it is that change is a constant property of life on Earth.

Population and Species Distribution Responses

Declines (or increases) in population size and abundance—observed through monitoring or other measures—and reductions (or increases) in overall range are often the "front lines" of species responses to local conditions. Although such changes are often assumed to be anthropogenic (e.g., in response to suppression of the natural fire regime, altered stream flow regimes, elimination of top predators), population change may also be natural species' responses to climate variability. For instance, Utah juniper and single leaf piñon expanding in Great Basin rangelands have been treated as exotic invasives, and measures have been taken to remove thousands of trees, even though these species have been present in the region throughout at least the past million years. Such population changes in native species can also be viewed as adaptive responses to changes in disturbance regimes and climate (Nowak et al. 1994).

Although changes in population size and distribution may be natural responses to climate change, causes are often difficult to untangle in practice. Lags in adjustment and other disequilibria between population distributions and climate mean that population increases or decreases may not be synchronous with climate variation, especially during periods when rapid climate changes occur over short periods of time (Jackson and Overpeck 2000; Overpeck and Cole 2006). Because individual plants, unlike animals, cannot "pick up and move" (intragenerational), they migrate and shift their range by dying in some areas while expanding in others (intergenerational). These processes may be messy on the landscape—with patchiness and irregularity characteristic, making the effects difficult to evaluate while they are happening (Schwartz 1993).

The range of a species is typically the basis for monitoring its condition, identifying favorable habitat, diagnosing threats and risks, determining restoration targets, and indicting some competing species as "exotic" (Jackson 1997). Viewed against historic changes in distribution and natural flux, however, the native range of a species must be considered a transient and dynamic property, capable of moving in space as climate shifts over the landscape (Falk et al. 1996). Recognizing that nonequilibrium conditions exist and vegetation lags climate variation means that, like Lewis Carroll's Red Queen, vegetation chases a target (climate) that is itself changing (van Valen 1977). Population abundances and species' distribution ranges may be relatively stable whenever climate is in a more stable phase and/or if the environment of a species offers considerable local heterogeneity (Thompson 1988; Williams et al. 2001). In these cases, shifts in climate may be tracked with relatively minor overall geographic changes. By contrast, in landscapes with less topographic diversity, even small shifts in climate may bring large changes in local population abundance. In coming decades, we can expect population demographics and ranges of many species to be highly unstable, including the dissolution and reassembly of multispecies communities, as species respond individualistically as well as interactively (Gleason 1926; Temperton et al. 2004) (chap. 9).

Reference Conditions and Restoration Targets

"Predisturbance" or "pre-Euro-American impact" conditions are used routinely as reference models and descriptions of desired targets for ecological restoration, and indeed constitute a foundational principle (Egan and Howell 2001). This assumes, however, that the climate template is unchanged between the benchmark target time and the present, and that human influence has not confounded historic conditions. These assumptions are tenuous, and the likelihood of their validity decreases with time between the historic target and present. For example, many contemporary forests originated during what is now identified as the Little Ice Age in parts of the Northern Hemisphere, and thus may provide problematic models for restoration (Fulé 2008; Millar 2014).

This does not mean that all aspects of climate or ecosystems of the past 500 years are irrelevant to restoration. The legacy of past ecosystems is extremely powerful, expressed in the form of dominant vegetation, regional species pools, community associations with major soil formations, broad-scale disturbance regimes, and general ecological genetic adaptations to regional climate (chap. 5). Indeed, throughout western North America there are large numbers of individual trees over 700 years old (and individuals of bristle cone pine, *Pinus longaeva*, that are approaching 5,000 years old), meaning that in their lifetimes they have persisted through multiple major episodes of drought, cold, and other climate extremes. Even as climate changes in coming decades, it is likely to do so progressively, working with the materials at hand and using adaptive processes that are millions of years old.

Restoration or Reorganization?

These considerations prompt reevaluation of some basic restoration assumptions and goals. As ecological resilience emerges as a new guiding concept in restoration ecology, its primary application may be to focus on sustaining future options for flexibility and adaptation to changing conditions, rather than attempting to maintain static composition or structure based on past distributions (Millar and Stephenson 2015). In practice, rather than emphasizing only time-specific historical ranges or predisturbance species assemblages, compositions, structures, and landscape patterns, a resilience approach to restoration embraces landscape macrodynamics that have characterized populations and species over long timeframes. These include the ability of species to shift locations significantly, fragment into refugia, expand or contract in range, coalesce with formerly disjunct populations, foster nonequilibrium genetic diversities, form novel plant associations, and accommodate population extirpations and colonizations—all in response to changing regional conditions. The question for restoration ecology thus becomes not if these changes will occur, but whether the restoration response will be to resist, stand back and watch, or facilitate such change (fig. 17-7).

