Forgotten Grasslands of the South

Natural History and Conservation

REED F. NOSS

Forgotten Grasslands of the South

Forgotten Grasslands of the South:
Natural History and Conservation

Reed F. Noss

With a foreword by Edward O. Wilson

Dedication

To my grandfather John Burlin Johnson,
dean of American metallurgy and amateur dendrologist,
who taught me the trees of Ohio and served as my scientist role model.

To the state natural heritage programs,
the last bastions of natural history–based conservation;
to NatureServe, the umbrella organization for these programs;
and to Bob Jenkins, the brilliant originator of the
natural heritage methodology, while serving as
vice-president for science for The Nature Conservancy
during many of the organization's most effective years.

Contents

Foreword

Reed Noss' excellent book took me home to the rich ecosystems to which I was imprinted as a young naturalist. The grasslands of the South, and in particular the Southeast, encompass a diversity of open habitats that beggar the more familiar iconic grasslands of the Great Plains. They are also far richer in species of plants and animals. In fact, acre by acre the Southern Grassland Biome, when it is properly defined to include the longleaf pine savanna and its intermittent hardwood bottomlands, is probably the richest terrestrial biome in all of North America. It is not unusual to find more than two hundred species of herbaceous plants per acre in the ground flora of the longleaf savanna, and the pitcher-plant bogs, with as many as fifty species of thin-stemmed and crowded herbaceous species *per square meter*, possibly hold the record for small-scale biodiversity in the world.

In addition, more species of amphibians and reptiles occur in the Southern Grassland Biome than any other region of North America. The central Gulf Coast region, if we include the rivers and streams, have per unit area the largest number of turtle species in the world.

The South is also one of the least explored major areas of North America. Although the Great Smoky Mountains National Park is largely forested, a tally of the biodiversity by its ongoing All Taxa Biodiversity Inventory (ATBI) gives a hint of what awaits when similar intensive studies are conducted elsewhere in the South: 60,000–80,000 species of plants and animals estimated to be present, of which to date 3,000 are new records for the park and more than 900 are entirely new to science.

Around the world, grasslands, savannas, and dry tropical forests are the most rapidly disappearing major habitats, their loss due chiefly to the ease with which they are converted into agricultural fields and rangelands. The American South is no exception. The longleaf pine savanna, which once covered 60 percent of the South, has been almost entirely cut over for timber extraction. Fortunately, the ground flora, where not replaced by cultivation (including tree farms), is for the most part intact.

To understand, cherish, and preserve the great natural heritage of the Southern Grassland Biome should be a priority goal in America's environmental movement. Reed Noss' book provides a valuable map to that end.

Edward O. Wilson
Harvard University

Preface

People in the South don't read. That's a slight exaggeration of what Barbara Dean, my friend and editor at Island Press, informed me when I approached her with a proposal for this book. Barbara's point was that I must try to make a book on southern grasslands appealing to a geographically broad audience, because surveys show that people in the southern states buy and read fewer books than in any other region of the United States. Indeed, I've known southerners who grew up in homes where the only book was the Bible. Based on attitudes toward scientific topics such as evolution and climate change, many southerners appear to believe that little, if any, reliable knowledge has emerged since biblical times. People in every region are full of superstitions, irrational beliefs, and contradictions. In North America these seem to reach an apogee in the South, because this is where fundamentalist Christianity is most prevalent, and education about ecology and evolution evidently most lacking. But the South is full of ironies. Some of the smartest, friendliest, most generous, most irreverent, politically incorrect, bawdy, and hilarious people I have ever met are southerners. Such contrasts make the South an interesting place to live.

Despite my conflicted feelings toward southern culture, I have always wanted to live here—at least for a good part of the year. Not least among the attractions is the weather. The North is just too cold for too long. As a kid in Ohio (just thirty-five miles north of the Kentucky line, where the cultural South begins, as I feel compelled to inform my southern friends), I always said, "When I grow up, I'm going to live someplace warm." During our family's

annual winter or spring trips to Florida, the brilliance of the sun made me feel happier. My sinus infections disappeared. I delighted in spending the long days catching lizards, exploring the "jungles" in vacant lots between motels, and swimming in the ocean. I was proud to learn that my great-grandparents moved to Sarasota, Florida, back in 1910. Although they lived here for only a portion of each year and ultimately ended up losing their property in the Wall Street crash of 1929 and moving back north, this family history makes me feel almost a legitimate southerner. As I grew up, I kept my eyes southward, looking for opportunities. The South ultimately drew me to graduate school at the University of Tennessee–Knoxville and later to the University of Florida in Gainesville. Especially at the latter, I discovered a wonderful thing about the Deep South—you can do field work all year long, and in relative comfort! We have no highly constrained "field season" that confines to the office our wretched colleagues up north. In the South, there is always an excuse to be out of the office. It is a wonder we accomplish anything.

It was during my graduate studies, especially the class field trips and regular jaunts with friends through the mountains, gorges, swamps, pine savannas, hammocks (hardwood forests), and seashores of the South, that one of the great empirical generalizations of biogeography came home to me—there are so many more kinds of macroscopic animals and plants down here than in the North. And so much of the diversity in the South is contributed by endemic species, each distributed over a relatively small area. Within the United States, only California might surpass the South as a hotspot of species richness and endemism (this is not known for certain, given the incomplete tally of organisms). In the South you can visit a single site and find species of plants that are known only from those two hundred acres or so, or perhaps from just a handful of other sites. Especially for plants, but also for many reptile, amphibian, and invertebrate groups, most of the endemics inhabit grasslands and related communities.

Why do I focus on grasslands? This is sometimes hard to explain, even to myself. I have always been a lover of trees. As a kid I played primarily "in the woods" and in the streams flowing through those woods. My graduate research for both my MS and PhD degrees addressed temperate forest bird communities. My last "ecosystem book" with Island Press was *The Redwood Forest: History, Ecology, and Conservation of the Coast Redwoods*. Despite my long love affair with forests, however, as a child and beyond I was always drawn to the openings within forests. I remember a limestone outcrop not far from my Ohio home, deep in the forest but jutting out as exposed Silurian bedrock on a hill embellished with grasses and cedars. There was one particularly large, gnarled

redcedar in this glade, no doubt ancient, which was easy to climb and afforded fine views of the landscape in all directions. Later, as a more mobile teenager and young adult, I discovered other such glades here and there in the forested hills of southern Ohio and Kentucky. When my family purchased a condominium in Sarasota in 1972, when I was twenty, I spent most of every visit exploring the pine flatwoods, dry prairie, oak hammocks, river, and lakes of nearby Myakka River State Park. The wide open space and distant horizons, reminiscent of the West, were magnificent.

When I try to explain to my dubious western friends why I am so fond of a place so inhumanly hot, humid, flat, mosquito-infested, and culturally depauperate as Florida, I invariably fall back on a simple statement: "The natural history here is so cool!" Of course, biodiversity everywhere is fascinating, whether it's lithophilic microbes living in the pore spaces in Antarctic rocks or the myriad species of trees, lianas, epiphytes, insects, herpetofauna, birds, and mammals in a tropical rainforest. One of the intriguing things about southern grasslands is the strange juxtaposition of species, not a few of them quite out of place or so it seems. In Florida, for example, we have a little piece of the West—ancient sand dunes, cacti, yucca, wild buckwheat, harvester ants, tortoises, scrub-jays, burrowing owls, caracara, and so on—tacked on to the East. This pattern reflects geological and climatic history, for instance when the Southeast was biogeographically linked with the American West and Mexico via a broad Gulf Coastal Corridor.

Endless fascination with nature—nothing more and nothing less—is the key to enlisting people in the fight to save biodiversity. We will save what we love; we must. If you are inclined toward natural history, a brief stroll through your backyard is an experience of paradise. The South offers such experiences in abundance, if only we take the time to seek them out. It is no coincidence that two of the most accomplished naturalists of our time—Ed Wilson and Archie Carr—hailed from the South. A stellar self-taught naturalist from an earlier generation, Herb Stoddard spent his formative childhood years in Chuluota, Florida, where I now live; indeed, Stoddard credits his experiences here as pivotal for his later career as an ornithologist, ecologist, and forester. Along with Aldo Leopold, Stoddard is considered a father of wildlife management.

I focus on southern grasslands as a case study of the central role of natural history for motivating and informing conservation practice. We need to know intimately that which we are trying to save, so that we can have some confidence that our conservation plans will meet the requirements for persistence of species and ecosystems. I hope that by bringing the natural history (in the broad sense of Humboldt and Darwin) of southern grasslands to a broader

audience, I will help move us closer toward the goal of widespread protection and restoration of wild grasslands. Aldo Leopold pointed out that "one of the penalties of an ecological education is that one lives alone in a world of wounds." You cannot know the ecological history of southern grasslands without feeling a profound sense of loss. But biologically significant and beautiful scraps remain, in some cases sizable ones, from which we can restore much of what has been degraded. If there is a more worthy cause than restoring and conserving ecosystems, with all their pieces, I have not heard of it.

SOME THINGS ABOUT THIS BOOK

This is not a scientific textbook, nor is it typical "popular" nonfiction. My intent is to provide an accessible, engaging, and yet scholarly account of southern grasslands that will be comprehensible to the educated general reader interested in ecology, natural history, or conservation. I want people to be aware of how biologically amazing and enchanting southern grasslands are. To this end, I combine discussion of current scientific knowledge, concepts, and debates in ecology and conservation biology with "straight" natural history and a personal narrative based on my exploration of these ecosystems in the field. I was fortunate to be guided by some of the best field biologists and naturalists in the South, whose intensive knowledge I try to convey secondhand. I use a fair bit of scientific terminology, but briefly define the more technical terms when first used. I provide common and scientific names for each species when first mentioned, and for plants when first noted in each chapter (because they are the most numerous species mentioned and their common names are less standardized than for vertebrates; some invertebrates mentioned have no common names). I provide a species list toward the end of the book.

The reference style for this book is unusual. In an effort to improve readability, I do not cite references in the usual "author (date)" style found in the technical literature. I also avoid the common alternative to this approach—endnotes—because I always find it annoying to flip back and forth between the text and the endnotes buried in the back of a book I'm reading. Instead, I refer to authors and studies in the text; then, at the end of each chapter I include a references section, which lists cited sources and other key references by topic and in chronological order. The topics are listed in the approximate order in which they appear in each chapter. Full references are then provided at the back of the book in the literature cited section.

Acknowledgments

I borrowed knowledge from many naturalists, living and dead, in the field and through correspondence and literature, in preparing this book. Botanists and ecologists currently or formerly with the state natural heritage programs were my single greatest source of assistance for this project. I could not have written this book without the guidance of Jim Allison, Roger Anderson, Wilson Baker, Larry Barden, Jerry Baskin, James Beck, Chris Bedel, Joyce Bender, Brian Bowen, Forbes Boyle, Keith Bradley, Chris Brantley, Edwin Bridges, Angie Carl, Susan Carr, Rebecca Chester, Steve Christman, Kyle Copas, Jim Cox, Jerry Davis, Jamie Donnellson, Linda Duever, Dwayne Estes, Marc Evans, Patti Faulkner, Bill Finch, Gary Fleming, Laura Fogo, Tom Foti, Cecil Frost, Laura Gadd, Paul Gagnon, Bill Garland, Toby Gray, Chris Gregory, Eric Grimm, Dennis Hardin, Larry Harris, Larry Hedrick, Chris Helzer, Sharon Hermann, Jovonn Hill, Richard Hilsenbeck, Ross Hinkle, Maynard Hiss, Malcolm Hodges, Walter Holmes, Greg Houseman, Fran James, Ann Johnson, Dan Jones, Philip Juras, Gary Kauffman, Travis Knowles, Lynn Kutner, Chris Ludwig, Jim Matthews, Rich McCarty, John McGuire, Bruce Means, Paul Miller, Jeff Mink, Mike Morrow, Judy Murray, Jim Neal, Chris Oberholster, Steve Orzell, Kyle Palmquist, Karen Patterson, Bob Peet, Tom Philipps, Bill Platt, David Printiss, Milo Pyne, Chris Reid, Jimi Sadle, Mike Schafale, Ed Schwartzman, Al Schotz, Nora Schubert, Jason Singhurst, Larry Smith, Latimore Smith, Frankie Snow, Bruce Sorrie, Mike Stambaugh, Jack Stout, Johnny Stowe, John Suther, Louis Suther, Walter Taylor, Johnny Townsend, Roger Troutman, Amy Truer-Kuhn,

Wayne Tyndall, Dale Wade, Andy Walker, Alan Weakley, George Willson, Theo Witsell, Rusty Woods, and many others I've met or spoken with briefly.

I thank David Stephens for preparing original figures and adaptations of others' figures for this book. Special thanks to Sam Shine for making a monetary contribution toward travel expenses early in this project and to the following fine folks who reviewed chapters or sections of chapters: Keith Bradley, Barbara Dean, Cecil Frost, Paul Gagnon, Bill Garland, Eric Grimm, Malcolm Hodges, Josh King, Travis Knowles, Marty Main, Steve Orzell, Bill Platt, Mike Schafale, Bruce Sorrie, Michael Soulé, Jack Stout, and Johnny Stowe.

CHAPTER 1

❦

Natural History of a Forgotten American Grassland

> We left the magnificent savanna and its delightful groves, passing through a level, open, airy pine forest, the stately trees scatteringly planted by nature, arising straight and erect from the green carpet, embellished with various grasses and flowering plants.
>
> William Bartram (1774, near present-day Gainesville, Florida)

Taking a break from after-dinner email, I stroll into the family room, glass of cabernet in hand, to find my family watching the Discovery Channel on TV. I almost never watch television, so I do not know what to expect when I encounter one of these strange machines. This time I see a view from a low-flying aircraft of a beautiful green prairie landscape somewhere in the Great Plains of North America. The low undulating hills and soft, waving grass roll into the distant horizon. It is an inviting and comforting sight, a verdant scene once common in the center of our continent but now hard to find due to conversion of millions of acres of prairie to agriculture. The narrator, a well-known actress who, my daughter informs me, has battled aliens in movies, repeats a well-worn refrain: "Grasslands occur where there is too much rain for desert, but not enough rain to support forest."

I hurry back to my computer to capture that quote, which can be found in various forms in countless textbooks. In a 1991 book series on ecosystems of the world, R. T. Coupland states that grasslands "occur along a climatic gradient between desert and forest." A textbook of biogeography by Mark Lomolino

1

and coauthors declares that "temperate grasslands are situated both geographi-
cally and climatically between the deserts and the temperate forests" (fig. 1.1).
These statements epitomize the paradox of grasslands in the rainy southeastern
United States: few people, even ecologists, know they exist or expect them to
be here. The South has more than enough rain to support forest. Whether a
particular landscape in the South supports forest or grassland depends on fac-
tors other than precipitation—especially fire—but also soils, herbivores, and
other influences. Ecologists describe this phenomenon as "alternative stable
states." Grassland was a common or dominant alternative state across much of
the South, but that fact has been largely forgotten.

   When educated people in North America hear the terms *grassland* or *prai-
rie,* most of them visualize the Great Plains—the scene I saw on television.
Here, grassland dominated a vast region or biome. Grassland is the largest of the
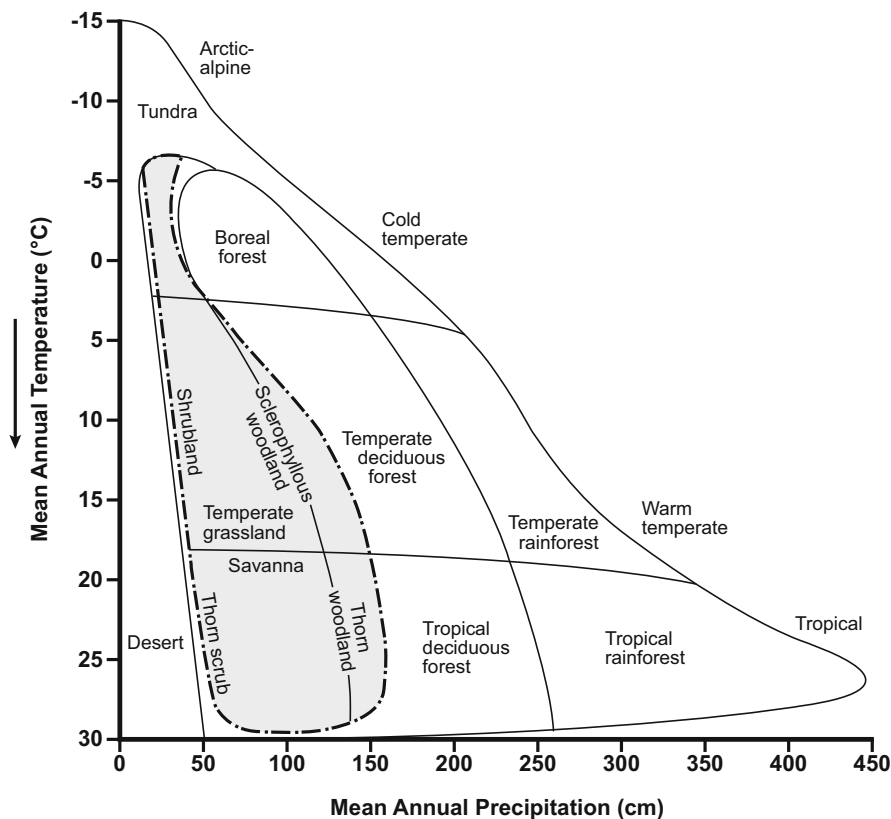
Figure 1.1. A climograph showing biome-scale relationships between climate and vegeta-
tion. Grassland/savanna is shaded. Grasslands in the southeastern United States do not fol-
low this pattern of being intermediate between desert and forest. Adapted from Lomolino
et al. (2006) after Whittaker (1975).

four major biomes on earth and the largest in North America, covering some 300 million hectares (ca. 750 million acres) before European settlement. (Note: I use English units in this book for the benefit of the general reader, but provide conversions from metric to English, as appropriate, where metric units are used in original sources.) The grassland biome (including savannas, which are grasslands with scattered trees) covers more than 40 percent of the land surface of the earth and is inhabited by more people than any other biome.

The climate of the South (fig. 1.2) varies greatly with latitude, longitude, and elevation, but none of it matches the traditional description of the grassland biome. Whereas most of the grassland biome of North America receives
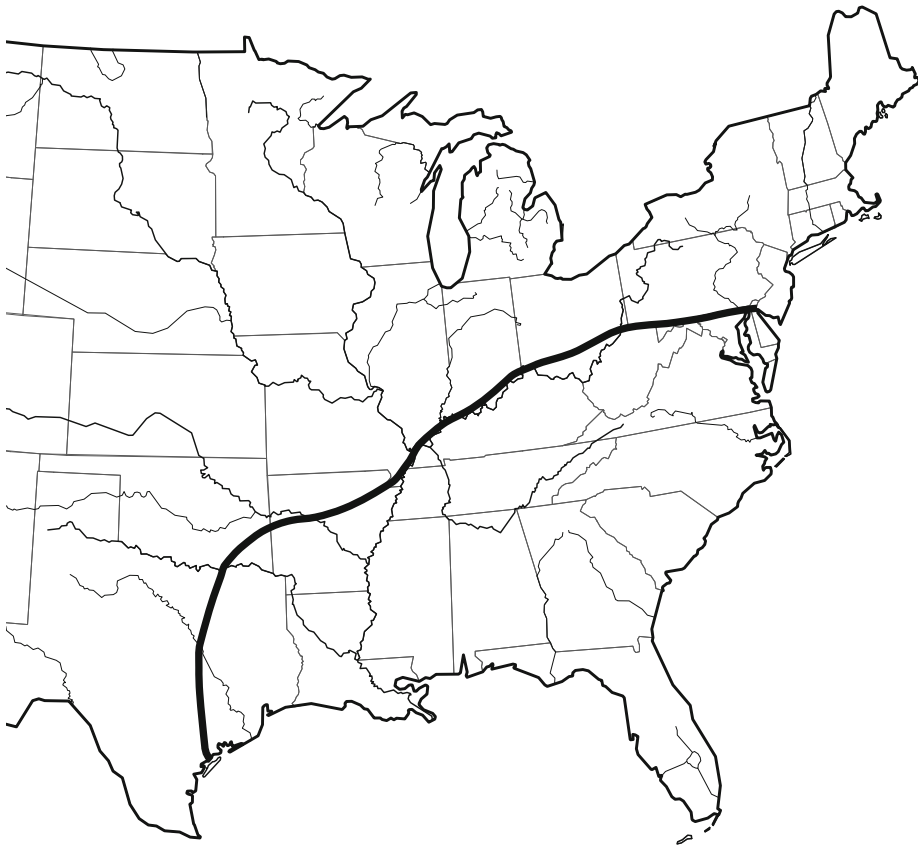
Figure 1.2. The study area, defined to encompass a variety of grasslands with southern (and often western) affinities. This entire region of the southeastern United States is referred to as "the South" in this book. "Southeast" and "southeastern" are used, where applicable, for the region east of the Mississippi River and to contrast this region with the southwestern and south-central United States.

well under forty inches of rain per year, the South gets about forty-eight to eighty inches. The climate, except at high elevations, is humid-temperate to warm-temperate from the Ohio Valley south to approximately the northern Florida Peninsula and Gulf of Mexico. Florida has a steep climatic gradient, with average temperature increasing rapidly with decreasing latitude. Northern Florida experiences regular freezes in winter; freezes decline sharply in frequency southward. South Florida is protected by the Gulf Stream, which originates as warm water from the tropical North Atlantic. Many biogeographic classifications designate south Florida as tropical, consistent with the dominance of south Florida (especially the Keys) by Antillean species. The climatic and physiographic diversity of the South partially explains the high species richness found in southern grasslands, but there is much more to it than that, as this book will explore.

NATURAL HISTORY FOR CONSERVATION

This book is about grasslands of the South, but it explores a bigger topic: how knowledge and practice of natural history are essential to the conservation of biological diversity. The logic is straightforward: to conserve wild living things and their habitats, we must know them and understand how they live and interact. Recognizing a species by name is essential to learning more; hence, it is deplorable that training in taxonomy is plummeting. Consider this example: Antje Ahrends and coauthors, in a paper called "Conservation and the botanist effect," show through a study of plant records from Tanzania that botanists with proper training in plant identification record more species (20 more species per 250 specimens) and more endemics (narrowly distributed species) and other taxa of conservation concern than botanists with inferior taxonomic skills. Poor training in natural history inevitably leads to second-rate conservation.

Natural history in the broad sense is not just identifying and naming things; it incorporates and intertwines biogeography, ecology, evolutionary biology, anatomy, physiology, taxonomy, systematics, paleontology, environmental history, geography, anthropology, archaeology, and other subjects, but with a focus on whole organisms and communities. What distinguishes natural history from most of current academic science is not just its acceptance of observation as a complement to experimentation, its rejection of extreme reductionism and hyperspecialization, or that much of it must be learned outdoors. More essentially, natural history insists on intimate familiarity with some aspect of biological diversity. A naturalist can be a generalist (familiar with many groups of

organisms or types of ecosystems) or a specialist (highly knowledgeable about one or a few groups or places)—we need both. Perhaps the ideal naturalist has broad knowledge complemented by specialized expertise on a particular taxonomic group or subject. The great ant biologist, all-round naturalist, and living legend Ed Wilson comes to mind, as does the generalist Charles Darwin with his special interest in barnacles, orchids, and earthworms, among other groups.

A modern tragedy is that we are losing naturalists as the old ones die off or retire and few new recruits are trained or hired. Schools and universities are eliminating field trips and field-based courses. At the same time—and the two trends are connected—major conservation organizations have shifted away from natural history and even from protecting biodiversity as a primary goal. Instead, they have moved into the vaguely defined territory of "ecosystem services," where nature is valued for its functional and economic services to human society, not for its beauty, fascinating peculiarities, or inherent dignity. This trend worries me, because a society that values nature only for its blunt utilitarian worth is not likely to care much about the extinction of species or the loss and degradation of natural communities that offer no tangible services. As extinction rates increase, so does the urgency of restoring natural history to its rightful place in science and conservation—at least on a par with concern for ecosystem services. Biodiversity and ecosystem services are complementary and should not be placed in competition with each other on the conservation agenda.

Beyond its importance for conservation, natural history provides a way for people to feel at home. Nothing alarms me more than someone who has no clue about what watershed she lives in and cannot name even five or ten species of plants and animals in her neighborhood. Such lack of awareness signals a pathological disconnection from nature. We need to know our nonhuman neighbors and come to see them as friends. Learning about the geologic history, flora, and fauna of the place we live in helps us feel that we belong here, regardless of our socioeconomic status, race, ethnicity, or whether or not we were born and raised in this place. Natural history is democratic—anyone can practice it—and it opens up limitless opportunities for joyful experiences. These experiences then circle back to conservation. We become more eager to save plants, animals, and places when they are familiar rather than strangers.

This book is a journey driven by curiosity, which is what being a naturalist is all about. From my first exposure to southern grasslands, I wondered why these places are so scarce in trees, whereas often adjacent to them are dense forests or swamps. As a beginning graduate student I learned that the pine savannas I viewed on field trips to Florida were the prevailing vegetation type of the Coastal Plain until quite recently. I did not yet know that the mixed hardwood

forests I saw through the car windows as a child during family trips to Florida, forests which now dominate much of the "undeveloped" parts of the region, are for the most part artifacts of fire exclusion or former agriculture. Many trained ecologists do not know this.