Assisted migration (AM) exemplifies new, strategic responses that have been proposed to maintain biological diversity through a period of climate change (Stone 2010). As the literature summarized earlier demonstrates, all species move in space and time throughout their ecological and evolutionary history, often in response to shifting climate. However, several factors raise concerns that the ability of many species to migrate in response to changing climate may be constrained under contemporary conditions. The first of these is the sheer pace of climatic change (IPCC 2014a). Depending on the rate of change (and recalling that mean temperature is only one of many climate dimensions), many species may not be able to migrate quickly enough on their own (fig. 17-8). Many other factors complicate this equation, especially landscape barriers to species movement (large multilane highways), natural and anthropogenic habitat fragmentation and degradation, absence of biotic dispersal vectors, and increased competition from nonnative species (Wilcove 2008; Vitt et al. 2010).

An intense debate surrounds the AM option, also referred to as assisted colonization and managed relocation (McLachlan et al. 2007). Objections to its use as "ecological gambling" (Ricciardi and Simberloff 2009) include concerns for inadvertently introducing species that could become locally invasive, displacing native biota, as has occurred multiple times with introductions to islands; lack of essential symbionts (such as pollinators or food plants) in the new location; contamination of locally-adapted gene pools; and the sheer number of species that may require assistance on a global scale, not to mention the high probability of failure. More conservative variations on AM include *facilitated migration*, in which habitat and migratory pathways are protected and restored to allow species populations to adjust on their own, a "build it and they will come" approach (Pearson and Dawson 2005; McLachlan et al. 2007). AM is being used as a forestry option, with extensive provenance adaptation trials in Canada and elsewhere (Pedlar et al. 2012).

Closing Remarks

The reality of global warming has raised much concern in the restoration and conservation communities. As we now understand, this is not something coming in the future, but something ecosystems are already experiencing. Abrupt climate change and vegetation response have been common in Earth's history, but it is an open question whether the pace and magnitude of change expected in the climate system in the next century exceed those of the ecologically relevant past. Certain responses, such as massive landscape mortality events, range expansions, minor and major population extirpations, shifts in native ranges, or changes in community composition, may appear catastrophic but may also be expressions of landscape-scale resilience and realignment to changing external forces.

Accommodating the realities of climate change will require rethinking our concepts about what and where native habitat is, what "healthy" communities are, and when changes in species ranges are acceptable and appropriate. These are unfamiliar and even uncomfortable questions for restoration ecology. Society may choose not to accept such consequences and manage instead for conditions based on past climates. In such cases we will have to consider that our management and conservation efforts may run counter to natural process, and thus restoration efforts may require continuing manipulative input to maintain desired conditions and the potential for sustainability (chap. 1, table 1-1) (Palmer and Ruhl 2015). For example, society (through land managers) may choose to maintain iconic species such as giant sequoia even where its climate envelope is shifting away from the current population location. The lessons implied from paleoclimatology and paleoecology suggest that making peace with physical and ecological change is

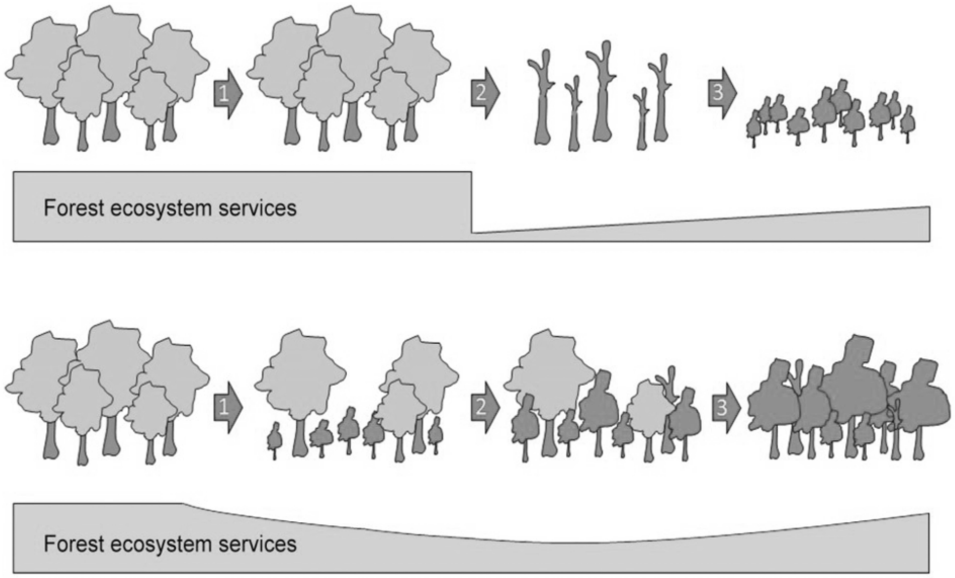


Figure 17-7. Management practices can influence the nature of transitions between forest types. Numbers represent forest transitions through time. *Top panel*: (1) Despite rapid directional environmental changes, managers strive to maintain forests within historical ranges of conditions and may initially succeed. (2) The forest may be more vulnerable to drought or wildfire in the new climate regime; once a threshold is exceeded, substantial mortality occurs, with an abrupt loss of ecosystem services. (3) After dieback, recovery of forest ecosystem is slow, and predisturbance forest structure may not be achieved. *Bottom panel*: (1) Managers anticipate and facilitate an impending forest transition by reducing the probability of sudden dieback (e.g., thinning to reduce competition for water and mitigate fire behavior) and by assisting establishment of species or genotypes better adapted to future conditions. (2) The transition is gradual rather than abrupt, and ecosystem services are maintained. (3) Forest ecosystem services are maintained closer to original levels, although species composition has shifted. Although some services are eventually lost in both cases, active management facilitates a gradual rather than abrupt transition. Modified from Millar and Stephenson (2015).

an important prerequisite to effective stewardship. Incorporating these ideas into new restoration ecology science and practice will require considerable difficult thought, discussion, experimentation, and research in coming years.

Such conclusions suggest that a rethinking of traditional concepts of sustainability and restoration targets is essential. We are challenged now to help species persist into the future by realigning populations with current and future anticipated conditions, and providing options to cope with uncertain futures with certain high variability (Foley et al. 2005; Hobbs and Suding 2009). The capacity for populations to grow, decline, migrate, and colonize has determined species survival during past periods of rapid change. Holding species and communities hostage to

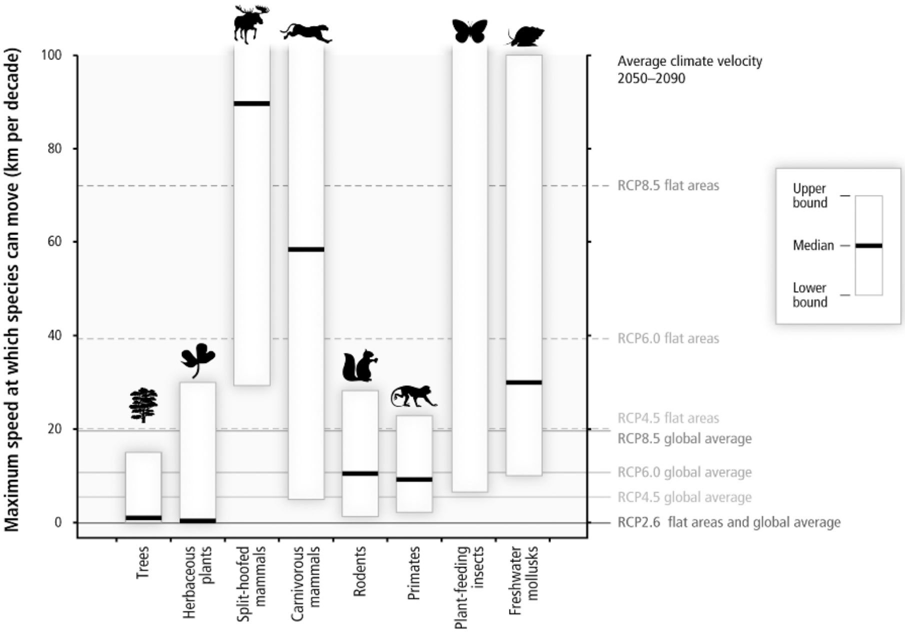


Figure 17-8. The average "climate velocity" in the late twenty-first century may exceed the maximum documented rate at which species can migrate across landscapes by natural processes. Climate velocity is higher in flat terrain than in more complex topography due to the lack of elevational diversity, which can absorb some of the poleward movement of climate envelopes. Some organism groups, such as large mammals, flighted insects, and freshwater mollusks may have sufficient migratory potential to match climate velocity, whereas others (most plants, smaller mammals) may not be able to keep up. Figure from IPCC (2014a).

specific locations and conditions may be both challenging and unproductive in a rapidly changing world. In some cases, it may be necessary to make the difficult choice to step away from a traditional restoration paradigm and find new models (Hobbs et al. 2015). Understanding that species have coped with change in the past suggests that restoration sciences have more important opportunities to help species cope with the dynamics of the current world.