Years later, while researching the status of endangered ecosystems across the United States, I discovered that grasslands are, in general, the most imperiled of all terrestrial ecosystems in the country. This is especially true when endangerment is measured as extent of decline since European settlement, but is also often true in terms of present and future threat. Some of these grassland ecosystems dominated entire physiographic regions, such as the Coastal Plain, Great Plains, and Palouse, whereas others, such as in the Appalachians, Midwest, and Northeast, occurred as relatively small patches in a matrix of dissimilar vegetation, usually forest. Learning about the plight of grasslands, I pledged to do what I could to protect them and help them recover their former glory. Such is the moral responsibility of a naturalist.

GRASSLANDS IN THE SOUTH?

I regularly meet professional ecologists, including some southerners, who give me a puzzled look when I mention that I am writing a book on southern grasslands. The lack of awareness of native grasslands in the South represents a case of collective amnesia. A few human generations ago, grasslands were abundant across much of the South; today they are rare. Driving through the region today, one mostly sees agricultural fields, pine plantations, dense and mostly young hardwood forests and swamps, and, increasingly, urban sprawl. One has to know where to go to find remnant southern grasslands. If you find one, you might be surprised—a few still cover tens of thousands of acres.

I am fortunate to live in Florida where, amazingly, given the obscenely large human population (approximately 20 million in 2012) and ravenous development pressure, more native grassland remains than in any other southeastern state. This fact was documented in a 1993 book chapter by Hal DeSelm and Nora Murdock on grass-dominated ecosystems in the South. Yet, we have lost much of our grassland in Florida, as elsewhere. Using General Land Office Survey records, Karen Stephenson calculated nearly 2 million acres of prairies and 40,000 acres of savanna (not including pine savannas and woodlands) in the Florida Peninsula during the nineteenth century. The largest area of grassland was in south-central Florida—the marvelous Florida dry prairie (plate 7). Exquisite historical accounts of the dry prairie were collected by botanist

Edwin Bridges and published in 2006. Historic Florida grasslands have been largely converted to agriculture and other human land uses; still, around 10 percent of their pre-European distribution remains, plus considerable acreage in longleaf and other pine savannas and woodlands.

In spite of studies documenting extensive historic grasslands in the South, many authors flatly deny the existence of prairies and other grasslands east of the Great Plains. For example, Rick Cech and Guy Tudor, in their otherwise excellent book, *Butterflies of the East Coast*, claim that "there are no true prairies in the East today" and that even the Florida dry prairie is "technically neither a prairie nor a grassland." Other authors acknowledge the existence of grasslands in the South, but claim they were all created by Native American use of fire or sprang up on abandoned agricultural land. Such opinions are misinformed. The authenticity and antiquity of southern grasslands are vividly demonstrated by the enormous number of species (species richness) and narrowly distributed species (endemism) of grassland plants and several animal groups in these communities. A simple juxtaposition makes the case: table 1.1 shows species numbers within five classic prairie plant genera of the Prairie region (the Great Plains and Midwest) compared with the South. The South beats the Prairie region hands down.

Table 1.1. Which is the hotspot of grassland biodiversity? For five classic plant genera characteristic of the Prairie Region, species richness is greater in the South.

	Prairie region	South
Andropogon (big bluestems)	2 spp.	19 spp. in Florida 16 spp. in North Carolina 11 spp. in Louisiana
Sorghastrum (Indiangrasses)	1 sp.	4 spp.
Schizachyrium (little bluestems)	1 sp.	10 spp. in Florida 3 spp. in North Carolina 5 spp. in Louisiana
Liatris (blazing-stars)	10 spp.	14 spp. in Florida 12 spp. in North Carolina 5 spp. in Louisiana
Echinacea (purple coneflowers)	3 spp.	9 spp.

Source: Alan Weakley, University of North Carolina Herbarium (personal communication).

The poor awareness of southern grasslands is partly a problem of perception and terminology. Although many grasslands are easily recognizable to ecologists and laypeople alike, there is little consensus about what to include in the category of "grassland." I favor a broad and straightforward definition, for example from Cecil Frost: "A grassland is any community in which the

grass layer, with its associated forbs is the dominant layer in terms of either total cover or biomass or both." This definition encompasses some communities that are not conventionally considered grasslands. For instance, many ecologists know that the Coastal Plain was once dominated by longleaf pine (*Pinus palustris*) communities, but in common parlance these are forests, not grasslands. In the National Vegetation Classification, these communities are considered woodlands or sparse woodlands (fig. 1.3). Ecologists, foresters, and others who conduct research or management in longleaf pine ecosystems increasingly recognize their true character: grasslands with varying densities of trees (fig. 1.4). A 2009 paper by plant ecologist Susan Carr and colleagues uses the term *pyrogenic grasslands* in reference to pine savannas and dry prairies in Florida, which depend on frequent fires promoted by their flammable native plants.

**PERCENT CANOPY COVER
OF VASCULAR VEGETATION**

LIFE-FORM/ HEIGHT	Crowns interlocking (100%–60%)	Crowns not touching (60%–25%)	Crowns widely spaced (25%–10%)	(< 10%)
Trees > 5 m	*Forest* →	*Woodland* →	*Sparse Woodland*	
Shrubs/Trees 0.5–5 m	*Shrubland (Scrub)*		*Sparse Shrubland*	
Dwarf Shrubs/ Shrubs/Trees < 0.5 m	*Dwarf Shrubland (Scrub)*		*Sparse Woodland*	
Herbs	*Herbaceous*			
	Sparsely Vegetated/Non-Vascular (1–10% Vascular Vegetation)			

Figure 1.3. General categories of the Standardized National Vegetation Classification System. Longleaf pine ecosystems fall into the Woodland and Sparse Woodland categories, whereas other "grasslands" covered in this book fall into the Herbaceous category, with some glades and outcrops falling into the Sparsely Vegetated/Non-Vascular category. Adapted from The Nature Conservancy (1994).

Figure 1.4. Is this a grassland? This virgin longleaf pine-wiregrass community on the Wade Tract near Thomasville, Georgia, might be called a forest or a woodland. The vast majority of the species here, however, reside in the grass–dominated groundcover, and this is where most of the key ecological processes operate.

Under natural, frequently burned conditions, canopy cover in most longleaf pine communities rarely exceeds 60 percent, which permits a grassy groundcover to flourish (plate 27). Consistent with my inclusive definition, Coupland defines vegetation types with scattered trees and shrubs as grasslands, the decisive criterion being the dominance of grasses in the groundcover: "In some instances shrubs or trees emerge above the canopy as scattered individuals to form savannas.…An ecosystem may be designated as grassland when the canopy of grasses is continuous or nearly so."

Botanists and travelers have long commented on the grassland character of southern pine ecosystems. As quoted in Lawrence Earley's *Looking for Longleaf*, E. W. Hilgard made this observation in Mississippi in 1860: "The herbaceous vegetation and undergrowth of the Longleaf Pine Region is hardly less characteristic than the timber. The pine forest is almost destitute of shrubby undergrowth, and during the growing season appears as a park, whose long grass is often very beautifully interspersed with brilliantly tinted flowers." Many animal ecologists also recognize the grassland character of longleaf ecosystems. As Bruce Means writes in *The Longleaf Pine Ecosystem,* "To understand the

vertebrate faunas of longleaf pine savannas, it is crucial to appreciate that long-leaf pine ecosystems are forests to only a handful of species, but that for most vertebrates, they are, or were, grasslands." Today, after decades of fire exclusion, many former longleaf pine grasslands are indeed forests, artificially thick with trees, including invading hardwoods. They are no longer spacious and park-like, and their groundcover is diminished. It is unsurprising that people do not recognize these overgrown communities as grasslands.

Besides longleaf pine communities, there are (or were) sundry other kinds of grassland across the South, from the pine rocklands and marl prairies of south Florida; to coastal grasslands of many varieties along the Atlantic and Gulf coasts; across the prairies and granitic flatrocks of the Piedmont and the grassy balds of the southern Appalachians; north to the Potomac riverscour prairies; the serpentine barrens of Maryland and southern Pennsylvania; the limestone prairies of the Ohio River Valley and the Big Barrens of Kentucky; then south and west across scattered limestone, shale, and sandstone glades to the shortleaf pine (*Pinus echinata*)–bluestem (*Andropogon gerardii*, *Schizachyrium scoparium*) communities of the Ouachita Mountains; the blackland prairies of Arkansas and Texas (which extend eastward to Alabama with outliers in Georgia); and the coastal prairies of Louisiana, Texas, and neighboring Mexico. These grasslands existed in the pre-EuroAmerican landscape despite plentiful rain. Although some grasslands were substantially expanded and maintained by Indian-set fires, there is little evidence to suggest that people can actually "create" grassland over large areas, and plenty of evidence that fires from lightning ignitions (plates 3 and 4), plus other factors such as extreme soils (plate 16) and flooding, are perfectly capable of favoring grassland over forest in the South. I explore the influence of these factors in subsequent chapters.

Regarding the traditional precipitation-based explanation for the distribution of temperate grasslands, it is not entirely accurate, even for the Great Plains. In a 1950 article in the *Journal of Range Management*, C. O. Sauer argued:

> The more we learn of climatic data the less success there is in identifying climate with grassland. There are grasslands with as little as ten inches of rain a year, and with as much as a hundred, with long dry seasons, with short dry seasons, with high and low temperature ranges.… Grasslands are found chiefly (a) where there are dry seasons or occasional short periods of dry weather during which the ground cover dries out, and (b) where the land surface is smooth to rolling.… The occurrence (of plains) all around the world points to one known factor that operates effectively across such

surfaces–fire. Recurrent fires, sweeping across surfaces of low relief, are competent to suppress woody vegetation.

Daniel Axelrod, in his 1985 monograph, "Rise of the grassland biome, central North America," heartily agreed with Sauer's "well-reasoned rejection of the notion that regional grasslands are controlled by climate." Nevertheless, seasonal drought is an important factor in the maintenance of many grasslands. The Great Plains are infamous for their droughts, such as during the Dust Bowl of the 1930s. Under droughty conditions, grasses and associated herbaceous plants—if not decimated by agriculture, as in the Dust Bowl phenomenon—can out compete most woody plants. As prairie ecologist Edgar Transeau put it in 1935, "Tall prairie grasses once established exclude forest seedlings both by shading and, during the annual droughts, by superior utilization of available water in the deeper layers of the soil." In this case Transeau was not talking about the Great Plains, but rather about areas of the Midwest with more abundant rain, his so-called Prairie Peninsula, on the edge of which I grew up in Ohio.

After living in several rainy regions of the South, I know firsthand that the desert–forest ecotone story does not apply here. I also suspect that seasonal drought cannot, by itself, explain tens to hundreds of millions of acres of grassland in the South at the time of EuroAmerican settlement. Even those scientists, such as Earle Ripley, writing in the 1991 *Ecosystems of the World* series, who consider climate the dominant force affecting the distribution of grasslands acknowledge other factors: "It must be kept in mind that the presence of grassland in a certain place may reflect not only the climate of the area, but also the topography, soil characteristics, the fire history, grazing pressure, human activity and perhaps an element of chance." Carla Staver and coauthors show that forest and savanna can be alternative stable states under the same environmental conditions, as mediated by fire within a broad range of rainfall.

Southern grasslands are distinctive for more than their relatively wet climate. They are among the biologically richest ecosystems on earth, especially for herbaceous plants and when measured on fine scales of one square meter to around a thousand square meters. Moreover, many southern grasslands—in contrast to the Great Plains—have a high proportion of narrow endemic species (plate 1). Most of these species probably evolved tens of thousands or more years in the past, long before humans entered the region a mere 15,000 or fewer years ago. The presence of numerous endemics strictly associated with these communities demonstrates that many grasslands of the South are ancient.

Factors other than a shortage of precipitation or manipulation of vegetation by humans must explain the origin and maintenance of these grasslands and their remarkable diversity and endemism.

WHAT AND WHERE ARE SOUTHERN GRASSLANDS?

Southern grasslands are ignored in many texts and maps of grasslands in North America. The definitive book on the terrestrial vegetation of North America, edited by Michael Barbour and William Dwight Billings, includes a chapter by Phillip Sims and Paul Risser on grasslands. Their map of the grassland biome shows it occupying the Great Plains, the western fringe of the Midwest, and the southern fringe of the southwestern United States and adjacent Mexico (desert grasslands), with outliers in the Northwest (the Palouse prairie), California, and coastal Louisiana west and south along the Texas coast to just south of the Mexican border (coastal prairie) (fig. 1.5). The coastal prairie is the only southern grassland recognized by Sims and Risser. According to these authors, the grassland biome, with the exception of the coastal prairie, occupies a region with twenty to a hundred centimeters (eight to thirty-nine inches) of annual rainfall. As noted earlier, the grasslands of the South receive forty-eight to eighty inches of rainfall per year.

Other authors acknowledge more grassland in the South. Roger Anderson and Marlin Bowles, writing about deep-soil savannas and barrens of the Midwest, describe the eastern prairie-forest transition zone, which occurred as a broad arc from Canada into Texas. Although they do not discuss southern grasslands, Anderson and Bowles provide a map of the prairie-forest transition showing the Big Barrens and other prairies of Kentucky, some of the grasslands of Tennessee and Arkansas, and, as outliers, the Jackson Prairie of Mississippi and the adjacent, crescent-shaped Black Belt Prairie (fig. 1.6, plate 9).

The Black Belt and Jackson prairies are examples of blackland prairie, also found in Arkansas, Texas, and a small part of Georgia. The Black Belt was the largest of the blackland prairies in the Southeast, extending more than three hundred miles from McNairy County, Tennessee, across Mississippi to Russell County, Alabama, and covering about 3.5 million acres as a mosaic of open prairie, chalk outcrop, and forest/woodland. It has been reduced since EuroAmerican settlement by more than 99 percent, to the point that some scholars have questioned whether it ever existed. According to Richard Brown of Mississippi State University, disjunct occurrences of plants, insects,
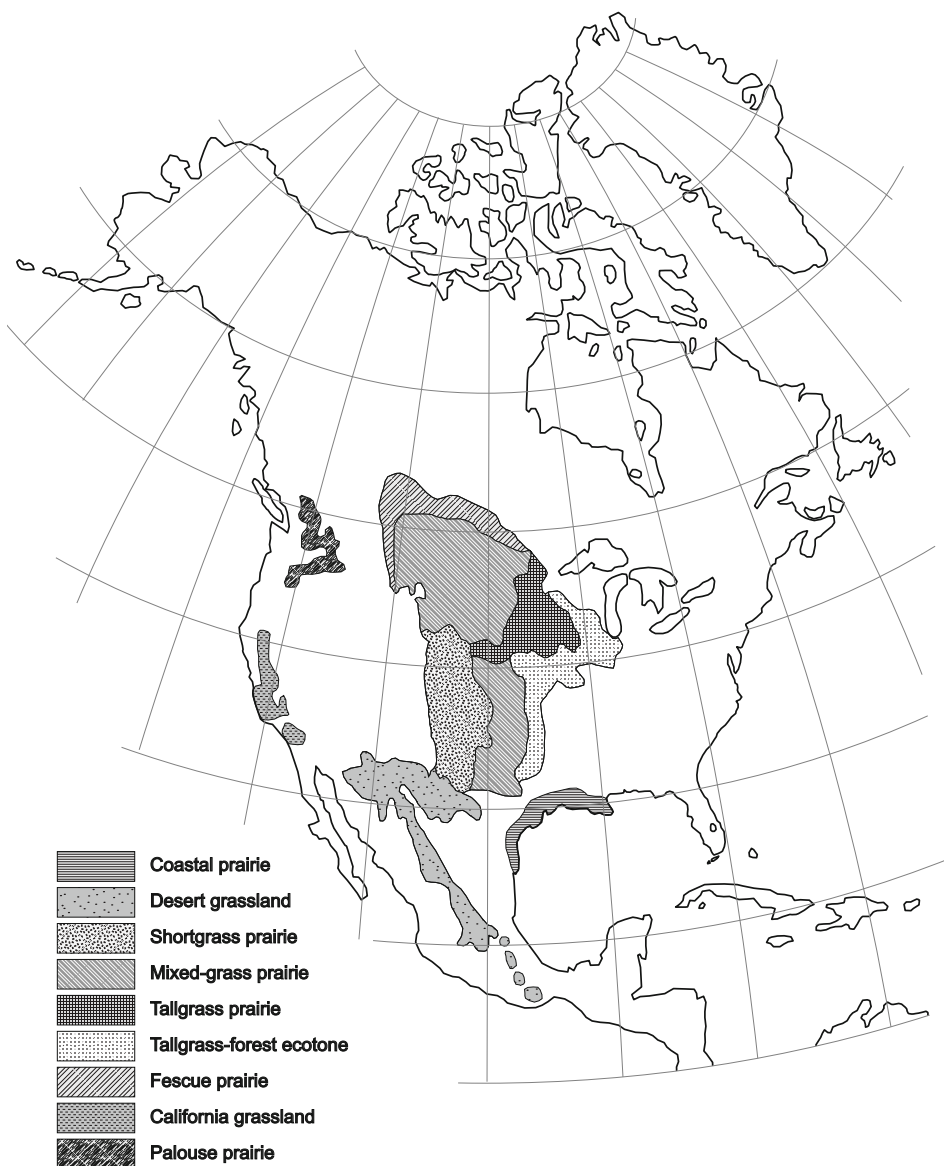
Figure 1.5. Major grassland types of North America, according to a textbook on vegetation of North America. The only southern grassland type recognized here is the coastal prairie of Texas and Louisiana. Adapted from Sims and Risser (2000) and reprinted with the permission of Cambridge University Press. © 1999 Cambridge University Press.

and extinct vertebrates between the Black Belt and the Great Plains suggest a prehistoric connection between the two regions, with the Black Belt perhaps serving as a refugium for Great Plains species during glacial episodes. Most of the grassland shown in figure 1.6 in Oklahoma and Texas lies to the west
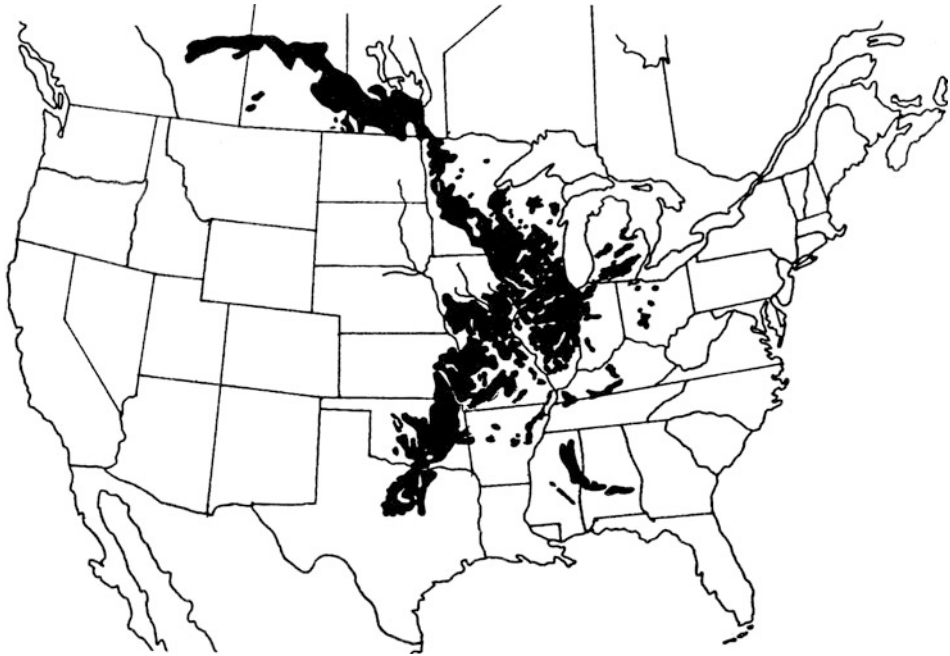
Figure 1.6. The eastern prairie-forest transition. Note the crescent-shaped Black Belt Prairie region of Mississippi and Alabama and, below it, the Jackson Prairie. From Anderson and Bowles (1999). Reprinted with the permission of Cambridge University Press. © 1999 Cambridge University Press.

of the southern grasslands covered in this book and is more similar to Great Plains grasslands.

The book chapter by DeSelm and Murdock provides a more comprehensive picture of the distribution of southern grasslands. Their map (fig. 1.7) shows "principal prairies, barrens, and additional small grassland areas" in several physiographic regions of the South. Absent from this map are the once-extensive prairies of the Piedmont of North and South Carolina, which extended into Virginia to the north and Georgia to the south. These prairies were described by European explorers as far back as Hernando de Soto's expedition in 1540. Larry Barden of the University of North Carolina reviewed the historic Piedmont prairies of the Carolinas in a 1997 article. That same year Philip Juras, whose painting graces the cover of this book, completed a master's thesis on presettlement Piedmont savannas at the University of Georgia. Barden and Juras, both largely on the basis of historical literature, concluded that prairies and savannas were common in the Piedmont at the time of European settlement, up through at least the end of the eighteenth century. Barden argued that the grasslands of the Piedmont were primarily the products of Indian burning
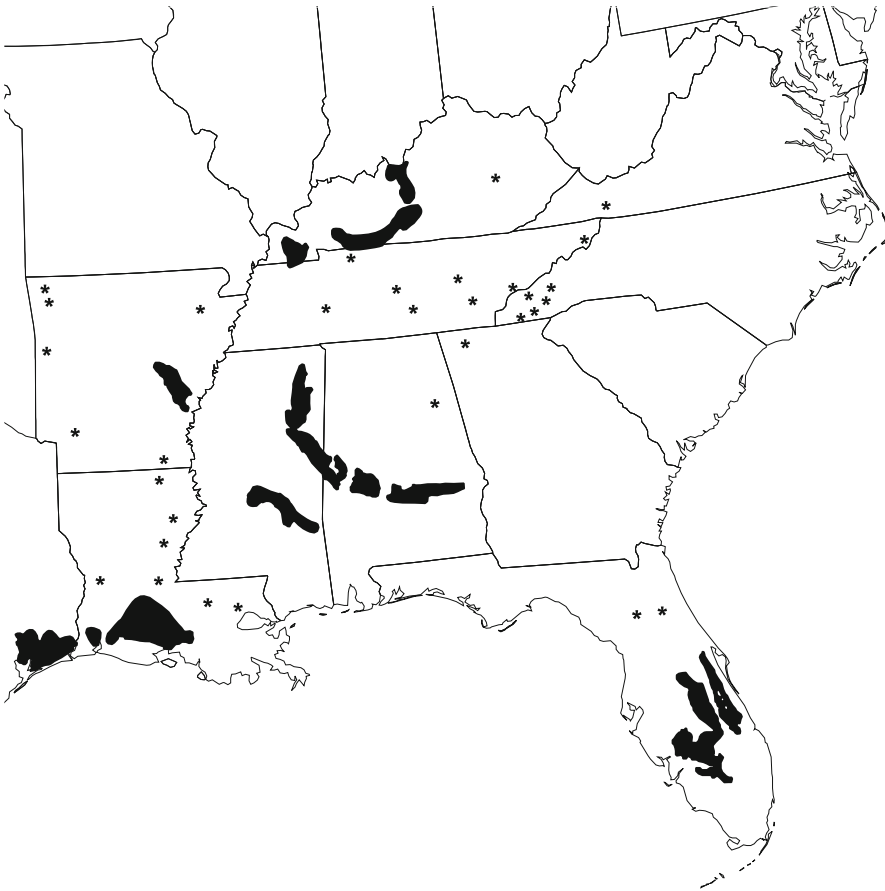
Figure 1.7. Grass–dominated areas of the South. Large grassland patches are shown as dark shapes, whereas small patches (mostly barrens) are indicated by asterisks. This map does not include Piedmont grasslands, longleaf pine ecosystems, or some other southern grasslands. Adapted from DeSelm and Murdock (1993).

and agriculture, whereas Juras allowed for other determining factors, especially soils and lightning fires. Other scholars dispute a purely anthropogenic origin based on the presence of Piedmont grassland endemics and other evidence that these ecosystems are more ancient than human presence in the region.