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PART V

Synthesis and Challenges

Chapter 18

Persistent and Emerging Themes in the Linkage of Theory to Restoration Practice

Margaret A. Palmer

Since the last edition of *Foundations* was written a decade ago, two factors have intersected resulting in transformative impacts on ecological science. First, the growth in the availability of data that is captivating scientists from all fields is also being felt by ecologists. The volume and types of ecological data being shared among researchers is growing, as are efforts to make data easily accessible to decision makers, practitioners, and natural resource managers. A plethora of new ecological models that take advantage of available data is emerging to focus on restoration-relevant topics as diverse as predicting the response of ecological communities to environmental change (Maguire et al. 2015), mapping the distribution of species migration patterns (Fujioka et al. 2014), and evaluating changes in ecosystem services following restoration (Peh et al. 2014).

The second transformative factor is that the demands on ecologists to contribute solutions to environmental problems continue to grow. This increase is contributing to tighter links between researchers and natural resource managers and policy makers. For example, many ecologists are extending their work beyond just exploring general theories of biodiversity, or undertaking studies to determine how much biodiversity has been lost, to address more pragmatic questions such as whether the functional consequences of biodiversity loss can be offset by restoring new assemblages (Laughlin et al. 2014). This is not a subtle epistemological shift, but rather a bold change in which questions are increasingly aimed at solving problems, not just discovering them. Of course practitioners and natural resource managers have already paved innovative paths in trying to solve environmental problems, and so it is exciting to see basic researchers engaging with them and jointly exploring new dimensions. Increasingly, such collaborations involve the implementation of adaptive management approaches that can be used to critically

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evaluate the utility of ecological theories, while growing the practice of restoration and pushing ecologists to revise or extend theory (Galat and Berkeley 2014).

The contributions in this book reflect this rapid period of change. Some ecological concepts and theories carry over from the first edition of this book, and will continue to persist in any future editions, because they are fundamental to understanding ecological systems and what it means to restore them; we begin by reviewing those in the first section. Nonetheless, new theoretical and empirical advances are apparent throughout this revised edition. Here, we reflect on those and the extent to which these have been linked to restoration in practice.

Persistent Themes

Certain ecological theories and concepts are timeless in their relevance to restoration (table 18-1). Theories and concepts such as these explain or unify many phenomena and generate predictions on the basis of minimal assumptions. Most of these persistent themes are integrated throughout this book, as well as the prior edition. We briefly describe some of them and devote subsections to themes that authors emphasize the most.

The important role of history is emphasized repeatedly in both editions, whether in relation to environmental conditions within which communities previously thrived, past species responses to natural climate change, historical disturbance regimes, or legacy effects of invasive species (e.g., chaps. 15 and 17). Although restoration ecologists increasingly debate appropriate targets for restoration in a highly altered world, the many roles of history remain useful in guiding restoration efforts (Higgs et al. 2014).

Genetic variation and diversity in all their forms are also emphasized in both editions of *Foundations*. This is not surprising because these are critical to restoring self-sustaining ecosystems, and they are also topics of deep interest in both basic and applied ecological research (e.g., chaps. 3 and 5). At the time of the first edition, there was enormous research interest in linking biodiversity to ecosystem function (Naeem 2006) with a focus on if/how species assemblages influence the rates of ecosystem-level processes such as primary production (Tilman et al. 2014). Today, much of this attention has shifted from a focus on ecosystem consequences of species diversity toward the consequences of trait or functional diversity (Gagic et al. 2015), as we discuss more fully later in this chapter.

The roles of *habitat heterogeneity* and *landscape context* that are treated specifically in chapters 4 and 10 are also common topics that appear throughout both editions, because they are critical to restoration prioritization, design, and outcome. In practice, restoration designs often incorporate aspects of variation, biodiversity, and habitat heterogeneity; less frequently, they identify alternative

Table 18-1.

Persistent themes in the linkage of theory to restoration
History plays a critical role in shaping ecological systems and determining what is possible in a restoration context.
Biological/genetic diversity reduces ecological vulnerability (e.g., to: extinction, invasion, disturbance, and wide fluctuations in the rates or direction of ecological processes).
Environmental heterogeneity at multiple scales can promote diversity, coexistence, persistence, and ecosystem function.
Landscape context and the spatial scale and arrangement of habitat patches are strong influences on the recovery of ecological patterns and processes.
Ecological systems, especially those dominated by nonnative species, can persist in altered or degraded states that are difficult to reverse.
Environmental filters and species interactions together determine restoration outcomes; some constraints can be overcome through restoration actions.
Ecological systems do not exhibit equilibrium dynamics except on very large spatial and temporal scales, and thus alternative states and multiple restoration trajectories are possible.

sites and priority landscape contexts to achieve restoration targets (Brudvig 2011; Tambosi et al. 2014). To some extent, this reflects the still opportunistic nature of many restoration projects; selecting restoration sites based on landscape context and spatially informed designs is less common than it should be, despite the extensive ecological theory and empirical findings that all point to these factors as critical to restoration outcomes (Rappaport et al. 2015).