Also missing from the DeSelm and Murdock map (fig. 1.7) and discussion are the most extensive grasslands of the entire South: the longleaf pine ecosystem. This ecosystem, composed of many plant associations, was the matrix vegetation of the Atlantic and Gulf Coastal Plain and extended up into portions of the Piedmont, Blue Ridge, Ridge and Valley, and Appalachian (Cumberland) Plateau provinces, as mapped in 1999 by William (Bill) Platt (fig. 1.8). The omission of longleaf pine ecosystems from the map of DeSelm and Murdock
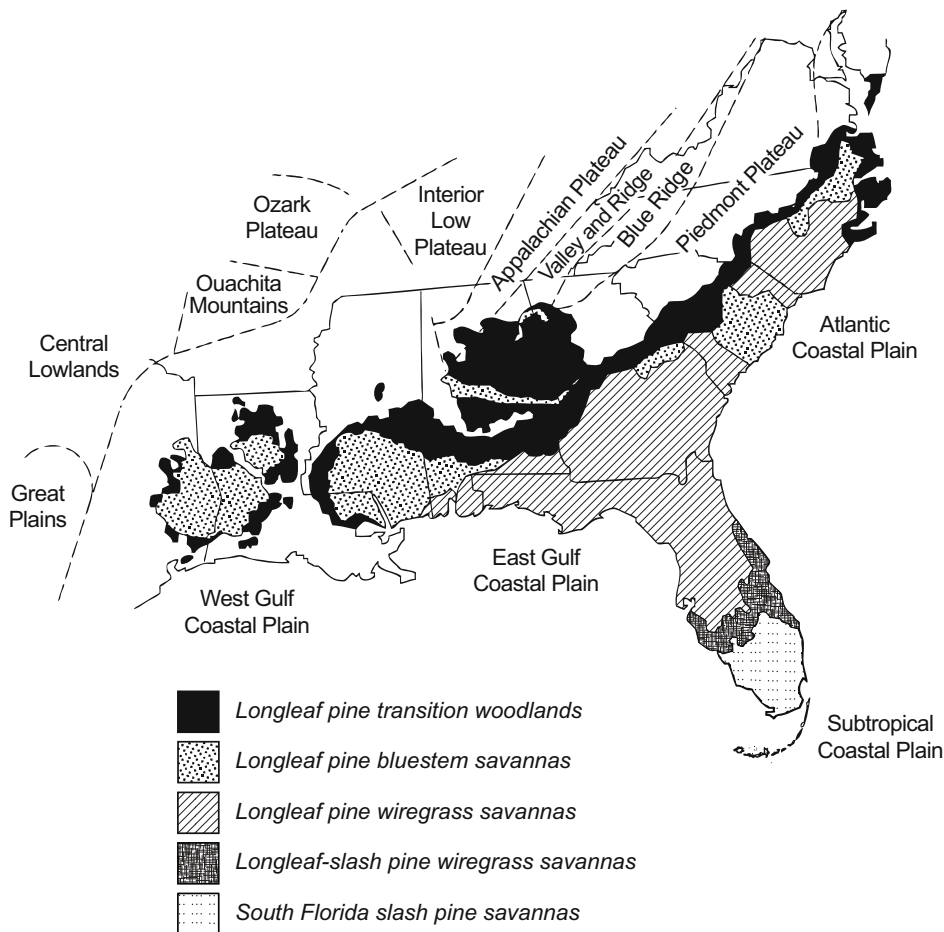
Figure 1.8. Distribution of pine savanna and woodland types in the southeastern United States. These communities formed the matrix vegetation across the Coastal Plain. Adapted from Platt (1999).

was intentional, as this ecosystem was addressed in two chapters of another volume of the same series: a chapter by Jack Stout and Wayne Marion on "pine flatwoods and xeric pine forests of the southern (lower) coastal plain" and a chapter by Stewart Ware, Cecil Frost, and Phillip Doerr on "southern mixed hardwood forest: the former longleaf pine forest." The title of the latter chapter is telling, as Ware and his coauthors were dissatisfied with the conventional label "southern mixed [hardwood] forest" for this region. They noted that "writers who emphasize the potential natural upland vegetation when fire is excluded name the region on the basis of the hardwoods that might ultimately dominate."

For example, the geographer A. W. Küchler, in his "potential natural vegetation" classification, published in 1964 and revised in 1985, mapped much of the

longleaf pine region as "southern mixed forest (*Fagus-Liquidambar-Magnolia-Pinus-Quercus*; i.e., beech–sweetgum–magnolia–pine–oak)." Earlier, in 1962, Elsie Quarterman and Catherine Keever published a monograph on the southern mixed hardwood forest, declaring it the climax vegetation of the Southeastern Coastal Plain, with pine communities being successional stages dependent on disturbance by fire. Most modern ecologists do not accept this interpretation, because fire is as natural a component of the ecosystem as climate or substrate. Nevertheless, Ware and coauthors were stuck with the "southern mixed forest" terminology because the organization of the book series was based upon Küchler's classification.

Why would Küchler misclassify longleaf pine ecosystems as southern mixed forest? It was not literally an error—it was the product of a false assumption. Küchler defined potential natural vegetation as "the vegetation that would exist today if man were removed from the scene and if the plant succession after his removal were telescoped into a single moment." Küchler assumed incorrectly that longleaf pine and similar grasslands of the South were maintained by anthropogenic fire; hence, they would quickly revert to hardwood forests if people stopped burning them. He was unaware of, or chose to ignore, evidence that the frequency of lightning strikes in this region is the highest in North America, north of Mexico (plate 4), and more than enough to account for dominance of the region by fire-dependent vegetation. Küchler also ignored the rich information on fire ecology in the Coastal Plain. Scientific understanding of the role of fire in southern pine and related ecosystems began with the natural history observations of Roland Harper, H. H. Chapman, and other botanists in the beginning of the twentieth century and continued through the work of Herb Stoddard and Ed Komarek of Tall Timbers Research Station—the site where the term *fire ecology* was coined and the field was born. In 1964, the same year that Küchler first published his map, Komarek wrote that "there has been much discussion, largely in ethnological or anthropological literature, on fire in grasslands, with little if any comment on the natural fires caused there-in by lightning…. That lightning is a major element in forest or grassland fires is now an accepted fact by most foresters…. Such a lightning factor…(exists) world-wide in nearly all vegetative types where there is enough fuel to burn."

Available evidence indicates decisively that grasslands were widespread in the southeastern United States at the time of European settlement, as well as in the more distant past, and they remained abundant into the twentieth century in some regions. In the northern and interior parts of the South, treeless grasslands were mostly rather small to moderate-sized openings in

a matrix of forest; they often reflected unusual geological or soil conditions. Other grasslands there were more extensive, and it appears that some, such as the Big Barrens of Kentucky, were maintained in part by Indian burning (albeit the relative contribution of lightning versus Indians as an ignition source remains controversial). Especially in the Coastal Plain, however, grasslands dependent on lightning fire formed the matrix vegetation of the region. The familiar fable of a squirrel being able to travel from the Atlantic coast to the Mississippi River without ever having to touch the ground—because the region was so densely forested—does not apply the farther south of the Mason-Dixon line one travels.

THE GRASSLANDS CONSIDERED
IN THIS BOOK

For the purposes of this book, a grassland is any natural community or ecosystem in which the herbaceous layer is dominated by grasses, other graminoid (grass-like) plants such as sedges, and associated forbs (other herbaceous flowering plants). This definition, consistent with Frost's and Coupland's given earlier, does not exclude trees, so long as the tree canopy is not dense enough to shade out the graminoid-dominated ground layer. More and more ecologists, especially in the South, use the term *grassland* to encompass prairies, savannas, and woodlands, in addition to sparsely vegetated communities, such as barrens and glades. The factors that allow or exclude trees from a grassland are not entirely understood, though there is no shortage of interesting hypotheses, many of which will be explored in this book. Commonly, especially in Florida, treeless prairies grade into savannas and woodlands or, alternately, patches or stringers of trees may occur in a grassland matrix or patches of prairie in a forest or woodland matrix. Nature is all about gradients and mosaics of communities of widely varying spatial scales of heterogeneity. Boundaries between vegetation types change over time—sometimes very rapidly with a stand-replacing disturbance, such as a major hurricane or landslide, but always, in the background, more slowly with changing climate, erosion, tectonic activity, and other geological phenomena, and with species colonizations and extinctions.

Table 1.2 provides a synopsis of the natural communities that I treat in this book. I group these communities into five main types: (1) prairies; (2) grassy balds; (3) savannas and woodlands; (4) barrens, glades, and outcrops; and (5) canebrakes.

The *coarse-filter* approach to conservation refers to the inventory and protection of natural communities and ecosystems, whereas the *fine filter* is the inventory and protection of individual imperiled taxa. The coarse filter is intended

Table 1.2. Definitions of main grassland types in the South as applied in this book.

Grassland type	Description and examples of ecological systems
Prairies	Dense herbaceous cover dominated by grasses or graminoid plants; treeless or nearly so.
	Examples of NatureServe ecological systems: Pennyroyal Karst Plain Prairie and Barrens Southern Ridge and Valley Patch Prairie Cumberland Riverscour Arkansas Valley Prairie and Woodland West Gulf Coastal Plain Southern Calcareous Prairie Southern Coastal Plain Blackland Prairie and Woodland Florida Dry Prairie Southwest Florida Dune and Coastal Grassland Central Florida Wet Prairie and Herbaceous Seep South Florida Wet Marl Prairie East Gulf Coastal Plain Savanna and Wet Prairie Southern Atlantic Coastal Plain Depression Pondshore Gulf and Atlantic Coastal Plain Tidal Marsh Systems Texas–Louisiana Coastal Prairie
Grassy Balds	Same description as prairies, but occurring on mountain crests or upper slopes in the southern Appalachians.
	NatureServe ecological system (i.e., just one defined): Southern Appalachian Grass and Shrub Bald
Savannas and Woodlands	Grasslands with trees; canopy cover varying widely depending on type, but generally in the range 5%–60% and occasionally up to 80% canopy cover (woodlands and sparse woodlands encompass this entire range in some classifications; other authors use woodland for the higher portion of canopy cover range and savanna for the lower portion).
	Examples of NatureServe ecological systems: Eastern Serpentine Woodland Ozark-Ouachita Shortleaf Pine–Bluestem Woodland Piedmont Hardpan Woodland and Forest Southern Appalachian Montane Pine Forest and Woodland Bluegrass Savanna and Woodland Lower Mississippi River Dune Woodland and Forest Southeastern Interior Longleaf Pine Woodland Atlantic Coastal Plain Fall-line Sandhills Longleaf Pine Woodland Florida Longleaf Pine Sandhill West Gulf Coastal Plain Upland Longleaf Pine Forest and Woodland Southern Atlantic Coastal Plain Wet Pine Savanna and Flatwoods Central Florida Pine Flatwoods South Florida Pine Rockland South Florida Dwarf Cypress Savanna

(table continues)

Table 1.2. continued

Grassland type	Description and examples of ecological systems
Barrens, Glades, and Outcrops	A highly diverse category with definitions varying widely among regions and authors; includes relatively shallow-soil prairies (barrens); savanna-like communities (often with redcedar, *Juniperus virginiana*) on very thin soils with abundant exposed rock and with lichens, bryophytes, and forbs sometimes more abundant than graminoids (glades); and exposed rock with patches or seams of herbaceous vegetation and usually abundant lichens and/or mosses (outcrops).
	Examples of NatureServe ecological systems: Appalachian Shale Barrens Alabama Ketona Glade and Woodland Nashville Basin Limestone Glade and Woodland Central Interior Highlands Calcareous Glade and Barrens Cumberland Sandstone Glade and Barrens Ouachita Novaculite Glade and Woodland Southern Ridge and Valley Calcareous Glade and Woodland Central Interior and Appalachian Sparsely Vegetated Systems Southern Appalachian Granitic Dome Southern Piedmont Granite Flatrock and Outcrop Panhandle Florida Limestone Glade South-Central Saline Glade East Gulf Coastal Plain Dry Chalk Bluff West Gulf Coastal Plain Catahoula Barrens
Canebrakes	Dense stands of cane (American bamboo, in the grass family: *Arundinaria gigantea* and *A. tecta*), which usually formed under disturbed canopies of trees in floodplains or on other fertile soils.
	NatureServe ecological systems (i.e., just two defined): Atlantic Coastal Plain Peatland Pocosin and Canebrake Mississippi River High Floodplain (Bottomland) Forest

Notes: Examples of NatureServe ecological systems that correspond to these types are given. Ecological systems are "groups of plant communities that tend to co-occur within landscapes with similar ecological processes, substrates, and/or environmental gradients" (www.natureserve.org/explorer/classeco.htm#terr_ecological). For a complete list of these types with descriptions and range information, see appendix 1.1 on the website: www.islandpress.org/forgotten-grasslands. For detailed information on any particular ecological system, search by that system's name at www.natureserve.org/explorer/servlet/NatureServe?init=Ecol.

to protect high-quality examples of all natural communities in a region. Hence, it requires a classification system, a topic I explore later. It is assumed, probably correctly, that the coarse filter will safeguard the vast majority of species without having to consider each species individually. The coarse filter is arguably most useful for taxonomic groups that have been poorly inventoried (for example, fungi, microorganisms, and most invertebrate groups) and for regions that have been inadequately surveyed. The fine filter remains essential for species that fall through the pores of the coarse filter—those that require individual attention because of their rarity or vulnerability (e.g., local endemics) or because they play pivotal roles in their respective ecosystems. Applied thoughtfully, the fine

and coarse filters are complementary; both are needed for conservation of a region's biodiversity.

I favor a coarse filter that combines vegetation with the physical properties and processes of ecosystems. As Robert Whittaker put it in his 1962 monograph on classification of natural communities, classification is most useful when "all aspects of ecosystems—physical environment, soil, vegetation, animal communities and, when appropriate, man himself, are considered together." A number of studies show that combining abiotic and biotic data in ecosystem classifications or representation analyses provides for a more robust coarse filter than either biotic or abiotic classifications alone. Especially with a rapidly changing climate, a coarse filter based entirely on vegetation would be ineffective because the species membership of vegetation types keeps changing. Recognizing the ephemeral nature of biotic communities in comparison with the physical environment, conservation scientists increasingly stress the utility of physical environmental features as coarse filters.

The logic of an abiotic coarse filter was argued by Malcolm (Mac) Hunter and colleagues in 1988. These authors noted that "most modern plant communities are less than eight thousand years old and therefore are not highly organized units reflecting long-term coevolution;" hence, they are not a reliable basis for a coarse filter during periods of climate change. As an alternative, they advocated "basing the coarse-filter approach on physical environments as 'arenas' of biological activity, rather than on communities, the temporary occupants of those arenas." They suggested climatic and soil variables for defining physical environments. Around the same time researchers in Canada and Australia argued for ecosystem representation schemes based on "enduring features" (landform, soils, etc.) and "environmental domains," respectively.

In a recent endorsement of this strategy, Mark Anderson and Charles Ferree of The Nature Conservancy (TNC) hypothesized that geologic factors take precedence over climate in explaining patterns of species diversity. They tested this idea for fourteen US states and three Canadian provinces and found that just four geophysical factors—the number of geological classes, latitude, elevation range, and the amount of calcareous bedrock—explained 94 percent of the variation in species diversity. In addition, 40 percent of 885 rare species were restricted to a single geology, and each geological class supported 5 to 95 endemic species. Calcareous bedrock and extreme elevations had significantly more rare species than expected by chance. This study makes a strong case for a geophysical coarse filter in conservation planning. It does not invalidate the use of vegetation as a coarse filter—especially when combined with geophysical features—or eliminate the need for a fine-filter safety net for

imperiled or local endemic taxa or for species that play key roles in their eco-systems. Anderson and Ferree acknowledge that "because species locations are so intertwined with geophysical properties, many current conservation areas chosen for a single population of a rare species, an unusual community type, or a taxonomic hotspot, already represent unique combinations of geophysical factors (e.g., serpentine barren or limestone fen) that benefit many species." As Cecil Frost pointed out to me, however, a geophysical coarse filter is insuffi-cient for fire-dependent species and communities; for instance, species depen-dent on frequent fire may disappear after just a few years of fire exclusion. "The coarse filter needs to be more complex," Cecil suggests; "the big thing missing …is the Process Filter."

Ecological classifications that combine vegetation and physical features include NatureServe's "ecological systems" classification and the natural com-munities classified by state natural heritage programs. In this type of classifica-tion, community membership can change considerably without altering the fundamental nature of the ecological system. Ecological systems are defined as "groups of plant communities that tend to co-occur within landscapes with similar ecological processes, substrates, and/or environmental gradients." I iden-tified 105 ecological systems in the NatureServe classification that correspond to my definition of grassland and that occur within my study area (appendix 1.1, on the website: www.islandpress.org/forgotten-grasslands). Included in table 1.2 are examples of ecological systems that correspond to the five main grassland types I recognize. A natural community can be defined as "a distinct and recur-ring assemblage of populations of plants, animals, fungi, and microorganisms naturally associated with each other and their physical environment." In table 1.3 (and see table 1.4 for the ranking system) I compare these two classification systems by means of a specific example for Florida: a crosswalk between the grasslands recognized in the NatureServe ecological systems classification and the natural communities recognized by the Florida Natural Areas Inventory. The classifications correspond well, but some discrepancies are evident.

An ecological system or natural community may encompass from one to dozens of associations, which provide a way to apply the coarse-filter approach on a finer scale. As defined in the US National Vegetation Clas-sification, associations are determined by "diagnostic species, usually from multiple growth forms or layers, and more narrowly similar composition that reflect topo-edaphic climate, substrates, hydrology, and disturbance regimes." For instance, the Southeastern Interior Longleaf Pine Woodland ecologi-cal system encompasses the following plant associations (a small number for southern grassland systems):

Table 1.3. Crosswalk between grasslands recognized in the NatureServe ecological systems classification (NatureServe, 2009 working draft) that occur in Florida and natural communities recognized by the Florida Natural Areas Inventory (FNAI 2010).

NatureServe Ecological Systems (grasslands only)	FNAI natural communities (grasslands only)
Prairies	
Florida Dry Prairie	Dry Prairie (G2/S2) Wet Prairie (G2/S2)[1]
Central Florida Wet Prairie and Herbaceous Seep	Wet Prairie (G2/S2)
Southern Coastal Plain Herbaceous Seep and Bog	Seepage Slope (G2/S2)
East Gulf Coastal Plain Savanna and Wet Prairie	Wet Prairie (G2/S2)
Central Florida Herbaceous Pondshore	Depression Marsh (G4/S4) Flatwoods/Prairie Lake (G4/S3) Marsh Lake (G4/S4) Sinkhole Lake (G3/S3)
South Florida Depression Pondshore	Depression Marsh (G4/S4)
Southern Atlantic Coastal Plain Depression Pondshore	Depression Marsh (G4/S4) Flatwoods/Prairie Lake (G4/S3) Marsh Lake (G4/S4)
East Gulf Coastal Plain Depression Pondshore	Depression Marsh (G4/S4) Flatwoods/Prairie Lake (G4/S3) Marsh Lake (G4/S4)
East Gulf Coastal Plain Sandhill Lakeshore Depression	Sandhill Upland Lake (G3/S2)
Floridian Highlands Freshwater Marsh	Basin Marsh (G4/S3)
South Florida Wet Marl Prairie	Marl Prairie (G3/S3)
Florida River Floodplain Marsh	Floodplain Marsh (G3/S3)
Atlantic Coastal Plain Indian River Lagoon Tidal Marsh	Freshwater Tidal Marsh (variant of Floodplain Marsh) (G3/S3)
Gulf and Atlantic Coastal Plain Tidal Marsh Systems	Freshwater Tidal Marsh (variant of Floodplain Marsh) (G3/S3)
Southern Atlantic Coastal Plain Fresh and Oligohaline Tidal Marsh	Freshwater Tidal Marsh (variant of Floodplain Marsh) (G3/S3)
Florida Big Bend Fresh and Oligohaline Tidal Marsh	Freshwater Tidal Marsh (variant of Floodplain Marsh) (G3/S3)
Southern Atlantic Coastal Plain Dune and Maritime Grassland	Beach Dune (G3/S2) Coastal Grassland (G3/S2)
East Gulf Coastal Plain Dune and Coastal Grassland	Beach Dune (G3/S2) Coastal Grassland (G3/S2)
Southwest Florida Dune and Coastal Grassland	Beach Dune (G3/S2) Coastal Grassland (G3/S2)
Florida Panhandle Beach Vegetation	Beach Dune (G3/S2)

(table continues)

Table 1.3 continued

NatureServe Ecological Systems (grasslands only)	FNAI natural communities (grasslands only)
Savannas and Woodlands	
Atlantic Coastal Plain Upland Longleaf Pine Woodland	Sandhill (G3/S2) Mesic Flatwoods (G4/S4)
East Gulf Coastal Plain Interior Upland Longleaf Pine Woodland	Upland Pine (G3/S2) Sandhill (G3/S2)
Florida Longleaf Pine Sandhill	Sandhill (G3/S2)
Southern Atlantic Coastal Plain Wet Pine Savanna and Flatwoods	Wet Flatwoods (G4/S4) Mesic Flatwoods (G4/S4)
East Gulf Coastal Plain Near-Coast Pine Flatwoods	Wet Flatwoods (G4/S4) Mesic Flatwoods (G4/S4) Scrubby Flatwoods (G2?/S2?)
Central Florida Pine Flatwoods	Wet Flatwoods (G4/S4) Mesic Flatwoods (G4/S4) Scrubby Flatwoods (G2?/S2?)
South Florida Pine Flatwoods	Wet Flatwoods (G4/S4) Mesic Flatwoods (G4/S4) Scrubby Flatwoods (G2?/S2?)
South Florida Pine Rockland	Pine Rockland (G1/S1)
South Florida Dwarf Cypress Savanna	Marl Prairie (G3/S3)
Barrens, Glades, and Outcrops	
Panhandle Florida Limestone Glade	Upland Glade (G1/S1)
(no adequate analog described)	Keys Cactus Barren (G1/S1)
South Florida Mangrove Swamp (*not an ideal analog*)	Keys Tidal Rock Barren (G3/S3?)
Canebrakes	
(none described for Florida)	*(none described)*

Note: Both classification systems use both vegetation and physical environmental features to classify system/community types. The Global (G) and State (S) ranks of conservation priority are given for natural communities, with "1" being the highest and "5" being the lowest (see table 1.4).
[1]Based on classification by Orzell and Bridges 2006b.

Pinus palustris–Pinus echinata–(Pinus virginiana)/Quercus marilandica–(Quercus prinus)/Vaccinium pallidum woodland

Pinus palustris–Pinus echinata/Quercus coccinea–Quercus georgiana woodland

Pinus palustris–Pinus echinata/Schizachyrium scoparium–Manfreda virginica Serpentine woodland

Pinus palustris–Pinus taeda–Pinus serotina/Chasmanthium laxum–Panicum virgatum Piedmont woodland

Quercus prinus–Pinus palustris forest

Table 1.4. NatureServe global ranking system for species, infraspecific taxa, and natural communities.

Rank	Definition
GX	**Presumed extinct** (species): Not located despite intensive searches and virtually no likelihood of rediscovery. **Eliminated** (ecological communities): Eliminated throughout its range, with no restoration potential due to extinction of dominant or characteristic taxa and/or elimination of the sites and disturbance factors on which the type depends.
GH	**Possibly extinct** (species) or **eliminated** (ecological communities and systems): Known from only historical occurrences but still some hope of rediscovery. There is evidence that the species may be extinct or the ecosystem may be eliminated throughout its range, but not enough to state this with certainty. Examples of such evidence include (1) that a species has not been documented in approximately 20–40 years despite some searching or some evidence of significant habitat loss or degradation; and (2) that a species or ecosystem has been searched for unsuccessfully, but not thoroughly enough to presume that it is extinct or eliminated throughout its range.[1]
G1	**Critically imperiled:** At very high risk of extinction due to extreme rarity (often 5 or fewer populations), very steep declines, or other factors.
G2	**Imperiled:** At high risk of extinction or elimination due to very restricted range, very few populations, steep declines, or other factors.
G3	**Vulnerable:** At moderate risk of extinction or elimination due to a restricted range, relatively few populations, recent and widespread declines, or other factors.
G4	**Apparently secure:** Uncommon but not rare; some cause for long-term concern due to declines or other factors.
G5	**Secure:** Common; widespread and abundant.
T#	**Infraspecific taxon (trinomial):** The status of infraspecific taxa (subspecies or varieties) are indicated by a "T-rank" following the species' global rank. Rules for assigning T-ranks follow the same principles outlined above. For example, the global rank of a critically imperiled subspecies of an otherwise widespread and common species would be G5T1. A T subrank cannot imply the subspecies or variety is more abundant than the species. For example, a G1T2 subrank should not occur. A vertebrate animal population (e.g., listed under the US Endangered Species Act or assigned candidate status) may be tracked as an infraspecific taxon and given a T-rank; in such cases a Q is used after the T-rank to denote the taxon's informal taxonomic status.

Note: Ranking criteria for national (N) or subnational/state (S) geographic scales are analogous. For example, a subspecies could be ranked G4T2S1. A subnational rank, however, cannot imply that the species or ecosystem is more secure at the state/province level than it is nationally or globally (e.g., a rank of G1S3 is invalid).
Source: NatureServe Explorer: http://www.natureserve.org/explorer/ranking.htm.
[1]Possibly eliminated ecological communities and systems may include ones presumed eliminated throughout their range, with no or virtually no likelihood of rediscovery, but with the potential for restoration, for example, American chestnut forest.

With climate change, we can expect the associations that compose a particular ecological system to change. Associations will drop in and out of ecological systems, and species composition will shift as species respond individualistically to change. Shifts in composition will ultimately proceed to the point where an

association, as originally described, no longer exists. I do not see this as a problem, either philosophically or practically. Indeed, it will be quite interesting and informative, for both ecological theory and conservation science, to track these shifts along environmental gradients in space and time. The general description of each ecological system (appendix 1.1) will remain valid for decades or even centuries, but the details of species composition and distribution will change at rates determined by the ecophysiological traits and dispersal capacities of individual species. Some species will go extinct, but over a long span of time, new species will originate. It is well within our ability as conservation scientists to monitor shifting species distributions and adjust our classifications in a dynamic world. It should even be fun.

JOSHUA CREEK

It is February 2011. My two dogs and I are on a late afternoon hike on the Florida Trail, a National Scenic Trail that I am fortunate to have pass within a mile of my home in central Florida. When not traveling I am on some portion of the Florida Trail at least a couple of times each week. On this occasion we are hiking the trail within the Joshua Creek Tract of the new Charles H. Bronson State Forest. A few years ago, as a governor-appointed member of the state's Acquisition and Restoration Council (ARC), I voted to approve purchase of this cattle ranch with state funds. At that glorious time, Florida was spending more money than any other state—and more than the entire federal government nationwide—for acquisition of conservation lands. That now seems unreal. Land acquisition by the state has stopped under a governor and a legislature more hostile to conservation than virtually any in Florida's history, perhaps since Governor Napoleon Bonaparte Broward was elected in 1904 on his campaign promise to create an "Empire of the Everglades" by draining that "pestilence-ridden swamp."

While in the field I seldom think of politics, and winter is a magical time in Florida. Even at this subtropical latitude, the low angle of the sun during much of the day makes the grasses, saw palmetto (*Serenoa repens*) fronds, and pine needles glisten sharply, every edge distinct with silvery and golden hues. I encounter one of the most delightful of southern grasses, splitbeard bluestem (*Andropogon ternarius*). Although the bright silvery luster of the late summer and fall inflorescences is gone, it is vivid in my memory. There is a chill in the air today, accentuated by a moderate breeze, but the late afternoon sun provides some warmth and the sky is brilliantly blue with a few puffy clouds. I could hike all day.

At the time of this winter visit, the Joshua Creek Tract was not yet open to the public. I had acquired a research permit to visit and record sightings of imperiled species, such as Sherman's fox squirrel (*Sciurus niger shermani*) and eastern indigo snake (*Drymarchon couperi*). This permit provides an opportunity to wander in a nice place near my home and keep track of the local flora and fauna. This is my diversion—natural history exploration—which many scientists find anachronistic. It may not be "real science" and is certainly not high-tech, but natural history gets me out of the office, away from machines, and helps me remember what the real world is like. Maybe that's important; the computer models that occupy the attention of most ecologists, however useful, are not real. Also, while in the field I learn interesting and useful things about the status of species and natural communities, and about life histories and behaviors—things that researchers stuck behind their computers never truly learn. Vicarious ecology pales before direct experience of nature.

Although damaged by past fire exclusion, logging, too many cows and feral hogs (both still abundant), and hunters who inexplicably are given the exclusive right to drive all over this conservation area during hunting season, the Joshua Creek Tract is one of my favorite places close to home. I am walking through a pine flatwoods, which on this site is dominated by a mix of pond pine (*Pinus serotina*) and longleaf pine in the overstory, indicative of seasonally wetter conditions than a pure longleaf pine flatwoods. The pond pine occupies lower portions of this site, which is most of it, and longleaf pine, the higher areas (I'm talking about only a few inches of elevation difference here). A few miles to the south, Tosohatchee Wildlife Management Area is dominated by slash pine (*P. elliottii*) flatwoods, probably reflecting its coastal position during past times of higher sea level (i.e., slash pine in central and north Florida is predominantly coastal in distribution).

Pine flatwoods of various types composed the matrix vegetation, within which other vegetation types were embedded, in much of Florida, including the landscape I now inhabit. Pioneer ornithologist, conservationist, and wildlife biologist Herb Stoddard described the pine woods of central Florida during the last decade of the nineteenth century: "Virgin stands of longleaf pine as far as one could see, marching on and on to infinity. The pinelands were quite open, with short grass and some palmetto ground cover, kept that way from time immemorial by frequent grass fires…one could see a deer a quarter of a mile away." A pine flatwoods is not a forest, although some people persist in calling it one. The canopy cover where I now walk is around 40 percent. It can range from much lower, 10 percent or less, up to 60 percent or so under natural conditions, making the flatwoods community a savanna/grassland. The

sky is big in pine flatwoods and sandhills (a related community on higher, drier ground) with their sparse tree cover.

I see a wall of thick vegetation ahead, where the pine flatwoods is interrupted by a broad strand of wet hardwood forest (a community known as hydric hammock) and, in the center, a strip of bald cypress (*Taxodium distichum*) swamp along Joshua Creek. As I leave the sunny flatwoods, enter the hammock, and proceed to the swamp, my mood changes in response to my surroundings. The broad, buttressed laurel oaks (*Quercus laurifolia*), live oaks (*Q. virginiana*), red maples (*Acer rubrum*), and sweetgums (*Liquidambar styraciflua*), interspersed with American elm (*Ulmus americanus*), cabbage palms (*Sabal palmetto*), many lianas (woody vines), abundant Spanish moss (*Tillandsia usneoides*), and other epiphytes impart a tropical flavor, but also an aura of mystery and foreboding. My senses are heightened, as if a predator lurks behind the next big tree. The cypress knees become denser and taller, some as tall as I am, as I near the sand-bottomed, tea-colored creek. The creek flows low and slow during the winter dry season, but by midsummer, if the rains come on schedule, it will overflow its banks and creep well up into the flatwoods.

Cypress trees, with sparse brown needles this time of year, are majestic even when of medium size like these, up to about 3 feet in diameter at breast height; this is a far cry from the record Florida cypress, "The Senator," which grew just twenty miles from where I now walk and measured 11 feet in diameter and 118 feet tall (*after* the top portion snapped off during a hurricane a few decades ago). Although the tree was largely hollow, the American Forestry Association was able to get a core in 1946 and estimated the tree at more than 3,500-years old, making it one of the oldest trees in the world and quite likely the oldest in eastern North America. In the days before massive logging, even bigger trees were apparently common. Sadly, The Senator mysteriously burned down in January 2012, as I was finishing this book. Arson seems likely, but the Florida Forest Service prefers an explanation of spontaneous combustion or ignition from a hypothetical lightning strike, despite no observed lightning in the area for several months. (An anonymous tip later led to the arrest of a woman who set a fire inside the hollow tree to facilitate her drug use.)

The Joshua Creek swamp is an enchanting place, and I linger to take in its melancholy. A barred owl (*Strix varia*) calls from down the creek, just beyond eyesight; they are nesting at this time of year. I hear a small flock of cedar waxwings (*Bombycilla cedrorum*) pass overhead; this species is just here for the winter. I walk a small log across the creek and then up the modest elevation gradient— a Florida mountain—from swamp to hydric hammock to mesic hammock

with its southern magnolias (*Magnolia grandiflora*) and big live oaks, and finally back into the fading sun of the pine savanna. The lovely aromatic flowers of the vine, yellow jessamine (*Gelsemium sempervirens*), pronounced "jasmine," hang from branches along the hammock-flatwoods edge.

A month or so later, in this same flatwoods, Bachman's sparrows (*Peucaea aestivalis*) sing from perches amidst the grasses and palmettos, while pine warblers (*Setophaga pinus*) trill and brown-headed nuthatches (*Sitta pusilla*) squeak from the treetops. Common ground-doves (*Columbina passerina*) plaintively "woot." These are characteristic grassland/pineland birds in our region. Red-cockaded woodpeckers (*Picoides borealis*), a federally listed endangered species, should be here, but there are too few pines old and internally soft enough with redheart fungus (*Phellinis* [*Fomes*] *pini*) disease for the birds to construct their nest cavities. I have heard only a few northern bobwhite (*Colinus virginianus*) in this vicinity recently, whereas only six or seven years ago they were still common; entire coveys occasionally flew into the mist nets in my yard. These quail have suffered a major decline, and the reasons are obscure. Fire exclusion is a known problem, but is probably not the whole story. The red imported fire ant (*Solenopsis invicta*) seems to become more abundant every year and is known to prey on nestlings of quail and other ground-nesting birds. Another rapidly declining species, also dependent on open, well-burned habitats, is Sherman's fox squirrel. This squirrel, the largest in the New World, is present in low densities on at least one corner of the Joshua Creek Tract. I have a special fondness and anguish for this mammal. I petitioned for listing it under the federal Endangered Species Act in the late 1980s. The US Fish and Wildlife Service evaluated my petition and determined that listing was warranted; then, a few months later, it decided that listing was "precluded by higher priority activities," placing the squirrel in a political trash bin from which it has yet to emerge.

On a steamy July day I discover a large population of Feay's prairie-clover (*Dalea feayi*), a beautiful grassland plant I had not seen previously in this general area. Also flowering is our common native palm, the cabbage palm (*Sabal palmetto*), whose gigantic inflorescences are buzzing with bees and other pollinators. I also find in bloom pale meadowbeauty (*Rhexia mariana*), tall meadowbeauty (*R. alifanus*), Nuttall's meadowbeauty (*R. nuttallii*), largeflower rosegentian (*Sabatia grandiflora*), Florida scrub skullcap (*Scutellaria arenicola*), rose-rush (*Lygodesmia aphylla*), roseling (*Cuthbertia* [*Callisia*] *ornata*—a Florida endemic), tread-softly (*Cnidoscolus stimulosus*), blackroot (*Pterocaulon pycnostachyum*), yellow bachelor's button (*Polygala rugelii*), yellow stargrass (*Hypoxis juncea*), Carolina yellow-eyed grass (*Xyris caroliniana*), St. Peter's-wort (*Hypericum tetrapetalum*),

matted sandweed (*H. reductum*), roundleaf thoroughwort (*Eupatorium rotundifolium*), rosy camphorweed (*Pluchea rosea*), and around a dozen other plants. These are my neighbors.

Later, in September, I discover just two individuals of a striking Florida endemic, celestial lily (*Nemastylis floridana*), which I have never seen before (plate 6). The violet-blue flowers of this "lily" (actually in the iris family: Iridaceae) open around 4:00 p.m. and close at dusk for a limited period between August and October. What pollinator does it attract with that bizarre strategy? Perhaps a moth? When not flowering, its few, inconspicuous, grasslike leaves would be difficult to see. The botanical wonders continue through September and October, with goldenasters (*Chrysopsis linearifolia*, *C. scabrella*), silkgrass (*Pityopsis graminifolia*), coastalplain honeycombhead (*Balduina angustifolia*), several blazing-stars (*Liatris spicata*, *L. gracilis*, *L. chapmanii*), chaffheads (*Carphephorus corymbosus*, *C. paniculatus*), blue curls (*Trichostema dichotomum*), false foxglove (*Agalinis fasciculata*), and many grasses in bloom, including the distinctive lopsided Indiangrass (*Sorghastrum secundum*). October is the time of year when the pasty Yankees begin to arrive in their golf clothes to get sunburned and clog the roads with their SUVs and minivans. I have learned to spend my time where these annoying tourists do not venture: in natural areas. Yet I am ambivalent, because in order to protect these areas, it is crucial that Florida residents and visitors alike experience and appreciate them.

Whenever I'm in an open savanna or other grassland with the full sky and breeze, I feel a sense of relief and freedom that is difficult to explain. John Muir felt this freedom, too, in the pine savannas of Georgia during his thousand-mile walk to the Gulf of Mexico in 1867: "The pines wide apart; the sunny spaces between full of beautiful abounding grasses, liatris, long wand-like solidago…. Here I sauntered in delightful freedom, meeting none of the cat-clawed vines, or shrubs, of the alluvial bottoms." I am persuaded by the evidence that early humans evolved in the African savanna, and that we still seek—or with our lawns and golf courses, attempt to create a semblance of—savanna environments today in order to satisfy an atavistic craving for openness, visibility against enemies, good hunting, and fewer bugs and diseases. A savanna feels like home.

The "savanna hypothesis" for human evolution was first proposed by anthropologist Raymond Dart in 1925. The hypothesis suggests that widespread environmental change (increased seasonality and drought) in the late Miocene, eight to six million years ago, converted many forests worldwide to savannas and other grasslands, and that this shift favored bipedalism in our hominin ancestors. Bipedalism freed the hands for tool use, favoring increased brain mass and intelligence, ultimately leading to modern humans. The hypothesis

has remained controversial, largely because plant fossils (including pollen) and other direct evidence of the vegetation composition in the areas where early hominins dwelled have been scarce, and because the term *savanna* has been applied disparately by different writers.

A 2011 paper in *Nature* provides powerful support for the savanna hypothesis. Thure Cerling and colleagues used stable carbon isotopes in ancient soils to determine the relative proportion of trees and grasses around hominin fossil sites in eastern Africa over the last six million years. Virtually all woody plants use the C_3 photosynthetic pathway, whereas warm-season grasses (which dominate African savannas as well as grasslands of the southern United States) use the C_4 photosynthetic pathway. The latter is more conservative of water under hot, dry conditions because it concentrates carbon dioxide in the plant cells and does not require that stomata (minute pores in leaves and stems) stay open for long periods for gas exchange. The C_3 and C_4 plants leave distinct and persistent carbon isotope signatures in soils after they decompose. By analyzing these isotope ratios in carefully dated soils, Cerling and colleagues determined that our earliest bipedal ancestors lived in an open savanna environment dominated by warm-season grasses and containing less than 40 percent woody cover. About 3.6 million years ago, woody cover increased somewhat in this region of Africa, followed by a return to more open grassland conditions beginning 3.6 million years ago and a peak in grassiness between 1.8 million and 10,000 years ago, as modern humans fully developed. We are truly and fundamentally grassland/savanna beasts.

Despite my deep genetic heritage as a grassland creature, I couldn't be satisfied experiencing only savanna or any other single kind of vegetation. For me the greatest aesthetic delight is found in moving among environments, experiencing the vivid contrast of dark and light, closed and open, proceeding back and forth from bright sunny places to dense mysterious places. This pattern of contrast is illustrative of what ecologists call spatial heterogeneity or horizontal patchiness. It can be observed and mapped from the scale of soil particles or anthills up to the extent of regions and continents. As heterogeneity increases across scales and in both horizontal and vertical dimensions, the diversity of species also increases. More habitats equal more species.

The southeastern United States is a heterogeneous region at many spatial scales, which helps explain its extraordinary species richness. We need to be careful, however, in interpreting the influence of heterogeneity on species diversity when setting objectives for conservation and management. High heterogeneity and diversity at a local scale—for example, a patchwork of forest and grassland blocks only acres in size—do not necessarily translate to high diversity

at a broader scale, in part because some species avoid the edges between distinct habitat types (whereas others specialize on the edges) or require very large patches of a certain structure and composition in order to maintain viable populations. This is especially true for vertebrates associated with naturally large-patch habitats. An example is the Florida grasshopper sparrow (*Ammodramus savannarum floridanus*, plate 8), which requires substantial blocks of treeless Florida dry prairie and seldom nests successfully less than 400 meters (1,312 feet) from a forest edge. Many factors are at work to determine biological diversity; I will attempt to explain some of them in this book, as they are what make life interesting.

REFERENCES

Global and North American grasslands: Coupland 1991, Sims and Risser 2000, White et al. 2000

Climate, fire, and other controlling factors: Sauer 1950, Whittaker 1975, Axelrod 1985, Ripley 1991, Frost 1998, Jacobs et al. 1999, Lomolino et al. 2006, Staver et al. 2011b

Savanna and human evolution: Dart 1925, Leakey 1994, Truett 2010, Cerling et al. 2011

Grass-tree competition: Transeau 1935, Riginos 2009

U.S. National Vegetation Classification: http://biology.usgs.gov/npsveg/nvcs.html

Longleaf pine ecosystems: Stoddard 1969, Means and Grow 1985, Noss 1988 and 1989, Earley 2004, Jose et al. 2006, Means 2006, Peet 2006, Carr et al. 2009 and 2010

Endangered ecosystems: Noss et al. 1995, Noss and Peters 1995, Samson and Knopf 1996, Hoekstra et al. 2005

Grassland distribution in North America and the South: Quarterman and Keever 1962, Küchler (1964) 1985, DeSelm and Murdock 1993, Stout and Marion 1993, Ware et al. 1993, Barden 1997, Juras 1997, Anderson and Bowles 1999, Platt 1999, Barbour and Billings 2000, Sims and Risser 2000, Brown 2003, Peacock and Schauwecker 2003, Cech and Tudor 2005, Bridges 2006a, Orzell and Bridges 2006b, Stephenson 2011

Plant taxonomy: Weakley 2008, Ahrends et al. 2011

Natural history: Bartram (1774) 1998, Noss 1996b, Greene 2005, Fleischner 2011

Coarse-filter approach: Jenkins 1985, Noss 1987, Hunter et al. 1988, Noss and Cooperrider 1994, Noss 1996a, Kintsch and Urban 2002, Noss et al. 2002, Anderson and Ferree 2010, Beier and Brost 2010

Vegetation, ecological systems, and natural community classifications: Gleason 1926, Whittaker 1962, Nature Conservancy 1994, Comer et al. 2003, Florida Natural Areas Inventory (FNAI) 2010, NatureServe (www.natureserve.org/explorer/classeco.htm#terr_ecological)

CHAPTER 2

❧

Origin and History

> We know now what was unknown to all the preceding caravan of generations: that men are only fellow-voyagers with other creatures in the odyssey of evolution.
>
> Aldo Leopold (1949)

If I hadn't gone into the field of ecology, I likely would have ended up a paleontologist or archaeologist. As a child, nothing thrilled me more than finding exquisite fossils or Indian artifacts and learning about the ancient history of the landscape around me. I was fortunate to spend my childhood on top of the absurdly fossiliferous Cincinnatian strata of southwestern Ohio. The bedrock is Paleozoic limestone and shale, mostly of Upper Ordovician age (about 450 million years old) and packed with incredible densities of brachiopods, bivalves, cephalopods, crinoids, bryozoans, corals, graptolites, and my favorites—trilobites (e.g., *Flexicalymene meeki*). Trapped in their death sediments, the animals often are so densely packed that they pile on top of one another, with hardly any bare sediment showing. I was more familiar with these extinct creatures than with living ones, with the notable exception of the local reptiles and amphibians. I spent hours examining broken slabs of bedrock along creeks and road cuts and imagining long-extinct animals crawling about on the ancient shallow sea floor. This personal contact with deep history made the area where I lived—and my place in the world—seem much more meaningful.

The area where I grew up also was a center of the mound-building cultures: the Adena, Hopewell, and Fort Ancient peoples of the Early to Late Woodland period and beyond (roughly from 1000 BCE to 1000 CE, and up to 1650 CE for

the Fort Ancient culture). With family and on school field trips, I regularly visited burial and ceremonial mounds and other earthworks. My favorite then and today is Serpent Mound, a bizarre quarter-mile-long effigy mound of an uncoiling serpent, its head aligned with the summer solstice sunset and the coils apparently to the winter solstice sunrise and the equinox sunrise. I cannot, to this day, visit Serpent Mound without getting goose bumps, and I sometimes see it in my dreams. As a college student I volunteered for some archaeological digs, and with dental tools I dug out the skull of a passenger pigeon (*Ectopistes migratorius*) from a refuse pit in a Fort Ancient village site along the Miami River near Dayton. Picturing these mysterious people, flocks of now-extinct pigeons, and big animals such as bear, puma, elk, and bison roaming the hills around my home was entertaining, but also sad. I wished I had lived a thousand years earlier, when life was richer.

Now, as a conservationist, I am interested in history not only because it helps me appreciate my place in the world. More important in the present context, knowledge about the origin and history of southern grasslands is directly germane to decisions that conservation planners and land managers must make to conserve these ecosystems. A challenge is to help people realize the relevance of history. I suggest that by understanding how the grasslands of the South came into being, how and why they waxed and waned over time, and what factors maintained them, or failed to, we can establish a scientifically sound basis for conserving and restoring these ecosystems today and into an uncertain future.

The history of the vegetation, flora, fauna, and ecological processes of a region can be reconstructed through a variety of methods, including interpretation of fossil pollen and charcoal collected in cores from the bottom of lakes and bogs, plant macrofossils, and the bones and teeth of vertebrates. For more recent history, we can also rely on archaeological findings and the reports of early explorers, settlers, land surveyors, and naturalists. Auspiciously, the South is rich in such evidence. The vertebrate fossil record for the South over tens of millions of years and fossil pollen over tens of thousands of years are about as good as one can find anywhere. In this chapter I review the history of southern grasslands, emphasizing factors important to their origin and maintenance and based on what I think are the most scientifically defensible interpretations.

A GENERAL MODEL

As discussed in chapter 1, the South is not intermediate in precipitation between desert and forest; hence, the presence of grassland here has puzzled many ecologists and led them to surmise that it is not the natural or "climax" vegetation of

the region. If climatic conditions today or in the past cannot fully explain the existence of grasslands in the South at the time of European settlement, what factors are responsible?

Southern grasslands encompass many types of communities with unique origins and histories. Even within a defined type, say longleaf pine woodland, different abiotic and biotic factors may be most influential for maintaining community composition and habitat structure at different sites or at the same site at different points in time. One factor may be primarily responsible for creating a grassland, whereas another combination of factors maintains the same grassland today (or did until the grassland was eliminated by modern humans). A common pattern is for grasslands to develop under a period of drier climate, often with assistance from lightning-set fires, but then be maintained during wetter climatic periods by continued fire, herbivores, or unusual properties of local soils or landforms.

Human activity, especially the use of fire, is another process that should be considered—and it is an enormously controversial topic. Parts of the South were rather densely populated by Native Americans, and this was also the first region of North America explored by Europeans. Contrary to common assumptions and claims, however, it has yet to be shown that humans have created grasslands anywhere on any substantial scale. Many southern grasslands show irrefutable evidence of existence long before humans arrived in North America. The evidence of antiquity includes pre-Pleistocene fossils of grassland-associated plants and animals, as well as current biogeographic patterns, such as high endemism of grassland species in the South and disjunctions of grassland taxa between the southeastern United States and the Great Plains and the southwestern United States and Mexico.

When attempting to explain patterns in ecology, we should consider both historical and modern factors, as well as regional versus local conditions and processes. If we limit ourselves from the outset to a single scale of space or time, we will probably miss something important. A fruitful approach to untangling the factors that could create or maintain grasslands is to develop a set of a priori hypotheses ("competing models") that might explain the pattern we observe. Then we try to determine how well each model is supported by empirical evidence. In seeking to verify or falsify hypotheses, we must be impartial and not "play favorites." This is in essence the "method of multiple working hypotheses" developed by geologist T. C. Chamberlin in the late nineteenth century. In contrast to traditional hypothesis-testing, the method of multiple working hypotheses explicitly recognizes that two or more hypotheses can simultaneously be correct. One of the most

annoying attributes of scientific discourse is the common assumption that alternative hypotheses are mutually exclusive; hence, scientists line up behind their favorite hypotheses and defend them against all others, often "cherry-picking" data or references to support their case. This is the flaw of the "ruling hypothesis" approach that Chamberlin criticized. If we instead recognize that multiple hypotheses have elements of truth, we can use modern statistical approaches to make inferences from several models that are simultaneously true, to greater or lesser extents.

A general model for the origin and maintenance of grasslands in the South may help ecologists and managers figure out what factors have been, and continue to be, influential in any particular case. Figure 2.1 presents such a model and encompasses many distinct but interacting hypotheses. Any of the factors identified in figure 2.1 could have a significant influence on grassland development and persistence, depending on the type of grassland and the period of time. The arrows should not be interpreted as signifying simple cause-effect relationships. Instead, the ecological structure, function, and composition of a grassland are shaped by multiple factors operating together. Positive and negative feedback loops and mutual causality (reciprocal relationships between factors) are fundamental to the maintenance and resilience of ecosystems.
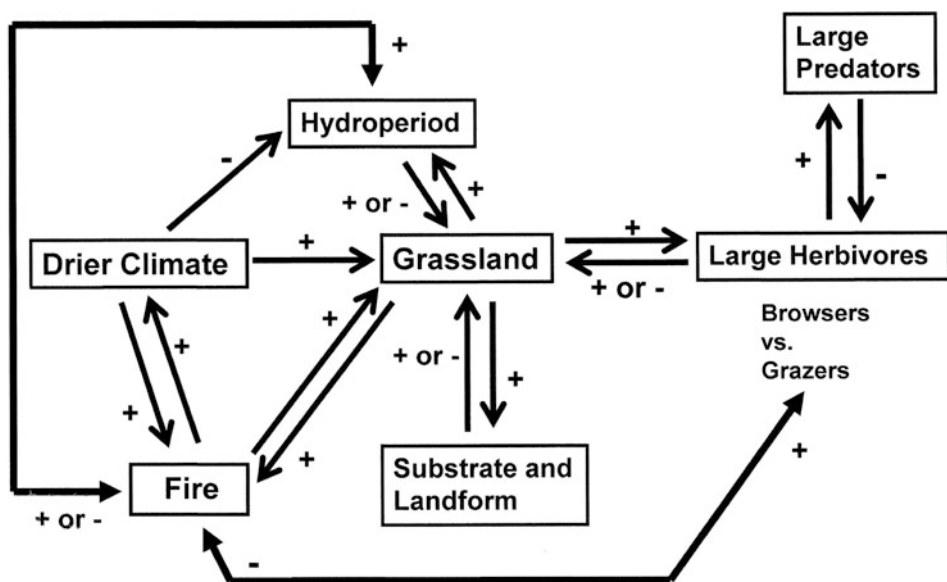
Figure 2.1. A general conceptual model for the origin and maintenance of southern grasslands. For particular cases, the influence of the factors identified here would vary widely. See text for explanation.