The concept of ecological filters first appeared in the literature in the seventies (Grime 1977; Southwood 1977) and ecologists have used it continually since that time to conceptualize environmental constraints on the establishment and restoration of populations and communities. In both editions of *Foundations*, authors discuss environmental constraints on recovery of populations or communities associated with ecophysiological requirements and life histories in the context of abiotic factors (e.g., chaps. 6, 12, 14, and 15 in this edition). Biotic factors such as dispersal and the presence of strong competitors, including many nonnative species, are also well known to influence the abundance and distribution of species (e.g., chaps. 2, 5, and 8). Simply mapping the distribution of species is not sufficient to distinguish biotic from abiotic constraints (Kraft et al. 2015) and thus practitioners may need to experiment to learn how to overcome the constraints. Fortunately, there is an ever growing body of literature on restoration approaches to overcome biotic, abiotic, and dispersal constraints to the reestablishment of ecological assemblages (e.g., Myers and Harm 2011; Hulvey and Aigner 2014). As Dennhardt et al. (2016) describe in chapter 16, newer approaches to modeling species distributions are better at representing multiple biotic and abiotic processes (see fuller discussion of species distribution modeling below.

Thresholds and shifts between different stable states (chap. 2) have been predicted theoretically for a long time, but until the early 2000s, few examples were widely accepted (Scheffer et al. 2001). Ecologists today are well aware of nonequilibrium dynamics in ecological systems, including the potential for thresholds and the frequency of nonlinear feedbacks (e.g., Kelly et al. 2015). These dynamics have been addressed conceptually by Suding and coauthors in both editions. The first edition also provided a few examples in the context of invasive species (D'Antonio and Chambers 2006). The increased emphasis on alternative states in this book reflects attempts by ecologists to operationalize theories on state changes. For example, researchers are now trying to develop methods to predict impending state changes and understand why some changes may be difficult to reverse (Brock and Carpenter 2012; Scheffer et al. 2012; Selkoe et al. 2015).

Insights into restoration of terrestrial and aquatic systems that exhibit state changes may come from an increased understanding of plant-soil feedbacks that influence soil nutrient status and stoichiometric imbalances in aquatic systems (chaps. 2, 12, and 14). However, much remains controversial on the topic of alternative states, for example, how common threshold transitions and regime shifts are in nature (e.g., Capon et al. 2015). Emerging research in this key area will undoubtedly inform restoration in the future (e.g., Yelenick 2015; Paz-Kagan et al. 2016).

Emerging Themes

Ecological research has entered a new era that is characterized by increasingly quantitative approaches, along with continuing efforts to apply ecological theory to solve problems. Thus, some of the themes called "emerging" in this section may be old in concept but reinvigorated through methodological advances or new insights.

Resilience Restoration

In discussing the dynamic nature of ecological systems, Suding and collaborators in both editions have provided an overview of resilience, a system's ability to absorb disturbance and persist over time by adapting under changing conditions. Aside from their discussions, however, resilience per se was not a theme in the first edition; although it is referred to briefly in the context of global change and resistance to invasion by nonnative species in some chapters (D'Antonio and Chambers 2006; Millar and Brubaker 2006). Since that time, interest in restoration *for* resilience has become prominent (e.g., Churchill et al. 2013; Lake 2013; FAO

TABLE 18-2.

Emerging themes in the linkage of theory to restoration practice
Enhanced ecosystem resilience is increasingly stated as a restoration goal. While ecological theory provides general guidelines to support this in practice, each context requires stakeholder–scientist collaborations to identify the range of acceptable ecosystem states, as well as rigorous empirical work to determine what factors act to stabilize or shift the ecosystem.
Species traits reflect responses to environmental conditions and provide insights into how changes in species composition may influence ecosystem-level processes and thus restoration outcomes.
Species shift their distributions in response to changes in the environment but these shifts can be modified by biotic interactions, dispersal, demographic processes, and other factors.
Strong feedbacks between plants, soils, and soil microbial communities influence ecosystem structure, function, and restoration.
The goods and services that ecological systems provide for humans are an increasing focus of restoration, but the targets selected may constrain the recovery of the full suite of ecological processes and structures, due to trade-offs.
Advances in applying quantitative approaches and methods in ecological contexts are improving our ability to assess potential restoration outcomes.
Environmental nonstationarity is a hallmark of climate change and the resulting instability in ecological systems challenges conventional notions of reference conditions for restoration projects.