Following the boxes and arrows in figure 2.1, the general model suggests that

(1) Climate is important. Strong paleoclimatic and paleoecological evidence shows that climate change can convert forest to grassland and vice versa. A drop in rainfall, seasonally or annually, as might occur with tectonic uplift and rain shadow effects, or with global changes such as reconfiguration of the continents or shifts in oceanic and atmospheric circulation patterns, can favor grasses over woody vegetation. Reduced precipitation promotes grassland because grasses and associated forbs are better competitors for scarce moisture (there are exceptions to this rule, e.g., desert shrubs). Even if annual rainfall does not change much, an increase in duration or intensity of drought (i.e., increased seasonality) can kill trees or inhibit growth of tree seedlings, allowing establishment or increases in abundance of warm-season (C_4) grasses.

Edgar Transeau hypothesized that the persistence of prairies in a forest matrix in the Prairie Peninsula of the Midwest, eastward to Ohio, with outliers all the way to the Atlantic coast, can be explained by summer drought. The most recent (9,000 to 5,000 years ago) major eastward expansion of prairies occurred during the warm, dry Holocene Climatic Optimum (Hypsithermal interval), although grasslands also may have expanded during previous or subsequent dry periods. Intense summer droughts in this region have allowed patches of grassland to persist despite an overall shift to a wetter climate. Transeau predicted that if droughts intensify, prairies will expand, but if droughts weaken, prairie patches will be overtaken by forest. In support of Transeau's hypothesis, W. Britton and A. Messenger showed that, during the big drought of 1933–34 (the "Dust Bowl" years), the region of the Midwest where deep-soil moisture was inadequately recharged corresponds closely to the Prairie Peninsula. Although the impact of the Hypsithermal on grassland development in more southern regions is debated, we can reasonably assume that this or other dry periods facilitated grassland expansion. As shown by the plus sign on the arrow leading from "drier climate" to "grassland" in figure 2.1, a drier or more droughty climate favors grassland over forest.

(2) Water is important, too. Hydroperiod is the seasonal pattern of water level—a plant community's "hydrologic signature." Especially in relatively flat terrain, hydroperiod has a strong influence on vegetation, such that plant communities (and not just those traditionally considered "wetlands") have characteristic hydroperiods. In the general model (fig. 2.1) the relationship between hydroperiod and grassland is complex and variable. A drier climate reduces hydroperiod (note negative arrow), but hydroperiod could have a positive or negative influence on development or persistence of grassland, depending on

seasonal contrast and other factors. A strong contrast between the dry and wet seasons may inhibit tree establishment and promote grassland. Grassland is predicted to have a positive effect, compared to forest, on hydroperiod because with lower total leaf area, grassland transpires less water than forest (note positive arrow).

(3) Fire is a major promoter of grasslands worldwide. The increased grassiness that accompanies a shift to a drier or more droughty climate enhances the flammability of an ecosystem. Many grasses are highly flammable and encourage the ignition and spread of fire. Given an ignition source such as lightning or people, increased flammability leads to an increase in fire frequency (positive arrow in fig. 2.1), in turn producing more grassland—a textbook-perfect positive feedback loop. Increased fire also changes climate, in that smoke, by reducing evaporation from the ground, suppresses cloud formation on a regional scale. By reducing the size of water droplets to the point where they are not heavy enough to fall as rain, smoke also reduces rainfall. Fire's drying effect on climate creates an additional positive feedback cycle (see arrows) that accelerates loss of forest and expansion of grassland. The result is a shift to a new stable state that is self-perpetuating. Fire has a relationship to hydroperiod in that heavy rains and flooding reduce the probability of fire; on the other hand, wet-dry cycles favor fire by producing abundant fine fuels (i.e., grasses and other herbaceous vegetation, increasing with rainfall), which are highly flammable after they dry out. Fire can increase hydroperiod by burning down into peat and lowering the local land surface.

(4) Wind and other disturbances that kill or damage trees and open the forest canopy will tend to benefit grasses and other plants in the groundcover that require abundant sunlight (positive arrow in fig. 2.1). Many tree species of savannas and woodlands, such as long-needled pines and certain oaks, are shade intolerant (as well as fire resistant as adults). The South is a windy place, with frequent, powerful hurricanes and tornados (plate 5). Paul Gagnon and Bill Platt hypothesize that large canebrakes, an ecosystem now essentially extinct, were maintained by fire or flood following a canopy-opening disturbance such as a hurricane, tornado, or ice storm.

(5) Substrate and landform can have a strong influence on the development of grasslands. Different kinds of rock weather differently, creating a variety of microhabitats for plants. Can extreme edaphic (i.e., soil-related) conditions— such as very thin or toxic soils—sustain prairie? Yes, in certain cases, by producing physiological drought or other stress that limits colonization or survival of woody vegetation. Many southern grasslands form on shallow soils that quickly dry out in the absence of rainfall, favoring grasses over trees. Trees die

off at the margins of glades and outcrops during drought, keeping them open and sunny. Unusual rock/soil types such as serpentine reduce effective moisture availability and have toxic effects on certain plants; many grasses prosper under these conditions of reduced competition (albeit they still usually require occasional fire). Clays and other fine-particle soils with distinct "shrink-swell" or "hydroxeric" properties also tend to favor grasses and associated forbs over trees. Over time, a productive grassland can build a deep soil (positive arrow in fig. 2.1); droughts favor grasses in competition with woody plants on these soils. A recent study of tropical savannas by Corinna Riginos concluded that competition from grasses may limit tree growth as much as herbivory and fire. Landform also can favor grassland maintenance; for example, erosion on steep slopes and the hotter and drier conditions on southwest-facing slopes favor grassland over forest (e.g., plate 14). The opposite is true in more sheltered landscape positions (hence, positive and negative arrows in fig. 2.1).

(6) An increase in grassland (including savannas and woodlands) across a region favors large grazing and browsing herbivores. These animals, through their feeding, rooting, and tree-destroying activities, create a positive feedback loop that favors savannas (positive arrows in both directions in fig. 2.1). Tree destruction by elephants, for example, is well known, and there were elephants (gomphotheres, mammoths, mastodons, and other proboscideans) in the South for a long time. Land managers have discovered that management of prairies with fire alone has a positive effect on grasses, but many forbs are declining, apparently because they are adapted to grazing and require the physical disturbance of trampling, digging, or wallowing to survive alongside superior competitors. Haying or mowing, which simulates herbivore activity in part, tends to increase forb diversity. Native large herbivores (most recently bison) are now missing from most southern grasslands, so this feedback loop no longer operates naturally.

(7) Large predators were probably important historically in southern grasslands (i.e., the negative arrow from predators to herbivores in fig. 2.1 suggests density-dependent top-down regulation). The largest herbivores of the Pleistocene may have been immune to predation as adults, but their young would have been vulnerable to a panoply of large, fierce carnivores. Without predators to keep them in check, megaherbivores would graze heavily, to the point of reducing fire frequency, as indicated by the negative arrow from herbivores to fire. A reduction in fire can release trees from competition and result in increased tree cover—unless controlled by browsing herbivores. Past a certain threshold, heavy grazing reduces the vigor of grasses and can lead to desertification, including replacement of grasses by shrubs, trees, and other

plants that are well defended by thorns or toxins against herbivores. Top–down regulation by large carnivores could prevent overgrazing and favor healthy grasslands. Like large native herbivores, however, large carnivores are reduced across the South, so any negative feedback control on herbivory (e.g., by live-stock) is now weak.

A conceptual model such as figure 2.1 allows predictions about the rel-ative influence of different controlling factors in any particular case. One might ask why there is no box or arrows for humans in figure 2.1. The answer is that this would be redundant. Humans, directly or indirectly, and over short or long periods of time, influence every factor and relationship depicted in the figure.

GEOLOGY, PHYSIOGRAPHY, AND PRE-NEOGENE HISTORY

Eastern North America is far less diverse topographically than the American West, but the topography is much older. The highest eastern mountains are the southern Appalachians, reaching 6,684 feet on Mt. Mitchell in North Carolina and 6,642 feet on Clingmans Dome in Tennessee. The Appalachians are an ancient mountain chain, first uplifted some 480 to 460 million years ago during the Ordovician Period. A later and principal uplift of the Appalachians occurred 300 to 250 million years ago during the middle Pennsylvanian to late Perm-ian periods. Subsequent to this uplift, the Appalachians underwent 250 million years of erosion, wearing them down to the rounded domes and relatively low elevations we see today. A frequently heard claim is that the Uwharrie Moun-tains, now in the Piedmont of North Carolina, were formed more than 500 million years ago, or even a billion years ago, but I can find no peer-reviewed confirmation of this claim. One reputable geological interpretation (from R. H. Kesel in 1974) is that the Uwharries are "inselbergs," the erosional remnants of a higher Miocene peneplain. The bedrock of the Uwharries is several hundred million years old, but the erosion that created the "mountains" is geologically young. The Ouachita Mountains of western Arkansas and adjacent Oklahoma, with a high point of 2,753 feet on Mount Magazine, arose between 325 and 310 million years ago during the Pennsylvanian Period and are geologically an outlier of the Appalachians. By contrast, the high western cordilleras are much younger, all arising between late Cretaceous and Pliocene times. For example, the Rocky Mountains began to rise around twenty million years ago; uplift

intensified twelve million years ago and was most dramatic between seven and four million years ago—just yesterday by geologic standards.

Other than the Appalachians, the Ouachitas, and a few isolated peaks—granite flatrocks and other hills, bluffs, knobs, and "monadnocks" (i.e., a Native American term for inselbergs) in the Piedmont—the South has modest topography. In Florida, the highest peak is Britton Hill near the town of Lakewood in the Panhandle, just south of Florala, Alabama, and a whopping 345 feet above mean sea level. A small park I visited, Lakewood Park, has a monument marking the spot: the lowest high point of any US state. In the Florida Peninsula, the highest point is Sugarloaf Mountain at 312 feet. This peak is on the northern section of the Lake Wales Ridge, which runs 150 miles north to south down the peninsula and is revered by biologists as a hotspot of endemism, especially within the Florida scrub community. The Lake Wales Ridge was an archipelago during times of high sea level, perhaps most recently about 2.6 million years ago, at the beginning of the Pleistocene Epoch. The isolation of these islands from each other and the mainland led to speciation within a number of taxa. In contrast to low-lying Florida, neighboring Alabama has a high point of 2,413 feet on Cheaha Mountain, which is part of the Talladega Mountains, the far southern segment of the Blue Ridge Physiographic Province. You can drive to the top and have lunch, which I did with my family on a hot July day in 2008. Neighboring Georgia has its high point in the Blue Ridge near the North Carolina line: Brasstown Bald at 4,784 feet. You can also drive to that peak. Being able to drive to mountain peaks is a product of industrial civilization that I find disconcerting.

Other major physiographic features of the southeastern United States are rivers and their valleys, and these evidently have had as strong an influence on biogeographic history as the mountain ranges. The Mississippi River and its southern tributaries, including the Ohio, Tennessee, Cumberland, Arkansas, and Red, drain most of the study area of this book. The Mississippi Alluvial Plain is the remnant of a large embayment (in turn, a remnant of the Cretaceous Sea) that served intermittently as a dispersal barrier for grassland and xeric-adapted taxa between the southeastern United States and areas westward. Rivers draining directly into the Atlantic Ocean and Gulf of Mexico, several of which have their headwaters in the Appalachians, also had a significant influence on the biogeographic history of the South. Paul and Hazel Delcourt of the University of Tennessee suggest that some of these river valleys served as dispersal corridors and refugia for warm-mesic species during the glaciations of the Pleistocene. In the Florida Panhandle, several wildflowers associated with mesic deciduous forest of the Appalachians and northward (e.g., columbine [*Aquilegia*

canadensis], cutleaf toothwort [*Cardamine concatenata*], May apple [*Podophyllum peltatum*], and blue phlox [*Phlox divaricata*]) occur as disjunct populations in counties along or very near the Apalachicola River, whose tributaries, the Flint and Chattahootchee, have their headwaters in the Blue Ridge Province of northern Georgia. The Apalachicola, like the Mississippi, also served as an east-west dispersal barrier or filter, as evidenced by genetic discontinuities within taxa on either side.

The wide open pine savannas and dry prairies of the Florida Peninsula are evocative of African savannas. Curiously, geologic evidence suggests that Florida was part of Gondwana (most likely what is now West Africa) during most or all of the Paleozoic. This is shown by several lines of evidence: (1) the correspondence of fossils, especially marine invertebrates, in sediments from the Suwannee Basin, the lower boundary of which is 504 million years ago, with those of Gondwana; (2) a paleolatitude (determined by paleomagnetic inclination) that matches West Africa rather than North America (the latter being farther south at that time); and (3) the correspondence in ages of detrital minerals between Florida and West Africa. Florida separated from Africa when Gondwana broke apart and the Atlantic Ocean formed at the end of the Paleozoic. Basement rocks of early Triassic age, the Tallahassee graben, apparently originated at the time Florida separated from Gondwana. The suspected suture zone where Florida connected to North America is the Brunswick magnetic anomaly found today in southern Georgia and Alabama.

By the Cretaceous Period of the Mesozoic Era, all of the major groups of life-forms—microbes, fungi, gymnosperms (including the conifers), angio-sperms (flowering plants), and all the major invertebrate taxa and vertebrate classes—had evolved. Flowering plants underwent an explosive radiation dur-ing the Cretaceous in coevolution with insect pollinators and herbivores. Grasses (Poaceae), the fourth largest family of plants with ca. 11,000 species, were thought to have first appeared between 70 and 55 million years ago. Recent evidence, in the form of phytoliths (silica bodies produced in epider-mal cells of grasses and a few other plants) embedded in coprolites (fossilized feces) from dinosaurs, suggests an earlier Cretaceous origin. Evidence also sug-gests that grasses first evolved in tropical and subtropical forests of the South-ern Hemisphere. Grasses were present in North America by the Paleocene/Eocene, with the major diversification occurring in open habitats during the mid-Cenozoic (around the beginning of the Neogene), with all major lineages present by mid–Miocene times.

The landscape of what is now the southeastern United States was quite different during the Cretaceous from what we see today. Most striking, by the

Middle Cretaceous (ca. 100 million years ago), a shallow midcontinental sea connected the Arctic Ocean to the Gulf of Mexico, separating western North America from eastern North America and Europe. This separation allowed numerous taxa, including many associated with grasslands, such as pines, to evolve independently. Sediments from the ancient Cretaceous Sea today support some significant grasslands of the South, including the Black Belt Prairie of Alabama and Mississippi and other blackland prairies of Louisiana, Arkansas, Texas, and Oklahoma. The soils derived from these sediments are typically chalky shrink-swell clays where grasses compete more successfully with woody plants. The Cretaceous Sea receded at the end of the Cretaceous, allowing floras and faunas from eastern and western North America, which had been separated for millions of years, to begin reconnecting; however, the Mississippi Embayment, a remnant of this sea, still posed a substantial barrier at low latitudes.

The Cretaceous was a period of very warm climate, correspondingly high sea level (which partly explains the midcontinental Cretaceous Sea), and tropical broad-leaved evergreen vegetation over much of North America. For much of geological history temperatures and sea level have been higher than today. Over the past few million years, only during glacial intervals was sea level lower than it is now. The present rise in sea level, tied to human-induced global warming, is in a sense bringing us back to a more "normal" land-sea configuration. Unfortunately for species and natural communities in low-lying coastal areas, current sea-level rise is increasingly rapid; most ominously, human land uses and infrastructure make it difficult for species to move away from the coasts. Natural history information on the habitat affinities and dispersal capacities of species will be crucial for developing adaptation strategies that reduce extinction rates during climate change and sea-level rise.

After a large meteorite struck the Yucatan coast 65 million years ago, an estimated one half of all species on earth went extinct. A "global winter," caused by dust ejected from the impact blocking out sunlight, made life challenging. Nevertheless, there were survivors within almost all major groups of organisms. Global climate rebounded to equable conditions relatively quickly. Among plants, ferns appear to have recovered the fastest and dominated many regions. The dinosaurs, as most people know them, went extinct, but many smaller dinosaurs—birds—survived. Mammals, released from competition and predation from nonavian dinosaurs, diversified; as we shall see, much of that diversification was later tied to the global expansion of grasslands during the Miocene.

Some periods of the distant past were amazingly similar to current conditions in the South. After rebounding from the meteorite incident, the climate of the early Paleogene Period (Paleocene through Early Eocene epochs) was

warm, with global temperature and humidity reaching maximal levels in the Early Eocene, about 52 million years ago. Temperatures then dropped relatively rapidly in the Middle Eocene. Pines were apparently limited to a series of refugia at this time, with one refugium being the southeastern Coastal Plain. Alan Graham, in *Late Cretaceous and Cenozoic History of North American Vegetation*, notes that the Middle Eocene, with its cooler and more seasonal winter–dry climate, represented a shift from "hothouse" to "icehouse" conditions and was "an important time in the modernization of North American plant communities." In the South the Middle Eocene was marked by a replacement of tropical rainforest by a semideciduous tropical dry forest; oak forest or woodland occurred on the Gulf Coastal Plain.

Graham describes some vegetation from the Middle Eocene much like that in Florida today: "On sandy sites *Pinus* and palmetto-like palms (*Sabal-Serenoa* type) were present and represent an earlier version of the modern sand pine scrub of the pine woods association." The cooling trend of the Middle Eocene was accompanied by an overall drying and a lowering of sea level, which led to a southward retreat of the Mississippi Embayment; by the end of the Paleogene, this remnant of the Cretaceous Sea had retreated to some 300 to 500 kilometers (186 to 310 miles) inland of the present coastline.

NEOGENE AND QUATERNARY HISTORY

Now we move into the period of time when grasslands similar to those we find remnants of today developed across the South. In this section I review the history of vegetation and associated flora and fauna, with particular attention to grasslands, from the Neogene Period (23 to 2.6 million years ago, including the Miocene and Pliocene epochs) through the Quaternary Period (2.6 million years ago to present, including the Pleistocene and Holocene epochs). During this time span substantial grasslands developed in the southeastern United States, thereafter waxing and waning with changes in climate and, ultimately, the influence of humans.

Neogene History (23 to 2.6 Million Years Ago)

By the Early Miocene, remnants of the Paleogene tropical flora remained only along the southern coasts. Components of pine woodland vegetation were present across a broad area of the southeastern United States, along with oak–chestnut, oak–hickory, southern mixed hardwoods, and floodplain forest. There is little evidence for extensive grassland at this time, though grasses were pres-

ent. Grassland began its major global expansion during the Middle Miocene, as global climate became cooler and more seasonal, with increased droughtiness. The expansion began with an increase in C_3 (cool season) savanna and woodland and was followed in the Late Miocene by a shift to C_4 (warm season) savanna and prairie over much of North America and the world. From the dentition and morphology of fossil vertebrates, and from stable isotope ratios in their tooth enamel (a very resistant material), we can infer whether they inhabited open grasslands, savannas, woodlands, or closed forests, and whether they ate primarily woody plants or grasses. As reviewed by Christine Janis and coauthors, the diversity of North American ungulates (hoofed mammals) peaked in the Middle Miocene, when there was a mix of grazing species with high-crowned teeth, browsing species with low-crowned teeth, and species with mixed diets and medium-crowned teeth (fig. 2.2). The grasslands at this time were primarily C_3 woodlands and savannas with no modern analogs.
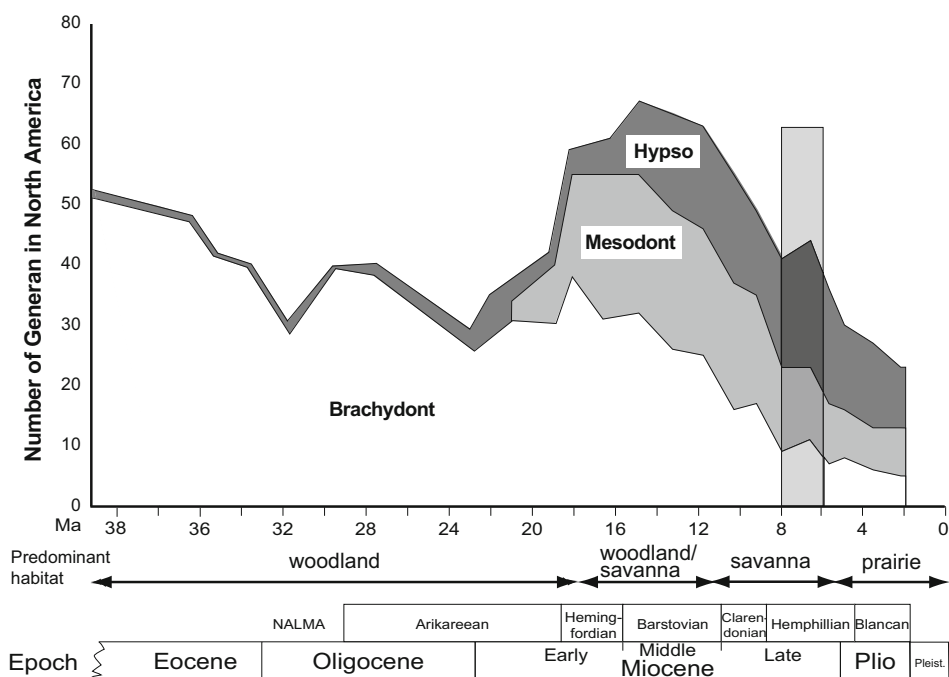
Figure 2.2. Continent-wide generic richness of North American ungulates, grouped by tooth crown height. Brachydont teeth are low-crowned and characteristic of browsers, which feed mostly on woody vegetation. Hypsodont teeth (Hypso) are high-crowned and adapted to grazing on grasses. Mesodont teeth are medium-crowned, indicating a mixed diet. The rectangle in the Late Miocene indicates the C_3/C_4 grass transition. Note that ungulate richness peaked in the Middle Miocene, a period characterized by C_3 woodlands and savannas. Reprinted from Janis et al. (2002) with the permission of Elsevier.

Modern laboratory techniques, such as stable isotope analysis, allow naturalists to understand vegetation history in much greater detail than was possible earlier. Plants with C_3 versus C_4 photosynthetic pathways contain different ratios of heavy and light stable isotopes of carbon in their tissues, and these signatures are passed on to the tissues of the herbivores that eat them. Evidence from stable carbon isotopes in the fossil tooth enamel of herbivores, supplemented in some regions by isotopes in fossil soils, document an explosion of C_4 grasses in the Late Miocene, six to eight million years ago (fig. 2.3). As described by
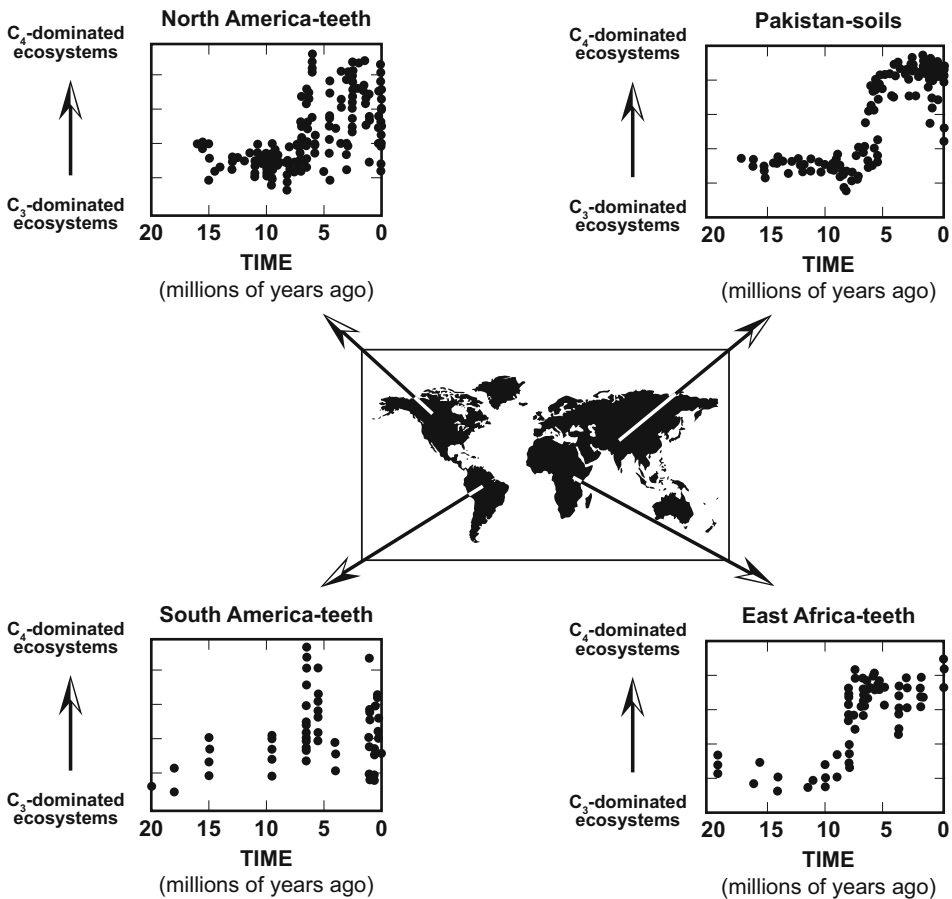
Figure 2.3. Evidence for the global explosion of C_4 (warm-season) grasses around eight million years ago, accompanied by a large-scale replacement of C_3 forests, woodlands, and savannas by C_4 savannas and prairies. The stable carbon isotopes recovered from the teeth of fossil vertebrates tell whether the animals fed on C_4 grasses or C_3 grasses, forbs, or other plants. The Pakistan example (upper right) shows that the dramatic increase in C_4 grasses is also recorded in some fossil soils. At this same time around 6,000–8,000 years ago, charcoal increased in ocean sediments a thousandfold. Adapted from Beerling (2007).

David Beerling in *The Emerald Planet*, this dramatic increase in C_4 grasses has been linked to a global-scale replacement of forests and woodlands by savannas and prairies in a positive feedback relationship with fire. The original competitive edge of C_4 over C_3 plants was likely favored by low atmospheric carbon dioxide concentrations, because C_4 plants concentrate carbon dioxide much more effectively in their cells for photosynthesis. Indeed, C_4 plants were more abundant during glacial maxima of the Pleistocene, when carbon dioxide concentrations were low (i.e., not much greenhouse effect). Paradoxically, however, because they do not need to keep their stomata (leaf pores) open as long to obtain sufficient carbon dioxide, C_4 plants have greater water-use efficiency and are highly competitive under warm, moisture-stressed conditions. Hence, as Beerling points out, "CO_2 starvation" does not explain the dominance of C_4 grasses over fire-sensitive vegetation under dry or warm climatic conditions.

As C_4 grasses gained a foothold in many ecosystems of the Late Miocene, their high flammability led to increased fire, which killed fire-sensitive trees and favored grasses and other fire-tolerant species associated with grasslands; these fire-adapted species included pines and oaks that form woodland/savanna vegetation, as well as the grasses and forbs of prairies. The worldwide increase in flammable ecosystems and frequency of fire during the same period that C_4 grasses exploded in abundance is confirmed by a thousandfold increase in charcoal in deep ocean sediments during this time (note: this was in spite of an abundance of megaherbivores, which tend to reduce fine fuels and fire frequency). The inhibition of tree recruitment by fire, facilitated by increases in grass cover during droughts, and subsequent competitive effects of grasses on tree seedlings may be more important than low carbon dioxide levels in favoring grasslands over closed forests. William Bond and Guy Midgely propose that as trees die in response to drought, grasses establish or increase in the gaps, increasing combustible loads of fine fuels and driving the positive feedback process. As noted by Bond and coauthors in 2005, fires fueled by the increase in C_4 grasses in the late Miocene essentially split biotas into fire-tolerant and fire-intolerant taxa. Grasslands prospered relative to forests.

Fossils tell engaging stories, and as vertebrate paleontologist S. David Webb pointed out in *Ecosystems of Florida*, "No state east of the Mississippi, and few to the west, can rival the abundance and variety of Florida's Cenozoic fossil heritage." If you ever need convincing that the Coastal Plain had considerable grassland for a long period of the Cenozoic, visit the vertebrate paleontology gallery at the Florida Museum of Natural History in Gainesville. I have spent hours there. This impressive exhibit leaves no doubt that large animals associated with savannas, woodlands, and prairies roamed Florida (and presumably

much of the rest of the Coastal Plain) for millions of years, up until their relatively abrupt disappearance soon after the first humans arrived around 14,000 to 15,000 years ago. Some of these megaherbivores—the tree destroyers—probably played a large role in maintaining grassland vegetation.

Vertebrates associated with grassland show up in the oldest terrestrial fossils in Florida, from the Middle Oligocene, about thirty million years ago. This assemblage, called the "I-75 Local Fauna" because it was discovered along Interstate 75 near Gainesville, includes fossils of a horse, a tortoise, and other animals associated with open environments. Early Miocene faunas are especially well represented in Florida. The richest Early Miocene site, Thomas Farm in Gilchrist County, is world-renowned for its collection of more than eighty vertebrate taxa. The terrestrial species, which include three kinds of horses, a rhinoceros, a horned cameloid, a peccary, an oreodont, a pocket mouse, a beardog, a Gila monster (*Heloderma* sp.), and a tortoise, suggest the environment was largely open, probably a mosaic of savanna, woodland, and forest. Middle Miocene sites are also rich in Florida and include many of the same or related taxa represented at Thomas Farm, such as Gila monster; *Geochelone* (giant tortoise); horses; camels; a giant ground sloth; and two elephant-sized proboscideans, *Gomphotherium* and *Miomastodon*. The horses and rhinoceros probably ate mostly grasses, whereas most other species were mixed feeders. These fossils suggest a mosaic of subtropical forest and savanna at that time.

A spectacular fossil site outside of Florida was discovered in the year 2000 in northeastern Tennessee, near the town of Gray, when unusual deposits turned up during a road-widening project. Called the Gray Fossil Site, and still barely excavated, it has yielded an amazing Late Miocene/Early Pliocene assemblage dating from 7 to 4.5 million years ago. When I visited the museum (which, ridiculously, was built on top of part of the unexcavated fossil site), I learned that this site has already produced the world's largest concentration of tapir fossils, the most complete skeleton of an ancient rhinoceros (*Teleoceras*) in eastern North America, shovel-tusked elephants, peccaries, and a new species of herbivorous badger. These animals indicate a mixed landscape of forest/woodland and savanna. Also found were remains (including a near-complete skeleton) of a new genus and species of red panda (*Pristinailurus bristoli*). I find this discovery tantalizing because red pandas have a specialized diet of bamboo. This suggests that canebrakes—stands of the American bamboo, *Arundinaria* sp. or an extinct relative—were present in the Late Miocene/Early Pliocene of the South.

The relatively brief Pliocene epoch (5.3 to 2.6 million years ago) shows a continuation of savanna-associated vertebrates in Florida, including taxa that had already gone extinct in the Great Plains. Webb interprets this as showing

that the well-watered subtropical savannas of Florida retained browsers as well as grazers during this time, whereas the Great Plains became arid and converted to prairie, thus losing browsers and mixed feeders. A long gap in the vertebrate fossil record then occurs in Florida, but Middle Pliocene sediments contain plant pollen suggesting a return of warmer temperatures; in Florida the trend was toward pine, grass, palms, and scrub vegetation, with tropical elements along the coasts. Late Pliocene vertebrate fossils show grazing and browsing species suggestive of a savanna/prairie environment, including horses, a proboscidean, and an abundance of pronghorn antelope (the family Antilocapridae, endemic to North America). Pronghorns are my favorite living ungulate. They can run as fast as cheetahs, up to around seventy miles per hour. It is no coincidence that a cheetah (*Miracinonyx*)—presumably the main predator of pronghorns, which selected for the latter's speed—also shows up in Florida fossils from the Pliocene and Pleistocene.

Quaternary History (2.6 Million Years Ago to Present)

The Quaternary Period comprises the Pleistocene and Holocene epochs, the most recent time in earth's history. The Pleistocene was characterized by a series of glacial-interglacial cycles, including eight over the last 740,000 years. During glacial maxima, sea level was about 120 meters (394 feet) lower than today and the width of the Florida Peninsula more than doubled, extending a hundred miles or more westward into the Gulf of Mexico (fig. 2.4). The east-west running Gulf coastline extended southward, with southern Louisiana and adjacent Texas at the same latitude as central Florida. As I discuss later, this broad extension of the Gulf Coastal Plain favored the dispersal of xeric-adapted western taxa into the Southeast (an invasion that began as early as the Middle Miocene). In contrast, during interglacials, sea level was much higher, around six meters (twenty feet) higher during the most recent interglacial, 120,000 years ago. The ancient beach on which I live in Chuluota, Florida, was on the Wicomico shoreline, which dates from the Early Pleistocene. The onset of the Holocene reflects the time when the effects of the last glaciation (the Wisconsinan) were essentially over and the present interglacial interval began. The demarcation between the Pleistocene and Holocene is now officially 11,700 years ago, as ratified in 2009 by the International Union of Geological Sciences; it is based on relatively abrupt changes in physical and chemical parameters within Greenland ice cores.

Scant direct information is available on vegetation change during the Early and Middle Quaternary in the South. Much can be inferred, however, from the fossils of vertebrates that remain diverse and abundant during this period.
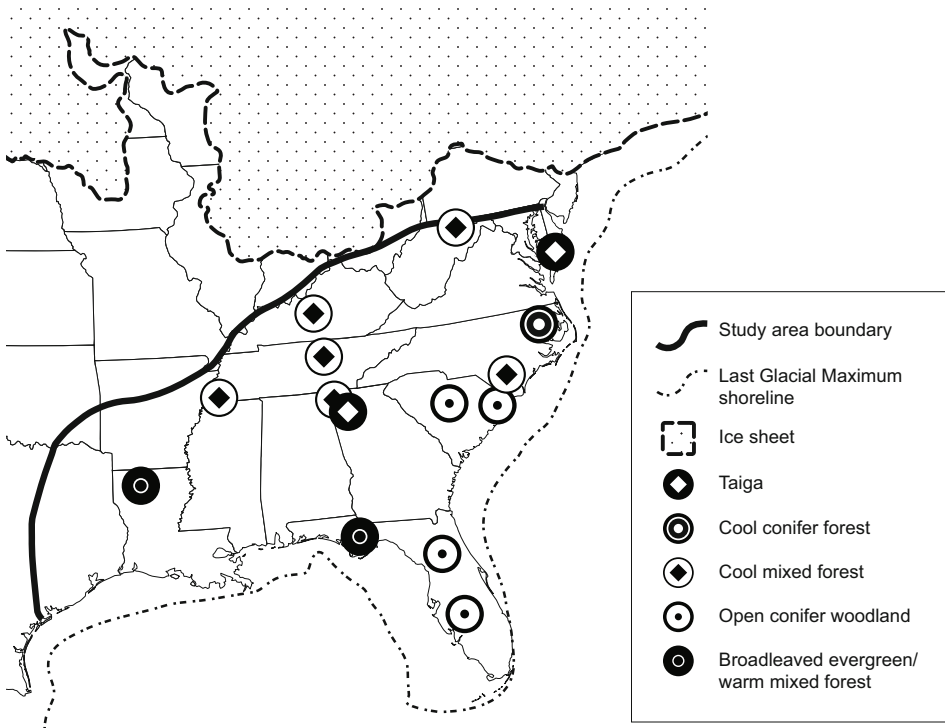
Figure 2.4. Shoreline, Laurentide ice sheet, and vegetation biomes (as suggested by fossil pollen samples from sites indicated by symbols) of the Last Glacial Maximum, 18,000 years ago. Adapted from Williams et al. (2000), who raised pollen thresholds to reduce the probability of misassignments, with full-glacial shoreline and ice sheet margin adapted from Delcourt and Delcourt (1981).

In Florida, a large grazing glyptodont (*Glyptotherium arizonae*), related to sloths and armadillos, was present 2.5 to 1.5 million years ago, and a grazing species, *Holmesina floridanus*, from a related group, the pampatheres, lived here from 2.2 to 1 million years ago. A Pleistocene horse (again, a grazer) and a large-headed llama (a mixed feeder) survived until the end-Pleistocene extinctions. These and other megafauna, including bison, tapir, mastodons, mammoths, giant ground sloths—and a condor (*Gymnogyps kofordi*), which fed on their carcasses—suggest a continuation of grassland and mixed environments through the Pleistocene.

In contrast to the Early and Middle Pleistocene, numerous sites with fossil pollen from the Late Pleistocene and Holocene occur in the South, as far back as 62,000 years ago. The longest and most continuous record of Quaternary vegetation is from lake cores in the Coastal Plain, particularly from peninsular Florida, although other sites across the South have yielded information. Figure

2.4, based on a paper in 2000 by John Williams and colleagues, infers biome types during the Last Glacial Maximum, 18,000 years ago, from fossil pollen collected at multiple sites, including fifteen sites within my study region. This figure makes no attempt to interpolate biome type between sites, which can be questionable. Vegetation ranges from boreal (taiga) and cool conifer forest in the northern part of my study region, through cool mixed forest, to broad-leaved evergreen/warm mixed forest and open conifer woodland (i.e., similar to the natural vegetation today) in the southern part of the region. This analysis confirms earlier studies suggesting the persistence of temperate vegetation across the lower Coastal Plain and temperate to subtropical vegetation in the Florida Peninsula.

The ecotone between boreal and temperate ecosystems, around 33 degrees to 34 degrees N latitude, was sharp during the Last Glacial Maximum. Spruce pollen has been found as far south as Camel Lake (30° 16' N), in the Florida Panhandle, occurring in sediments from a cold period 14,000 to 12,000 years ago and mixed with pollen from oak, hickory, beech, and other temperate trees. Most of the lower Coastal Plain was presumably temperate hardwoods during much of the Pleistocene, except peninsular Florida, which was largely pine/grassland (woodland) and oak scrub. At around 12,500 years ago a temperature tolerance threshold for boreal taxa was reached and boreal forests were gradually replaced by temperate vegetation across the South. An important finding from paleoecological studies, however, is that biome-scale reconstructions can be misleading. Not only are fine-scale vegetation mosaics not captured by such maps; more fundamentally, species respond individualistically to environmental change, with many past associations of species having no analog in the modern vegetation.

The pollen record for Lake Tulane, within the town of Avon Park on the Lake Wales Ridge of central Florida, extends back 62,000 years (fig. 2.5). These data show that the Florida Peninsula remained temperate or warmer throughout the glacial–interglacial cycles, as was suggested earlier by the Delcourts for the lower Coastal Plain in general. Based on the Lake Tulane data, Eric Grimm and coauthors reported in a 2006 paper that the full-glacial climate of peninsular Florida was warm and wet, as it is today, and that

> the Pleistocene flora of the Lake Wales Ridge is similar to today. Only the quantities differ. The Lake Tulane record does not indicate major shifts in range distributions. Although more northern species of *Pinus*, *Quercus*, or *Carya* may conceivably have appeared during the Pleistocene, no identifiable northern taxa occurred.
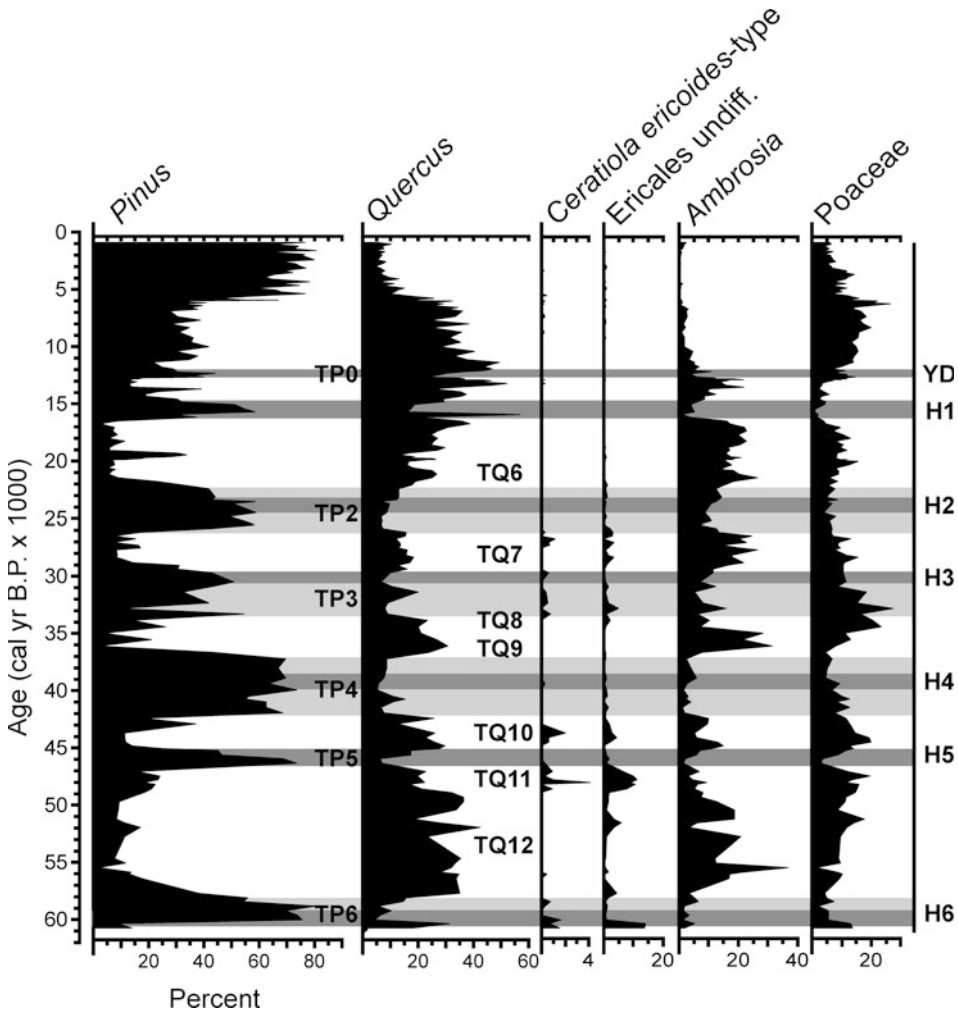
Figure 2.5. Fossil pollen record from Lake Tulane in central Florida (Avon Park on the Lake Wales Ridge) over the last 62,000 years. Note fluctuating dominance of pine (*Pinus*) vs. oak (*Quercus*) in response to glacial/interglacial cycles (see text for explanation). Courtesy of Eric Grimm, adapted from Grimm et al. (2006).

It was a surprise for Grimm to discover, based on pollen analysis, that the stadial (glacial advance) periods during the last 62,000 years were warm and wet; earlier studies had suggested that stadial periods were cool and wet. A persuasive hypothesis for why stadial periods in Florida (and, by extension, other portions of the lower Atlantic and Gulf Coastal Plain near the ocean) remained warm is that, when the northern part of the North Atlantic Ocean was gripped in full-glacial frigid conditions, the Gulf Stream shut down. The Gulf Stream acts as a heat conveyor belt; when it shuts down, heat is retained in the lower

latitudes of the Atlantic, Gulf of Mexico, and Caribbean Sea. Recalling that the east-west Gulf coastline lay as much as one hundred miles south of its present position, at about the same latitude as central Florida, during stadial periods of low sea level, we can infer that areas close to the coast were quite warm, likely as warm as the Lake Tulane site. No direct evidence exists of the vegetation near the coast during such times, however, because this area now lies inaccessibly some 120 meters (394 feet) below the sea surface.

What is the history of the ecosystem that dominated the Coastal Plain at the time of European settlement—longleaf pine? A common myth is that the longleaf pine ecosystem is very young, developing only over the last 5,000 or so years; it is often added that this ecosystem is a "cultural ecosystem" that arose in response to human-set fires. According to fossil pollen data, the most recent period of pine dominance of the Coastal Plain indeed began around 6,000 to 5,000 years ago. Looking at longer-term data, however, periods of pine dominance and oak dominance alternated in cycles of 5,000 to 10,000 years over tens of thousands of years in the Florida Peninsula (fig. 2.5) and probably in other areas of the lower Coastal Plain that are now submerged. A Pleistocene refugium for longleaf pine in the Florida Peninsula seems likely, especially given the specialized adaptations to frequent fire seen in longleaf pine (e.g., the extended seedling or "grass" stage) and its codependent species (see chap. 5). Evolution of such extreme traits takes time and is not likely to happen over just a few thousand years.

The charcoal record is poor for the Coastal Plain, but available data suggest low charcoal influx during the Last Glacial Maximum. This may seem incompatible with the idea that longleaf pine and other fire-dependent ecosystems (e.g., scrub) dominated the Florida Peninsula at this time, but it is consistent with the hypothesis that large populations of megafauna kept fine fuel loads low, reducing fire frequency during the Late Pleistocene. When these animals declined and ultimately disappeared, fire probably assumed the role of maintaining savanna conditions as fine-fuel loads rapidly recovered. Research reported in 2009 by Jacqueline Gill and colleagues, from fossil pollen/spore sites in Indiana and New York, shows that megafaunal populations collapsed between 14,800 and 13,700 years ago, before the final extinctions around 13,500 to 13,000 years ago. As megaherbivores declined, charcoal in sediments increased, indicating increased fire frequency. This and a number of other recent studies suggest that the extinction of herbivores was not a rapid "blitzkrieg" of overhunting by people of the Clovis culture, who are not known before 13,000 years ago. Rather, pre-Clovis people were also efficient hunters of such large beasts as mammoths and mastodons and may have been

responsible for a gradual collapse of megafaunal populations over a period of 1,000 years or more before the Clovis people arrived. Nevertheless, the Clovis may have dealt the final blow.

In a 1998 paper, Schmidtling and Hipkins speculate that "during the late Pleistocene, longleaf pine (*Pinus palustris*) was undoubtedly absent from the lower Coastal Plain of the southeastern United States and the area was dominated by a type of boreal forest (Watts 1983)." On the basis of allozyme (different forms of enzymes) data showing a longitudinal decrease in genetic diversity from west to east, Schmidtling and Hipkins propose that longleaf pine entered the southeastern Coastal Plain at the close of the Pleistocene from a single refugium in southern Texas or northeastern Mexico. This is conceivable, but unlikely. Schmidtling and Hipkins misinterpret Watts, who never stated that the lower Coastal Plain was dominated by boreal forest during glacial maxima; his 1983 paper and others show temperate vegetation in Florida during stadial periods of the Pleistocene. Watts described the Last Glacial Maximum pollen flora of a site in north-central Florida (Sheelar Lake) as "up to 80% *Pinus*, with *Quercus* and *Carya* present in significant quantity.... Herbs, especially herbs of prairies and sand hills, make up 10% or more of the pollen." Watts concluded (and later confirmed) that although *Picea*, mixed with temperate deciduous trees, may have reached the Gulf coast (as we know it today—not the Gulf coast in its southward glacial position), he described pure boreal vegetation only for sites north of about the 33 degrees to 34 degrees N latitude ecotone identified by the Delcourts.

Based on macrofossil evidence, Jonathan Overpeck and colleagues concluded that southern pines in the Southeast were restricted to Florida until about 9,000 years ago, "when southeast pine forests, similar to modern forests, spread northward." With the Coastal Plain extending far out into what is now the Gulf of Mexico during glacial intervals, however, pine savannas could have occupied a broad range of longitude to the West Gulf Coastal Plain of Louisiana and Texas. David Webb surmised that the Early Pleistocene was marked by "extensive development of longleaf pine habitats," but the species-level identity of the pines has not been verified. If the ancient pine-dominated vegetation in Florida was not at least partially longleaf pine, it must have included a species very similar ecologically, perhaps south Florida slash pine (*Pinus elliottii* var. *densa*). As Bill Platt and Bruce Means have pointed out, the presence of longleaf pine-associated fauna, including the highly specialized red-cockaded woodpecker (*Picoides borealis*), in deposits 180,000 to 120,000 years old in central Florida, strongly suggests ancient vegetation not very different from that at the time of European settlement.

The antiquity of the longleaf pine–associated grassland flora in the Coastal Plain is also suggested by the high level of plant endemism and monotypic genera found there (see chap. 3).

DISJUNCTIONS AND THE GULF COASTAL CORRIDOR

One of the most intriguing biogeographic patterns of the South is the presence of species in the eastern part of the region, especially Florida but also north to Virginia, whose closest relatives are in the West, including the Great Plains, the southwestern United States, California, and Mexico. Some of the eastern taxa are still extant, whereas others went extinct during the Pleistocene or earlier. In most cases there is a gap between the western and southeastern representatives, making the eastern taxa disjunct, while sometimes one or more species bridge the gap. Most of the disjunct eastern representatives of western taxa are adapted to sandy habitats, which are "physiological deserts" because of their low water availability; their western relatives inhabit areas of arid to semiarid climate.

These fascinating disjunctions are best explained by a long-term, though intermittent, presence of savanna in the lower Coastal Plain along a Gulf Coastal Corridor. This corridor was first proposed by David Webb in 1977, on the basis of vertebrate fossils, and was further discussed in his 1990 book chapter. During the Miocene, a savanna flora known as the Madro-Tertiary Geoflora developed, with its center on the Mexican Plateau. Savanna-adapted vertebrates of that period were distributed from Mexico through the Chihuahuan Desert to the southern Great Plains; from there, by the Middle to Late Miocene, the fauna had spread eastward along the Gulf coast to Florida. The continuity of savanna apparently persisted through most of the Pliocene and into the Early Pleistocene. As shown by Peter Meylan in 1982, some thirty-one species of Early Pleistocene xeric-adapted herpetofauna from Inglis, Florida, document a link between Florida and the semiarid West.

Evidence of this ancient connection of xeric-adapted plants and animals can be seen in patterns of disjunction of many taxa (table 2.1). The Gulf Coastal Corridor would have been especially wide—and the distance between peninsular Florida and Texas much shorter—during times of lower sea level, such as during the Late Miocene and the Pleistocene glacial maxima, when the Gulf coastline extended much farther seaward (and for the Florida Peninsula, westward) (fig. 2.4). The continuity of savanna between Florida and the West weakened considerably by the mid-Pleistocene as the mesic Mississippi Alluvial

Table 2.1. Examples of disjunctions of western and Neotropical taxa in the southeastern United States (especially Florida).