2015; Laughlin et al. 2016), and many of the new chapters have entire sections on the topic, while others include specific examples of research focused on ecological resistance or resilience resulting from, or as the goal of, restoration (chaps. 2, 3, 4, 8, 10, 11, 16, and 17). Falk and Millar (chap. 17, page 501) describe what such a goal might imply:

> Rather than emphasizing only time-specific historical ranges or predisturbance species assemblages, compositions, structures, and landscape patterns, a resilience approach to restoration embraces landscape macrodynamics that have characterized populations and species over long timeframes. . . . The question for restoration ecology thus becomes not if these [climate] changes will occur, but whether the restoration response will be to resist, stand back and watch, or facilitate such change.

This new edition also includes discussion of factors that might promote resilience in a restoration context (e.g., chaps. 4, 8, 10, and 11) by identifying underlying mechanisms that link directly to ecological concepts, including theories of fluctuating resources, niche-based and functional ecology, landscape and spatial ecology, biodiversity (especially for resilience to invasion by nonnatives), metapopulation dynamics, environmental heterogeneity, and “bet-hedging” in an evolutionary context. The increased attention to the linkage between ecological theory and the potential to restore *for* resilience helps set the stage for ecologists to collaborate with social scientists to actually operationalize restoration *for* resilience (e.g., Quinlan et al. 2015; Stone-Jovicich 2015).

Trait-Based and Functional Ecology

Trait-based community ecology approaches (Suding et al. 2008) have emerged as a major focus in ecology in the last decade, and this is reflected in the new edition. Naeem (chap. 3), Kimball et al. (chap. 6), D'Antonio et al. (chap. 8), and Temperton et al. (chap. 9) provide extensive discussions on the relevance of trait-based ecology to restoration, including its underlying assumptions. As Laughlin (2014) emphasizes: "A trait-based framework provides restoration ecology with a robust scaffold on which to apply fundamental ecological theory to maintain resilient and functioning ecosystems in a rapidly changing world." Trait-based approaches have been applied fairly broadly to plant communities; however, it is not trivial to identify species' traits along relevant environmental axes for many other types of communities. Whereas phylogenetic relatedness may be an appealing surrogate for niche differences that allow species coexistence, emerging research indicates relatedness is a poor predictor of stabilizing niche differences for use in restoration planning (Godoy et al. 2014; Kraft et al. 2015).

Interest in trait *functional* diversity is growing (chap. 3) largely due to the growing interest in functional outcomes or targets for restoration that may be associated with the delivery of desired ecosystem services (see below). Baer et al. (chap. 12) and Marín-Spiotta and Ostertag (chap. 13) both provide specific examples of how plant traits can be used to establish communities that promote carbon sequestration. Since the distribution of functional traits is tied strongly to environmental conditions and competitive interactions, they may also provide information on which species can persist together—information highly relevant to restoration in a changing world. *Response-and-effect* trait-based approaches (chap. 3) offer the possibility of using functional trait targets to accomplish restoration goals (Burylo et al. 2014; Laughlin 2014). Ecosystem function appeared as a concept many times in the prior edition, but this was largely in the context of how factors like species composition and/or environmental heterogeneity may effect ecosystem-level processes, such as total productivity or rates of biogeochemical processes (e.g., Larkin et al. 2006; Menninger and Palmer 2006).

Species Distributions

Mathematical, statistical, and modeling approaches are increasingly revealing new insights into ecological problems of high relevance to restoration. As Urban (2006) emphasized in the earlier edition of *Foundations*, modeling is integral to restoration, and he forecast a trend toward increasing integration of spatial data and multiscale analyses into models. Indeed, the level of innovation in this arena has been immense, particularly that associated with predicting the effects of global change on species distributions. Distribution or bioclimatic-envelope models are being applied to predict future species' distributions as a function of expected climates (chap. 16) and may offer some guidance to restoration ecologists in terms of appropriate targets (chap. 17). As alluded to earlier, the use of species distribution models (SDMs) is extending beyond predicting suitable future ranges to incorporating other types of information, including biotic interactions, dispersal, and genetics (chaps. 5 and 16). Additionally, information on environmental heterogeneity at the landscape scale along with genetic analysis can be combined with SDMs to identify those landscape variables that may limit genetic connectivity and thus population persistence (see the chapter 5 discussion on the emerging field of landscape genetics). Extending SDMs to include biotic interactions allows for the detection of how, for example, mutualistic interactions may alleviate abiotic stress, resulting in broader range limits than expected in their absence (Afkhami et al. 2014).