Taxa	Western pattern	Southeastern pattern
Pliocene–Pleistocene vertebrates, now extinct globally, extinct in the Southeast, or represented by disjunct taxa	*Thomomys* pocket gophers widely distributed, with 9 species recognized.	*Thomomys* pocket gopher reached Florida from the west in Early Pleistocene, then went extinct. Plains pocket gopher (*Geomys bursarius*) present in Appalachians in Late Pleistocene, now in Illinois, Missouri, and westward. *G. pinetis* (5 subspecies) extant from southern Georgia and southeastern Alabama to central Florida.
	Jackrabbits (*Lepus*), pronghorns (Antilocapridae), tapir (*Tapirus*), peccaries (*Pecari*), ground squirrels (*Spermophilus*), capybara (*Hydrochoerus*), jaguar (*Panthera onca*), ocelot (*Leopardus pardalis*), margay (*Leopardus wiedii* or *L. amnicola*), pallid bat (*Antrozous pallidus*), greater prairie-chicken (*Tympanuchus cupido*), black-billed magpie (*Pica pica*), great-tailed grackle (*Quiscalus mexicanus*), and many tropical bats remain extant in southern Great Plains, southwestern US, or Mexico/Central America. Giant ground sloth (*Eremotherium eomigrans*) of Neotropical origin present in Plio-Pleistocene, now extinct.	American badger (*Taxidea taxus*) and thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*) in Appalachians in Late Pleistocene; now farther west or north.
		Jackrabbits, pronghorns, tapir, peccaries, ground squirrels, capybara, jaguar, ocelot, margay, pallid bat, prairie-chickens, magpies, great-tailed grackle, etc., present in Plio-Pliocene in Florida; now extinct here. Giant ground sloth extinct. Some Pleistocene tropical bats (including narrow endemic Florida mastiff bat, *Eumops floridanus*) extant, but many (e.g., vampire bat; *Desmodus archaeodaptes*) extinct.
	Teratorns (*Teratornis merriami*), of South American origin, present in Pleistocene, now extinct globally.	Teratorns present in Pleistocene, now extinct globally.
		Podomys floridanus (Florida mouse, an endemic species and genus) has Neotropical affinities, remains extant.
Tortoises (*Gopherus*)	Extant Texas tortoise (*Gopherus berlandieri*) of southern Texas and Mexico; 2 species of desert tortoise: Agassiz's desert tortoise (*Gopherus agassizii*) of the Mojave Desert and Morafka's desert tortoise (*Gopherus morafkai*) of the Sonoran Desert; the Bolson tortoise or Mexican giant tortoise (*Gopherus flavomarginatus*) of the Chihuahuan Desert.	Various tortoises, including giant tortoise (*Geochelone*) from the Miocene onwards. Extant is only the gopher tortoise (*Gopherus polyphemus*) of Atlantic and Gulf Coastal Plain, from South Carolina to eastern Louisiana.

Table 2.1. continued.

Taxa	Western pattern	Southeastern pattern
Xeric-adapted lizards and snakes	Numerous species of xeric-adapted skinks (*Plestiodon*), whiptails (*Aspidoscelis*), whipsnakes (*Masticophis*) extant in the West and Neotropics.	Early Pleistocene Inglis IA site in Florida contains 31 snake and lizard species, including western alligator lizard (*Gerrhonotus* sp.), western hognose snake (*Heterodon nasicus*).
	Indigo snake (*Drymarchon* spp.) extant from southern Texas to Argentina.	Five subspecies of endemic xeric-adapted mole skinks (*Plestiodon egregious* ssp.) extant in Florida in sandy habitats, one of which (*P.e. similis*) ranges into Georgia and Alabama. Sand skink (*Plestiodon reynoldsi*) endemic to Florida.
		Six-lined racerunner (*Aspidoscelis s. sexlineatus*) in Southeast west to eastern Texas; westward is prairie racerunner (*A.s. viridis*).
		Whipsnakes now represented in the South only by the Eastern Coachwhip (*Masticophis flagellum flagellum*).
		Eastern indigo snake (*Drymarchon couperi*) disjunct and endemic to Florida, southern Georgia and Alabama, and a small area of Mississippi.
		The snakes *Aniloides, Calamagras, Pseudocemophora,* and *Ogmophis*; the lizards *Ophisaurus, Eumeces* (*Plestiodon*), and *Cnemidophorus* (*Aspidoscelis*); and the rhineurid amphisbaenians (worm lizards) found in Miocene deposits in both Florida and the Great Plains.
Diamondback rattlesnakes	Western diamondback rattlesnake (*Crotalus atrox*) extant from southeastern California to western Arkansas and south into Mexico.	Eastern diamondback rattlesnake (*Crotalus adamanteus*) extant from southern North Carolina to south-eastern Louisiana; presumably split from *C. atrox* by the Mississippi River barrier.
White-tailed kite (*Elanus leucurus*)	Extant in California (and uncommonly Oregon) and Texas, Mexico, and Central America.	Disjunct population extant in south and south-central Florida; time and place of origin of population uncertain.
Crested caracara (*Caracara cheriway*)	Extant from southern Arizona and south-central Texas south through Mexico and patchily through Central America and South America, south to Argentina and Chile.	Disjunct population extant in central Florida and marginally in south Florida (first collected in 1831 by John James Audubon in St. Johns River marshes, northeast Florida).

(table continues)

Table 2.1. continued.

Taxa	Western pattern	Southeastern pattern
Condors	California condor (*Gymnogyps californianus*) extant (reintroduced) in California and Arizona; occurred historically (until nineteenth century) throughout much of the West, from southern British Columbia and Alberta to northern Mexico, east to Colorado.	Extinct Pleistocene *Gymnogyps kofordi* has western affinities.
Nuthatches	Pygmy nuthatch (*Sitta pygmaea*) extant in ponderosa pine and related long-needled pine forests patchily throughout western US and north and central Mexico.	Brown-headed nuthatch (*Sitta pusilla*), a sister species of structurally and functionally similar longleaf pine and other southern pine forests, extant from Virginia to eastern Texas, with a gap in the Mississippi Valley. An endemic subspecies (*S.p. insularis*) occurs in *Pinus caribaea* savannas on Grand Bahama.
Burrowing owl (*Athene cunicularia*)	Breeds in arid West, from prairie regions of southern Canada, eastern Washington and Oregon, and California, east to Great Plains and south to northern Mexico.	Disjunct populations in peninsular Florida, a small area of Cuba, and Hispaniola.
Scrub-jays	Western scrub-jay (*Aphelocoma californica*, probably soon to be split into 2–3 species) extant from central Texas patchily to Pacific coast and northern and central Mexico; narrow endemic island scrub-jay (*Aphelocoma insularis*) extant on Santa Cruz Island, California.	Florida scrub-jay (*Aphelocoma coerulescens*) extant in peninsular Florida—Florida's only endemic full species of bird.
Hymenoptera: Ants, bees and ichneumonid wasps	Numerous ant species of xeric or semiarid habitat, including 21 species of extant harvester ants (*Pogonomyrmex*). Digger bees (*Centris* spp.): 110 species extant from Kansas to Argentina. Unlike most ichneumonids, most *Polycyrtidea* spp. adapted to semiarid desert or thorn scrub; distribution mostly Neoropical.	Several species of ants with western affinities, e.g., the Florida harvester ant (*Pogonomyrmex badius*), the only harvester ant east of the Mississippi; extant from Florida north to North Carolina and west to Louisiana; a native fire ant (*Solenopsis globularia littoralis*), *Leptothorax texanus*, *Pheidole floridana*, *P. sitarches littoralis*, Florida carpenter ant (*Camponotus abdominalis*), *C. tortuganus*, orange ant (*Aphaenogaster floridanus*), *A. flemingi*, trap-jaw ant (*Odontomachus clarus*); probably restricted to xeric upland refugia in Florida during glacial times and some species subsequently spread across a broader area of the Southeast.

Table 2.1. continued.

Taxa	Western pattern	Southeastern pattern
Hymenoptera: Ants, bees and ichneumonid wasps, continued		Digger bee, *Centris lanosa*, disjunct in Florida from Oklahoma, Texas, California, and Mexico.
		Polycyrtidea limitis, a semiarid-adapted ichneumonid, disjunct in north-central Florida from Central America, Mexico, and southern tip of Texas.
Blattodea: Sand cockroaches (*Arenivaga* spp.)	Several species in semiarid sandy areas in western US.	*Arenivaga floridensis*, endemic to sandy ridges of central and western peninsular Florida.
Grama grasses (*Bouteloua* spp.)	19 species of *Bouteloua* in western US.	Side-oats grama (*Bouteloua curtipendula*) extant in several disjunct populations in South, from Maryland and western Virginia to western North Carolina, northwestern Georgia, the Florida Panhandle, and westward.
		Hairy grama (*Bouteloua hirsuta*) disjunct in coastal grasslands on islands in southwestern Florida and some interior locations; introduced populations reported from Georgia, South Carolina, and northward.
Yuccas and Spanish bayonet (*Yucca* spp.)	Ca. 40 species, mostly in southwestern US and northern Mexico.	4 or 5 species (depending on taxonomy) in Southeast, from Virginia to Florida and west to Louisiana.
Beargrass (*Nolina* spp.)	12 species in southwestern US and northern Mexico, to Great Plains (Colorado, Oklahoma, Texas).	3 species (*Nolina georgiana*, *N. atopocarpa*, and *N. brittoniana*) extant in Southeast, with latter 2 (Florida beargrass and Britton's beargrass) endemic to Florida.
Jujube (*Ziziphus* spp.)	Ca. 40 species in warm-temperate and subtropical regions globally, including 2 species in southwestern US and Mexico.	Scrub ziziphus (*Ziziphus celata*) is only native extant species, endemic to south-central Florida and most closely related to southwestern US/Mexico taxa.
Wild-buckwheat (*Eriogonum* spp.)	Ca. 250 species in western North America (including northern Mexico).	3 species (*Eriogonum allenii*, *E. tomentosum*, and *E. longifolium*) in Southeast; shale-barren wild-buckwheat (*E. alleni*) endemic to western Virginia and eastern West Virginia; Florida's longleaf wild-buckwheat (*E. longifolium*) is the endemic variety *gnaphalifolium*.
Milkvetches (*Astragalus* spp.)	380 species in North America, with vast majority in arid western regions, including 94 species in California alone (including many rare endemics).	8 species in Southeast, including narrow endemics (e.g., Pyne's ground plum, *Astragalus bibullatus*, of limestone glades in central Tennessee); few species occurring between West and Southeast.

(table continues)

Table 2.1. continued.

Taxa	Western pattern	Southeastern pattern
Endemic plants of limestone (cedar) glades	Ancestors of cedar glade endemic taxa listed to the right have centers of distribution in the western US; *Leavenworthia* may be most closely related to western genus *Selenia* and entered the Southeast from the Ozarks or Southwest.	*Astragalus* (see above), *Dalea*, *Delphinium*, *Echinacea*, *Lesquerella*, *Onosmodium*, *Pediomelum*, *Penstemon*, *Phemeranthus*, *Leavenworthia*.
Cacti (Cactaceae)	34 genera and 189 species in North America, north of Mexico, most in the southwestern states.	3 native full species in southeastern US south to northern Florida; 12+ native full species in Florida; southwestern and Antillean affinities.
Xeric-adapted ferns (Pteridaceae)	Various genera and species associated with xeric sites.	Chestnut lip-fern (*Cheilanthes castanea*) disjunct in Virginia and West Virginia from main range in southwestern Texas to southern Arizona; slender lip-fern (*C. feei*) disjunct in Kentucky and Virginia from main range from British Columbia and Alberta south to northern Mexico.
		Forked spleenwort (*Asplenium septentrionale*) disjunct in West Virginia from western North America.
		Hybrid cloakfern (*Astrolepis integerrima*), disjunct in Ketona glades of central Alabama from Texas (700 miles).

Note: Present disjunctions represent a mixture of relicts from the Gulf Coastal Corridor savanna, long-distance dispersal, and a combination of the two.

Sources: Porter (1975), Meylan (1982), Baskin and Baskin (1986), Deyrup and Trager (1986), Deyrup (1989), Deyrup (1990), Webb (1990), Hickman (1993), Weakley (2008), Hall and Ascher (2010), Morgan and Emslie (2010), Wunderlin and Hansen (2011), Flora of North America (www.efloras.org), and sources therein.

Valley became a greater dispersal barrier for grassland-adapted taxa. Some western taxa, such as pronghorns and jackrabbits, disappeared from the South during the Middle Pleistocene, while others, including a number of reptiles, birds, and plants, persisted as disjunct relicts.

Gary Morgan and Steven Emslie document numerous vertebrate taxa of western origin in Florida during the Plio-Pleistocene, which are extinct or disjunct here today (table 2.1). These authors reveal a similar pattern for many extinct or disjunct Florida vertebrates of Neotropical origin. The northward and then eastward expansion of tropical species from South America followed the completion of the Central American Land Bridge (Isthmus of Panama) and the ensuing Great American Biotic Interchange, which began about 3.5 million years ago (Middle Pliocene). These taxa probably dispersed eastward

along the Gulf Coastal Corridor, the warmest route, into the southeastern United States. The coexistence of species from the semiarid West and the Neotropics in Florida and elsewhere in the lower Atlantic and Gulf Coastal Plain is yet another example of no-analog assemblages of species that are not found together at present. Morgan and Emslie agree with Webb that the Gulf Coastal Corridor was mostly savanna (plus thorn scrub) during the Plio-Pleistocene and that it would have been wider and more effective during times of low sea level.

HUMAN HISTORY IN THE SOUTH, AS IT RELATES TO GRASSLANDS

A debate has raged for decades over the extent to which Native Americans transformed American landscapes. Geographer William Denevan fired up the recent argument with a paper in 1992, "The Pristine Myth: The Landscape in the Americas in 1492," in which he claimed that "the Native American landscape of the early sixteenth century was a humanized landscape almost everywhere." Denevan provides anecdotes from throughout the Western Hemisphere to show the extent of modification of the landscape by Indian burning, agriculture, earthworks, hunting, and other activities. As far as I can tell, most of his examples are legitimate. The problem is that they are very selective—he avoids mention of the many regions that show little or no evidence of significant modification by Indians. I accept the closing sentence of his abstract: "A good argument can be made that the human presence was less visible in 1750 than it was in 1492." It would have been prudent to stick to that line of reasoning rather than asserting on the basis of patchy and selective data that landscapes "almost everywhere" were wholly transformed by Native Americans.

Among the responses to Denevan was a paper by Thomas Vale titled "The Myth of the Humanized Landscape: An Example from Yosemite National Park." Vale was selective in his examples, too, but was explicit about his focus on Yosemite. Vale summarizes his thesis commendably as follows:

> The desire to visualize humanized landscapes in the pre-European era derives from social ideologies, rather than from careful assessment of ecological facts…. The model of the pristine landscape has merit—its applicability in any given locale being an empirically testable proposition—and it should serve as a guide for management of natural areas.

The most recent volley in this debate was launched with the publication, in 2005, of Charles Mann's *1491: New Revelations of the Americas before Columbus*, which quickly became a national best seller. Unfortunately, the book displays limited understanding of the nonhuman physical factors and ecological processes that shape ecosystems. Regarding fire, for example, Mann overstates its ubiquity but understates its history, in saying that "for more than ten thousand years, most North American ecosystems have been dominated by fire." Actually, many North American ecosystems are "dominated" by forces other than fire, but fire-dependent vegetation and adaptations of species to fire developed many millions of years before humans arrived on the scene. Completely ignoring geographical data on thunderstorm and lightning frequency (plates 3 and 4; see chap. 5), Mann claims that "in North America, lightning fire is most common in the western mountains." In reality, lightning fire frequency is highest by far in the Coastal Plain, peaking in Florida.

Mann tries to make the case that, outside of the western mountains, most fire in the pre-European landscape was anthropogenic, to wit: "Carrying their flints and torches, Native Americans were living in balance with Nature—but they had their thumbs on the scale." In a literally incredible map (fig. 2.6), Mann depicts the entire Florida Peninsula (as well as most of the Mississippi River watershed and much of the Gulf Coast and east Texas) as a "humanized landscape" in 1491, "dominated by anthropogenic fire." To the contrary, the first European explorers to travel through much of Florida—the party led by Alvar Núñez Cabeza de Vaca, who landed in 1528 near present-day Sarasota and walked northward up the Peninsula and then westward across the Panhandle and ultimately to Mexico—described Florida as sparsely populated. The only humanized landscape they encountered was the agriculture-based Chiefdom of Apalachee, located in the area between the Aucilla and Ochlockonee Rivers in the Florida Panhandle, near present-day Tallahassee (an Indian word for old fields). Historian Andrés Reséndez describes this portion of Cabeza de Vaca's journey in his book, *A Land So Strange*:

> Apalachee was indeed the largest and most complex chiefdom of the entire Florida peninsula. In fact, it was something of an anomaly. Thus far the Spaniards had encountered native peoples organized in small villages scattered over large areas. The size of these communities was dictated by the amount of food available. Although some of these groups cultivated maize, they were primarily hunters and gatherers.… By the sixteenth century, the people of Apalachee had cleared large fields that stretched for miles and were regularly cultivated by communal labor.

AREAS DOMINATED BY ANTHROPOGENIC FIRE

WIDESPREAD FOREST CLEARING FOR AGRICULTURE
OR GAME MANAGEMENT
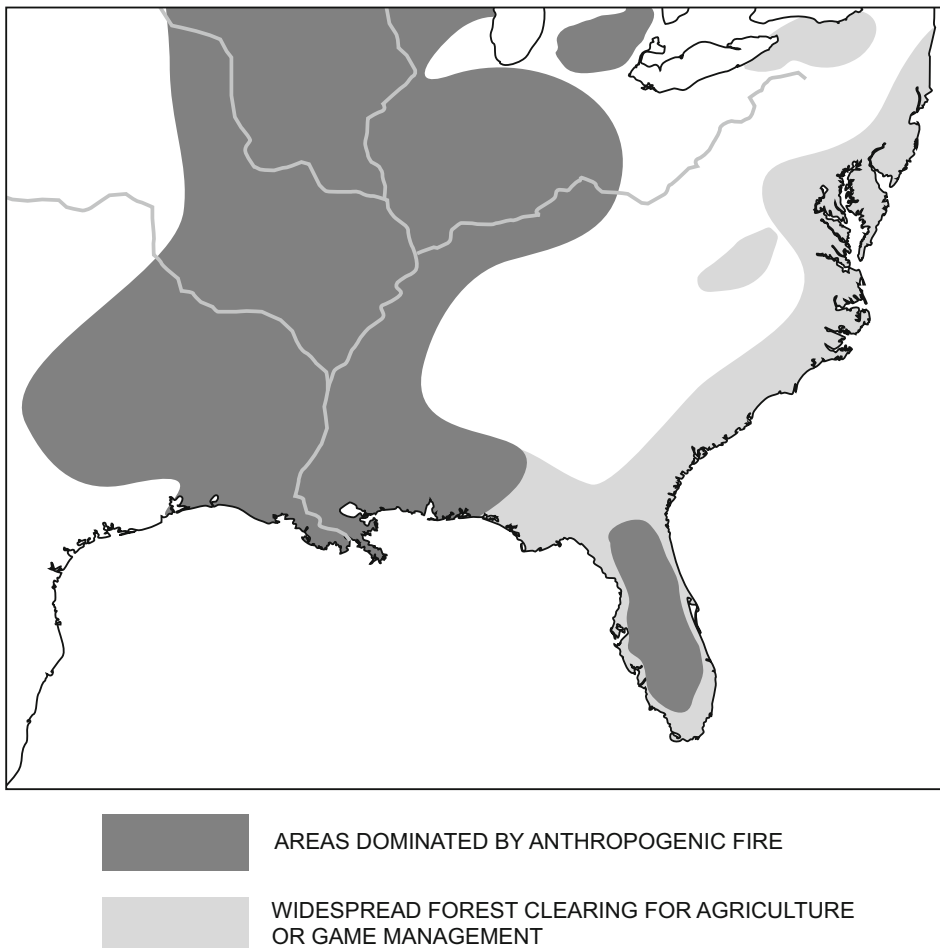
Figure 2.6. Humanized landscapes in the South, as imagined by Charles Mann (after Mann 2005), including areas dominated by anthropogenic fire and by widespread forest clearing for agriculture or game management. Mann's interpretation is highly speculative, and in the case of the Florida Peninsula, demonstrably wrong; abundant evidence indicates that lightning was the primary ignition source for fires there and across the Coastal Plain.

Although Reséndez refers to the "Florida peninsula" above, the area he describes is in the Florida Panhandle. No evidence exists for humanized land-scapes this extensive on the Florida Peninsula. Further, Indian-set fires were apparently rare in Florida because fires ignited by lightning were so frequent (i.e., every one to three years for the dominant upland vegetation) that there would have been little fuel to burn. Fire ecologists overwhelmingly agree that lightning frequency in the Coastal Plain is more than enough to explain domi-nance of the region by pyrogenic vegetation prior to EuroAmerican settlement;

any fires set by Indians would have been virtually superfluous. A physical chemistry and climate model developed by Richard Guyette and colleagues shows that, even ignoring ignitions, temperature and other physical variables predict high fire frequency (less than two to four years) across most of the South. At the 2011 meeting of the Ecological Society of America, fire history authority Mitchell Power of the University of Utah showed Mann's map in his presentation, implying that he found it suspect. He asked Mann for his data, but got no response. I interpret that as no data.

When humans first entered the South is unclear, but available evidence suggests around 14,000 to 15,000 years ago. Most scholars believe it not coincidental that the extraordinary Pleistocene megafauna, the last representation of the richest assemblage of large mammals (plus giant tortoises, etc.) known in earth's history, went extinct around 13,500 to 13,000 years ago. Overhunting is probably a major cause of the mass extinction, but climate change played a role. The relative role of the two factors has been a topic of controversy, but a 2011 paper by Eline Lorenzen and coauthors shows that the relative influence of climate and humans on megafaunal extinction in Eurasia and North America varies by species.

I do not have space to review the subsequent history of Indians in the South, but a comprehensive and highly readable treatment of their "prehistory, social institutions, and history" can be found in Charles Hudson's 1976 book, *The Southeastern Indians*. The impact of Indian cultures on the landscape is the explicit topic of a book by Paul and Hazel Delcourt, *Prehistoric Native Americans and Ecological Change*.

How much Native Americans modified their environment remains contentious, but it definitely varied geographically. Much depends on the size of their populations in various regions. Denevan suggested a total population of 53.9 million in the Western Hemisphere, including 3.8 million in North America. Many scholars find these numbers improbably high, and indeed Denevan had little or no data to back up his estimates. Charles Kay far outdid him, claiming in 1994 that North America "was home to tens of millions of aboriginal peoples before European-introduced diseases decimated their numbers." This estimate is extremely far-fetched. Perhaps the best-researched estimate, similar to Denevan's for North America, was provided by Shepard Krech II in *The Ecological Indian: Myth and History* (1999). Krech suggests that

> the most sensible figures are four to seven million.… Most people lived in the Southwest, Northeast, California, and Southeast.… The most densely settled regions were California and the Northwest Coast; the least densely settled, the Subarctic, Arctic, and Great Basin.

The Delcourts document an increasing intensity of Indian impact on landscapes over time. The Paleo-Indians of the Early Holocene were hunter-gatherers with some small-scale agriculture and small population sizes. By the late Holocene, beginning 4,500 years ago after the Hypsithermal ended, agriculture had expanded and substantial impacts of a larger population, deforestation, use of fire, and hunting were evident. Land clearance was confined for a long time to the vicinity of villages and along major waterways, but by 1,000 years ago the Mississippian culture had created a large agriculture-based civilization, with its center in the Cahokia metropolis in the American Bottom of present-day southern Illinois, across the river from St. Louis. Cahokia, at its peak, may have held as many as fifty thousand people. A large area of the Central Mississippi Alluvial Valley around Cahokia was abandoned by 550 years ago, leaving a "vacant quarter" within the former heart of the culture (fig. 2.7). Overpopulation, depletion of soil fertility due to intensive agriculture, shortages of wood resulting from deforestation, climate change (the "Little Ice Age"), warfare, and other factors have been hypothesized to account for the collapse, which began before Europeans and their diseases entered the New World and dealt the final blow.

More recent archaeological research, reviewed in a 2011 "News Focus" in *Science* by Andrew Lawler, reveals a prominent role of what is now the southern United States in the history of civilization in the New World. The foundation for the astounding North American mound-building tradition now appears to have been established by Native Americans in the Lower Mississippi Valley some 5,500 years ago—an amazing 2,000 years earlier than the first cities (of the Olmec) appeared in Mexico. Excavated sites from 3,500 to 2,500 BCE in northeastern Louisiana indicate high earthen mounds flanked by flat plazas reminiscent of the classic architecture of Mesoamerica. Some scholars suggest a direct link from these people to the later mound-building cultures to the north and Mesoamerican civilizations to the south. At this point, to my knowledge, no evidence exists for the use of fire by these people to manage vegetation.