Whereas phrases like "distribution modeling" are not generally used when practitioners describe restoration designs, the concepts associated with predicting species distributions are widely considered in deciding what to plant based on species requirements and life histories (e.g., Angelieri et al. 2016; chap. 15) and what species to remove that are known competitors of species being restored (chaps. 6 and 8). Seeding and reintroductions to restore plant and wildlife populations expected to thrive in a region are well established in restoration (e.g., Cole et al. 2011; Huber et al. 2014), but only recently has attention been placed on their potential role for restoring nonfishery aquatic communities that often have depauperate regional species pools (Tonkin et al. 2014).

Plant-Soil Feedbacks

Strong interactions among vegetation, soil, and precipitation that have feedback effects on the persistence and composition of that vegetation have been long recognized (chap. 14). Less studied, and a topic of increasing focus, is microbial ecology, particularly the tight linkages between soil microbes and plants (Martiny et al. 2015). Over half of the chapters in this edition discuss some aspect of these interactions and their relevance to restoration. Baer (chap. 12) covers several examples in depth (fig. 12-2 and box 12-2).

This change in coverage stems from significant advances in recent years in understanding the role microbial communities play in ecosystem dynamics, and the recognition that their recovery may be critical to restoration (Putten et al. 2013;

Singh 2015). Kimball et al. (chap. 6) provide examples of using microbial inocula in restoration, and Baer et al. (chap. 12) describe how the stoichiometry of soil microbial biomass is useful in understanding nutrient limitation in soils and its relevance to restoration.

Ecosystem Services

A dominant theme today in the environmental literature, as well as in management discussions, is ecosystem services: how to protect, restore, and manage them. Indeed, ecosystem services have now progressed from the conceptual stage—as a way to emphasize the value of nature to people—to becoming operationalized (Arkema et al. 2015; Wong et al. 2015). Although the latter is certainly not mature scientifically, efforts are moving restoration in that direction. This is reflected throughout the book and in contrast to the prior edition in which the phrase "ecosystem services" appeared only twelve times, and then in very general ways. This edition not only refers many times to ecosystem services in the majority of chapters, but also has sections explicitly devoted to the topic (chaps. 3 and 10) or to ecological processes in support of services, such as carbon sequestration and nitrogen removal in aquatic systems (chaps. 12, 13, and 14). This reflects tremendous interest in ecosystem services in general and more specifically in identifying ecological metrics that can be used to evaluate the potential for delivering ecosystem services (Wortley et al. 2013; Olander et al. 2015) via restoration, conservation, or management (e.g., Reynolds et al. 2016).

In both editions of the book, Naeem points out the importance of distinguishing between functions and services, and while he devotes more discussion to ecosystem services in this edition, he cautions readers about going too far in this direction (chap. 3). Certainly, a major challenge in restoration ecology today is to develop empirically supported, quantitative relationships between restoration actions, the response of ecosystem processes and structures, and the potential delivery of ecosystem services (Bullock et al. 2011; Olander et al. 2015; Palmer and Ruhl 2015).

New Quantitative Approaches

Ecology has never been more quantitative, nor has the pace of methods development been greater. Growth in the sophistication of remote sensing and the use of geospatial methods has been enormous and of obvious direct benefit to restoration planning and design, especially using theories from landscape ecology (chap. 4). For example, GIS data are being linked with demographic and dispersal data to model recovering populations (chap. 7), with landscape data to identify seed sources for restoration sites (chap. 9), and with precipitation and soils data to model run-off and erosion potential of a site (chap. 14). New quantitative genomic tools are also of benefit to restoration ecology, as they can provide linkages across levels of biodiversity (gene to genotype, to population, to species, to plant family, to community); the use of such tools will likely increase into the future (e.g., "restoration genomics," Stockwell et al., chap. 15).

Pronounced growth in the use of advanced models of many types, including, but not limited to, structural equation, hierarchical, state-space, and fully distributed hydrologic models (chaps. 2, 3, 5, 7, 10, 13, and 16), is apparent in the new edition. These models can both inform the design of restoration projects and forecast outcomes. As one example, Integral Projection Models (IPM) (Merow et al. 2014) are being used to link environmental factors to individual variation in vital rates to population dynamics and fitness landscapes in order to predict future states and their spatial distribution (chap. 7). Because vital rates can be modeled as a function of continuous environmental factors, IPMs can be used to forecast spatial variation in vital rates and thus extend predictions to broader scales (chap. 7). These methods are powerful in that they can provide information on population- and community-level responses to multiple factors, simultaneously in space and time.

Hierarchical models, especially those implemented under a Bayesian inferential framework (chaps. 3 and 7) are statistical models written in a hierarchical form (e.g., several levels of observational units) that are implemented using a Bayesian method (e.g., combining prior information about an ecological parameter with sample data to make an inference about that parameter). These models not only provide more accurate and precise estimates of ecological parameters, but perhaps more importantly they can also provide broader estimates of process variation around the parameters in question (Hobbs and Hooten 2015). Such approaches have been used, for example, to quantify the extent to which soil properties in restored sites of different ages are similar to soils in reference sites (Gasch et al.2014) and to predict ecological responses to flow restoration in rivers (Webb et al. 2015). Another benefit of Bayesian models is that they can incorporate practitioner experience and opinions to inform prior probability distributions that can be used in estimating the probability [likelihood] of a certain restoration outcome, that is, the Bayesian approach facilitates incorporation of what has been learned into the design of future projects (Martin et al. 2012).

Climate Change and Restoration

There has been a strong decadal trend to move beyond a sole focus on how climate change will impact ecosystems to a focus on the role ecological systems can play in reducing the impacts of climate change. Both editions of *Foundations* have a chapter devoted to climate change that includes a primer on the topic (Millar and Brubaker 2006; chap. 17), but this edition devotes much more space and in-depth coverage to the implications for restoration, including anticipating changes in species distributions due to climate change (see "Species Distributions" above) and adapting conservation and restoration strategies to maximize species' adaptation abilities (chap. 15). The evolutionary challenges associated with the latter are significant (Smith et al. 2014). As Stockwell and coauthors state (chap. 15, page 441):

> the field of 'eco-evolutionary dynamics' has blossomed, examining the reciprocal interactions and feedbacks of contemporary evolution and ecology. . . . Theory and empirical studies now provide evidence of many ways in which evolution might promote not only evolutionary rescue, but can also influence community structure and ecosystem function . . . , and thus affect restoration outcomes beyond the scale of the focal species.

Many populations will be highly unstable because the adjustment of ecological systems lags behind changes in climate, and because other factors confound their responses. Altered use of lands and waters as well as other anthropogenic impacts and complications due to population demographics, all render the job of a restorationist difficult (chap. 17). The implications for restoration include the need to manage for genetically diverse populations (chaps. 5, 15, and 17), incorporate habitat features and landscape structures that promote long range dispersal for at least some individuals, consider the possibility of assisted migration, and plan for continual manipulations (both abiotic and biotic) to maintain desired assemblages (chaps. 5, 15, and 17).

Closing Remarks

In looking back to the first edition of this book, what strikes me is the vigorous and exciting growth in ecological science—theory and empiricism—since then that has the *potential* to advance restoration practice enormously. Consider the possibilities of combining knowledge on the functional structure of ecological communities and their interactions to spatially explicit, probabilistic assessments of future environmental conditions in order to guide on-the-ground restoration efforts. While much of this forecasting is still limited to research contexts or at best is being tested using plot-scale manipulative experiments, moving to the "real-world," operational stage can be envisioned. For this to be realized, a great deal of work remains to forge ever closer ties between researchers and those who make decisions about *how* to restore ecological systems.

The first sentence in my remarks included an emphasis on the word "potential" [to advance restoration] because information on the extent to which ecological theories help practitioners frame and/or implement restoration projects is difficult to obtain. Practitioners undertake heroic efforts to recover damaged ecosystems but rarely have the time or funds to publish their results much less keep up with the rapidly changing scholarly literature. Collaborative efforts between scientists and practitioners to document restoration methods and outcomes are resulting in the accumulation of data that can be used to test ecological theory, but this is a slow process. As a result, progress in linking theory to practice has not advanced nearly as fast as has growth in the implementation of restoration projects.

Researchers of the science-policy link have emphasized the significant lag time between fundamental research and its application, but for those of us who conduct ecological research and work actively with practitioners, there is a sense that we must decrease that lag time. As my coauthor Joy Zedler argues, "adaptive restoration" is critical—research and restoration can proceed simultaneously by establishing large field plots to test alternative approaches to restore various targets. Then, the high-performing approach(es) can be adopted and expanded in subsequent restoration phases, adding new tests as the need arises (Zedler and Callaway 2003). Practitioners can set up test plots for later study even if researchers aren't available to take immediate advantage of field comparisons. The existence of a series of replicate test plots would facilitate a researcher's ability to obtain the necessary funding.

There is no need for restoration improvements to lag behind discovery; there is every need for the practice to keep pace with new knowledge.

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