It is undeniable that later use of fire by Native Americans had substantial impacts on vegetation in some areas, with the proportional human impact generally increasing from the Coastal Plain (with its extremely high lightning frequency) inland and northward. The Delcourts compared fossil pollen, charcoal, and archaeological data for a site in the Appalachian highlands of North Carolina, Horse Cove Bog, over the last 3,900 years. They concluded that Indian-set fires were focused on particular portions of the landscape, helped maintain fire-dependent plant species and communities (e.g., chestnut [*Castanea*] and
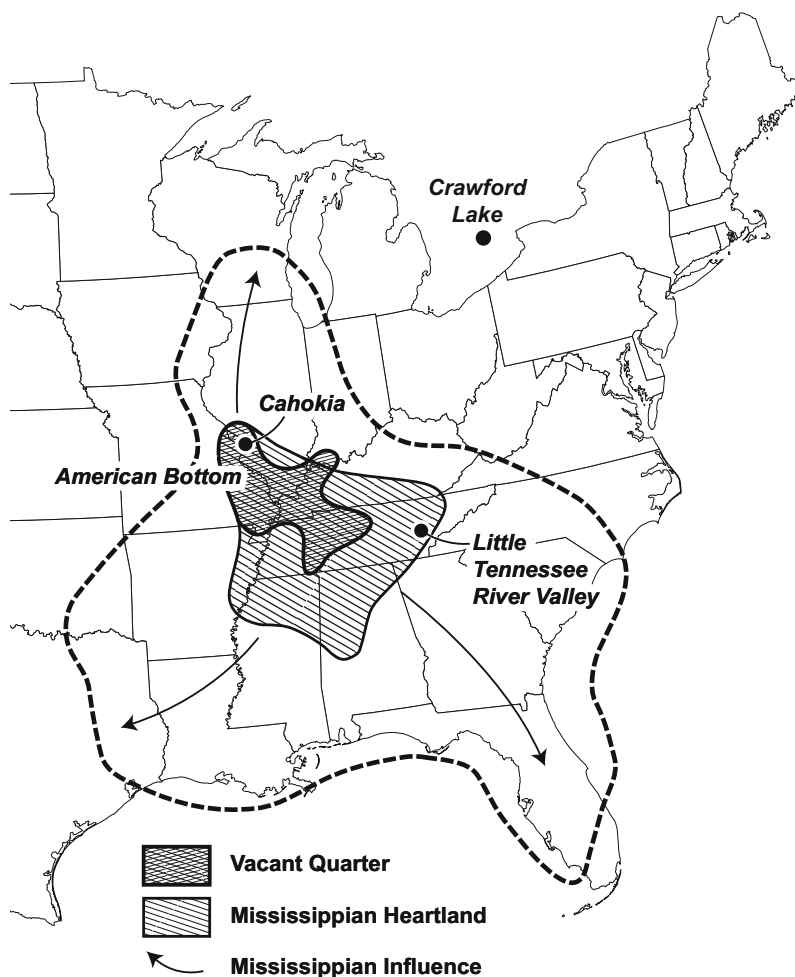
Figure 2.7. The demise of the Mississippian culture was marked by a vacating of a large agrarian area spreading out from the major city of Cahokia about 550 years ago. The Mississippian Heartland had been dominated by agriculture from about 1,000 years ago until its demise about a century before the arrival of European settlements. Smaller Mississippian settlements survived until after the arrival of Europeans. Adapted from Delcourt and Delcourt (2004).

oak [*Quercus*] forests/woodlands with grassy understories, and stands of table mountain pine [*Pinus pungens*] and pitch pine [*P. rigida*]), and increased overall landscape heterogeneity. Jerry Baskin and colleagues suggest an anthropogenic origin for the Big Barrens vegetation of western Kentucky and a small part of adjacent Tennessee. They base this conclusion on a dramatic rise in grass pollen in cores from ponds in this area around 2,000 years ago, well after the close of the dry Hypsithermal Interval about 5,000 years ago. Deliberate burning by

Indians is a parsimonious explanation for the development of this major grassland. Nevertheless, I question whether Indians literally created grassland here or anywhere versus simply (but significantly) expanding grassy openings that were already present, perhaps as remnants from the Hypsithermal that were too small and scattered to contribute much pollen to sampled cores.

As a final example, Larry Barden amassed considerable historical information to show that the prairies observed on the Piedmont of North and South Carolina by the first European explorers (going back to Hernando de Soto in 1540) and later settlers were shaped by fires set by Indians. He also documents extensive agriculture in the region, which would have favored open vegetation. Many of the early Europeans directly observed Indians setting fires. For example, in the 1720s, famed naturalist Mark Catesby noted in the interior of the Carolinas that "in February and March the inhabitants have a custom of burning the woods…an annual custom of the Indians in their huntings, of setting the woods on fire many miles in extent." Catesby also observed bison foraging in the burned "savannas" (a term used at that time in reference to prairies). University of North Carolina ecologist Robert (Bob) Peet estimates that most of the Piedmont had a grassy understory at the time the first Europeans arrived. A plausible hypothesis is that the Indians needed "something to work with," that is, natural grasslands or at least grassy openings with flammable properties, which they then expanded through their use of fire and agriculture. That humans have a capacity to diversify a landscape, acting perhaps as keystone species in the most positive sense, is something I find comforting.

Cecil Frost, in *The Longleaf Pine Ecosystem*, provides an authoritative review of the history of EuroAmerican exploration, exploitation, and settlement in the Atlantic and Gulf coastal states from Virginia to east Texas. The temporal pattern of settlement was highly uneven, with some areas (such as the Coastal Plain and Piedmont of Virginia and the Carolinas) having two or more people per square mile before 1770, whereas other areas (including the vast majority of Florida) remained under this threshold until 1890 or later (fig. 2.8). As Frost notes, the 256-year tenure of the Spanish in Florida, from the establishment of St. Augustine in 1565 until ceding to the United States in 1821, was marked by a profound lack of immigration and development. By 1821 the entire population of Florida was only around 20,000 people, and most of the Peninsula and the Gulf coast interior were near-pristine. Even by 1850 the native ecosystems of the six Gulf states were largely intact, with the exception of areas with cotton plantations.

As whites settled the South, many mimicked the Indian habit of "burning
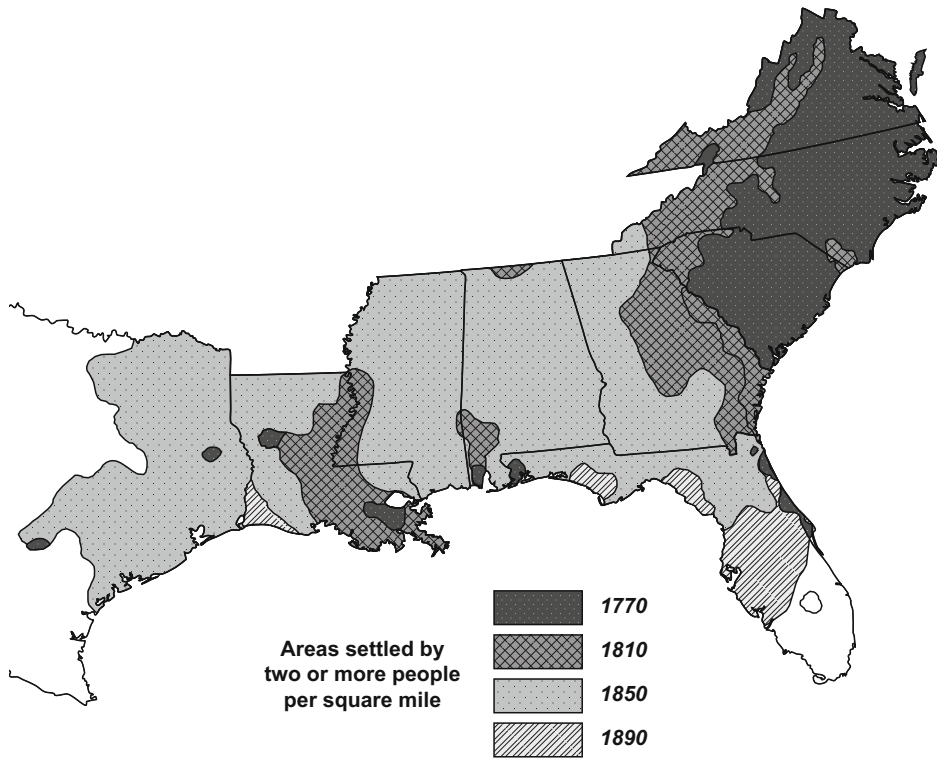
Figure 2.8. EuroAmerican settlement patterns within the longleaf pine region, 1770–1890, as indicated by two or more people per square mile. The Coastal Plain and Piedmont of Virginia and the Carolinas were settled first, along with a few isolated areas around settlements in other states. South Florida was not settled until after 1890. Adapted from Frost (1993).

the woods." Outside the Coastal Plain with its abundant lightning ignitions, these settlers probably kept fire frequencies higher than would have occurred under a lightning regime. Francis (Jack) Putz, one of my former professors at the University of Florida, concludes that "rednecks" are the "unsung heroes of ecosystem management" because of their habitat of keeping beneficial fire on the southern landscape. Country people set fires, according to Putz, "to improve hunting, to kill ticks, because the mower won't start, to expose snakes, and for fun." Although white settlers, like the Indians, generally burned in the winter, which is not the ideal season because it promotes shrubs more than many native grasses and other grassland plants, they at least kept the woods open and, in many places, prevented succession to hardwood forest. Unfortunately, this largely beneficial management did not last long. Beginning in the early twentieth century, the American Forestry Association and the Ad Agency,

sponsored by the US government, initiated a massive propaganda campaign, which included the "Dixie Crusaders" and Smokey Bear, in an effort to curtail burning by rural people. Sadly, they largely succeeded, and the great grasslands of the South were replaced by unnatural hardwood forest.

MILLS CREEK

Some people need a wild place close to home—their own Walden. My personal Walden, at present, is the Mills Creek tract, owned by the US Forest Service and the closest place to my home through which the Florida Trail passes. Henry David Thoreau's Walden Pond is only 1.38 miles from the center of Concord, Massachusetts. Mills Creek, which flows out of Lake Mills through a cypress swamp, is about the same distance from my house outside Chuluota. I can strap on a backpack, walk out my front door, and camp out, now even in an official primitive campsite that virtually no one else uses except my sons and me. Mills Creek is a place filled with natural and human history. As noted earlier, Herb Stoddard spent the formative years of his youth in my community. I find it heartening that Stoddard played in the woods at Mills Creek where I now walk, though the scene was different then. Stoddard arrived in Chuluota in 1893 when he was four years old and, to his dismay, had to leave with his parents just seven years later, but his recollections from his time here are keen. He summarizes his departure:

> Then, blinded by tears, I crawled onto the train in Oviedo with Mother, Dick, and Marge in February, 1900. I had not had shoes on my feet for seven of the most wonderful years a boy ever lived. The calluses on the bottoms of my feet were so tough that only between my toes was I vulnerable to the spines of sandspurs. I was a small wild creature about to leave a beloved land to take up life in a city teeming with man.

Stoddard describes central Florida as an open landscape dominated by fire-maintained longleaf pine savannas. Huge cattle drives were run from here to south Florida. Ancient cypress swamps surrounded every lake and creek. Stoddard's first sighting of an ivory-billed woodpecker (*Campephilus principalis*) occurred on a huge cypress on the edge of Lake Mills, from which Mills Creek flows; between 1896 and 1900 he saw twelve or fifteen individuals here. The ivory-billed woodpecker is primarily a bird of old-growth bottomland hardwood and cypress forests and swamps. Considering that these communities were embedded within a longleaf pine matrix over much of the woodpecker's

range, it is not surprising that Cornell ornithologist Arthur Allen and his graduate student Peter Paul Kellogg reported in the 1930s that ivory-billed woodpeckers fed on fire-killed trees in Florida pine savannas. Another of Allen's students, Jim Tanner, whom I was fortunate to have on my graduate committee at the University of Tennessee, wrote the definitive text on the bird for his PhD dissertation. In that book he speculated that the abundance of upland pine habitats in Florida may explain why the woodpecker was relatively more abundant here than elsewhere within its range.

Besides the cypress swamp (now second growth) where Stoddard observed his ivorybills, the Mills Creek tract is now mostly hardwood forest. By reading the land, however, I see that it was once old-growth longleaf pine savanna. Remnant longleaf pines, perhaps too young to log in Stoddard's time, but now perhaps around 150 to 200 years old, tower above a canopy of live oaks, water oaks (*Quercus nigra*), laurel oaks, southern magnolias, pignut hickories (*Carya glabra*), and other trees. A few old turkey oaks (*Q. laevis*) also occur as scattered remnants of the former pine sandhill community. Deeply cut old roadbeds wind through the forest, but frequent patches of wiregrass show that this area was never completely cultivated (i.e., wiregrass does not return, on a human timescale, to plowed land). I surmise that this was "unimproved pasture," an area where the settlers let their cattle graze; they probably also raised crops in small patches near their home sites. Today, after more than a century of fire exclusion, the site has converted to hardwood forest.

This is the story of so much of the former longleaf ecosystem and other grasslands of the South. Yet Mills Creek retains some of its original elements. In addition to the remnant old longleaf pines, emergent above the canopy of hardwoods, younger longleafs and quite a few grasses and grassland forbs occur in open patches throughout the area, mostly on the whitest, least fertile sands. Furthermore, over the last year I have observed two characteristic and imperiled large reptiles of the longleaf pine ecosystem here: (1) a five-foot eastern indigo snake along the Florida Trail in the center of the tract, in a small opening with a gopher tortoise (*Gopherus polyphemus*) burrow; and (2) an eastern diamondback rattlesnake (*Crotalus adamanteus*) dead on the road just outside the site. These species are the largest nonvenomous and venomous snakes, respectively, in all of North America; they can each exceed eight feet in length. As long as these impressive reptiles persist here, the spirit of the ancient longleaf pine savanna lives on.

REFERENCES

Multiple working hypotheses: Chamberlin 1890, Burnham and Anderson 2002, Elliott and Brook 2007

Physiography, geologic and vegetation history: Kesel 1974, Delcourt 1979, Davis 1981, Delcourt and Delcourt 1981, Watts 1983, Delcourt and Delcourt 1984, Webb 1990, Overpeck et al. 1992, Watts et al. 1992, Brouillet and Whetstone 1993, Delcourt and Delcourt 1993, Graham 1993, Watts and Hansen 1994, Heatherington and Mueller 1997, Schmidtling and Hipkins 1998, Graham 1999, Jackson et al. 2000, Pan Terra, Inc. 2000, Williams et al. 2000, Davis and Shaw 2001, Williams et al. 2004, Grimm et al. 2006, Huang et al. 2006, Beerling 2007

Fossil animals, Gulf Coastal Corridor, Southeast–West disjunctions, phylogeography: Webb 1977, Meylan 1982, Webb 1990, MacFadden 1997, Janis et al. 2002, Wallace and Wang 2004, Means 2006, Soltis et al. 2006, Gill et al. 2009, Morgan and Emslie 2010

Rise of C_4 grasses, effects of fire on climate: Beerling 2007

Droughts favor grasslands: Transeau 1935, Britton and Messenger 1969, Beerling 2007

Fire-grassland positive feedback: Bond and Midgley 2000, Bond et al. 2005

Grass–tree competition: Transeau 1935, Riginos 2009

Human history (and fire): Cabeza de Vaca (1542) 1993, Tanner 1942, Stoddard 1969, Hudson 1976, Denevan 1992, Kay 1994, Delcourt and Delcourt 1997, Barden 1997, Vale 1998, Krech 1999, Putz 2003, Delcourt and Delcourt 2004, Mann 2005, Frost 2006, Reséndez 2007, Lawler 2011, Guyette et al. 2012

Extinctions: Jablonski 2001, Lorenzen et al. 2011

CHAPTER 3

Biological Hotspots and Endangered Ecosystems

> The grass grows three feet high. And hill and valley are studded all over with flowers of every hue. The flora of this section of the State and thence down to the sea board is rich beyond description.
>
> Mississippi Congressman John F. H. Clairborne (1841)

More than any other attribute, except perhaps pure aesthetics, discovery is what makes natural history so irresistible to naturalists. Given its impressive biodiversity, the South holds many rewards for professional and amateur naturalists who take the time to explore their backyards and beyond. The South has been traveled extensively by botanists, zoologists, and other naturalists for centuries, yet every year species new to science are discovered here. Whereas some new species are "split" from previously recognized taxa on the basis of newly discovered differences, other new species are completely new in the sense of never having been recorded before. These are usually narrow endemics discovered in a place that no previous naturalist with sufficient taxonomic expertise had explored intensively.

DISCOVERING LOST WORLDS

Finding a species completely new to science is a privilege reserved for the very skilled and the very lucky. In 1992 Georgia botanist Jim Allison was conducting surveys in Alabama for a rare plant, Georgia rockcress (*Arabis georgiana*). Allison

73

and three friends were canoeing down the Little Cahaba River in central Alabama, on the southern fringe of the Ridge and Valley Physiographic Province, where they were delighted to find several previously unknown populations of Coosa Barbara's-buttons (*Marshallia mohrii*), a federally threatened species, disjunct from its main distribution in the Coosa prairies of northeastern Alabama and adjacent Georgia. This was exciting enough. But then they noticed, high above the bank of the river, a rocky slope dominated by grassland (plate 11). There were scattered longleaf pines and other woody plants, including eastern redcedar (*Juniperus virginianus*); chinkapin oak (*Quercus muehlenbergii*); dwarf palmetto (*Sabal minor*); Missouri maidenbush (*Leptopus phyllanthoides*), which is disjunct in Alabama from further west; and the rare Alabama croton (*Croton alabamensis* var. *alabamensis*). Mostly, however, the site was very open, with considerable exposed rock and a sparse groundcover dominated by little bluestem (*Schizachyrium scoparium*).

In general appearance, the site that Jim Allison and friends discovered along the Little Cahaba resembled the limestone "cedar glades" of Tennessee, Kentucky, Alabama, and Georgia. Closer inspection, however, revealed that this site was different and of enormous biological value, surpassing even the famously endemic-rich cedar glades of the Central Basin of Tennessee. Subsequent surveys, aided by inspection of topographic maps (on which glades show up as irregular white patches in a green matrix) and infrared aerial photographs, led to the delineation of some forty sites along an eleven-mile stretch of river. The glades ranged from small outcrops to a 12-acre patch, totaling a little less than 250 acres of open glade. Botanical exploration of this site by Jim Allison and colleagues (especially Tim Stevens, his coauthor on the 2001 article describing their finds) led to a plant list that included more than sixty rare species, including eight taxa—five full species and three varieties—that proved to be totally new to science and restricted to these glades (table 3.1, plate 12). Allison aptly labeled the Ketona Glades a "botanical lost world."

In addition to these endemics, the rare taxa discovered on the Ketona Glades in 1992 include seven state records, such as Carolina horsenettle (*Solanum pumilum*), which was last collected in 1837 and presumed extinct; hybrid cloakfern (*Astrolepis integerrima*), disjunct from Texas; and yellow nailwort (*Paronychia virginica*), for which this site bridges a distributional gap between Virginia and Arkansas. New discoveries are still being made from the Ketona Glades.

What is responsible for this incredible collection of rare, endemic, and disjunct plants on a couple hundred acres of glade in central Alabama? It is possible that some of these taxa once had wider distributions and contracted to these odd glades, although this scenario appears unlikely for most of them.

Table 3.1. Recently described plant taxa endemic to Ketona Glades of Bibb County, Alabama.

Alabama gentian-pinkroot	*Spigelia gentianoides* var. *alabamensis*
Cahaba daisy fleabane	*Erigeron strigosus* var. *dolomiticola*
Cahaba paintbrush	*Castilleja kraliana*
Cahaba prairie-clover	*Dalea cahaba*
Cahaba torch	*Liatris oligocephala*
Deceptive marbleseed	*Onosmodium decipiens*
Ketona tickseed	*Coreopsis grandiflora* var. *inclinata*
Sticky rosinweed	*Silphium glutinosum*

Source: Allison and Stevens (2001).

Some species, such as the hybrid cloakfern from Texas, probably got here by long-distance dispersal. The primary explanation for this strange collection of plants, however, surely has to do with the substrate. A geological map of Alabama shows that all of these newly discovered glades occur on Ketona dolomite. This rock, Upper Cambrian in age (ca. 500 to 540 million years old), is a dark gray and exceptionally pure form of dolomite. Ketona dolomite is unusually rich in magnesium, which in high concentrations is toxic to plants. The soil derived from this distinct bedrock is shallow and droughty, creating extreme growing conditions. To survive here, a plant has to be tolerant of high magnesium and low moisture levels, either through previously acquired adaptations or as a result of the strong selective pressures that such an extreme site imposes. These tolerant plants are then able to outcompete less tolerant plants in the struggle for survival.

Jim Allison knew that these glades were unique. University of Kentucky botanist Jerry Baskin, an authority on limestone glades, and colleagues attempted to clarify the confusing terminology used to describe limestone glades and barrens. In a 1994 article, they settled on three general categories: limestone glade, xeric limestone prairie, and barrens. Allison noted that the Ketona Glades are most similar to the xeric limestone prairie class, but are different: they are on dolomite rather than on limestone (albeit dolomite is considered a high-magnesium form of limestone), and their flora is distinct. This flora includes many taxa not found in the limestone glades, but it also lacks a number of endemic or characteristic elements of limestone glades. Allison suggested that a fourth category of calcareous glades be established to accommodate the Ketona Glades, but Baskin and colleagues still consider these glades a form of xeric limestone prairie.

I was fortunate to visit the Ketona Glades twice while working on this project. My first visit was in mid-May 2008, in the company of Bill Finch, conservation director for the Alabama office of The Nature Conservancy (TNC).

Wisely, TNC made conservation of the Ketona Glades a high priority and so far has protected more than half of the open glades within a 480-acre preserve. The US Fish and Wildlife Service created an adjacent conservation area, the Cahaba River National Wildlife Preserve, to protect the outstanding endemic aquatic fauna, as well as imperiled terrestrial species.

Bill Finch and I spent most of a drizzly morning at the Prairie Grove Glades TNC Preserve in northwestern Alabama, the largest complex of limestone cedar glades remaining in Alabama. Alabama gladecress (*Leavenworthia alabamensis*) is the main endemic here, but we were too late in the season to see it in bloom. We did get to see flowering Alabama larkspur (*Delphinium alabamicum*), which is endemic to central and north Alabama and a bit of northwestern Georgia. We also enjoyed Gattinger's prairie-clover or purpletassels (*Dalea gattingeri*), longsepal beardtongue (*Penstemon calycosus*), Nashville breadroot (*Pediomelum subacaule*), sunnybells (*Schoenolirion croceum*), fragrant sumac (*Rhus aromatica*), and green antelopehorn (*Asclepias viridis*), plus other glades/grassland plants in bloom.

Then we traveled to the Ketona Glades. I must say that I was not prepared for the preposterous endemicity and overall weirdness here. It is breathtaking. I was able to get reasonably good photographs of several of the endemic and rare species, including the Alabama gentian-pinkroot, Cahaba prairie-clover, deceptive marbleseed, Coosa Barbara's-buttons, whiteleaf leatherflower (*Clematis glaucophylla*—not all that rare, but gorgeous and a first for me), and Alabama croton. The last species is endemic to four counties in central Alabama and a single county in central Tennessee; its other variety (*texensis*) is on the Edwards Plateau of Texas. On a second trip to the Ketona Glades in mid-July 2008, I was able to locate and photograph two more endemics in bloom: Cahaba torch and sticky rosinweed. The Cahaba torch—the rarest and probably most phylogenetically distinct of all the single-site endemics here and one of the rarest plants in the world—was irresistible to black swallowtail (*Papilio polyxenes*) butterflies.

Discovery of a suite of entirely new species on a single site, as on the Ketona Glades, does not happen often for well-surveyed groups, such as vascular plants or vertebrates, even in the tropics. Less dramatic discoveries are more common, but are still exciting and important to science. As noted earlier, new species are discovered when previously known taxa are "split" into two or more taxa on the basis of novel morphological or genetic studies; sometimes the newly split taxa are also shown to differ ecologically. From as early as 1900, botanists had noticed that the native bamboo on mountain slopes in the southern Appalachians was morphologically and ecologically different from the giant cane (*Arundinaria gigantea*) and switch cane (*A. tecta*) found in flood-

plains and wetlands at lower elevations. It was not until 2006, however, that J. K. Triplett and coauthors formally described this bamboo as a new species, hill cane (*A. appalachiana*). With increasing use of molecular tools, new "cryptic species," which look identical to their sister species but differ in their DNA and often in aspects of their life histories, are being identified in many places. Importantly, our definition of "species" and our methods for distinguishing species and other taxa have conservation implications. Patterns of species richness and endemism vary somewhat depending on the species concept that is applied, which in turn affects endangered species-listing decisions and identification of geographic conservation priorities.

Discovery of a "new species" also can mean finding a known species in a new place, for example a county record, a species new to Tennessee, or perhaps just a species new to your neighborhood. Every serious naturalist can expect to make these fun discoveries, and such finds have value. For instance, naturalists are documenting range expansions and contractions in response to climate change, in addition to changes in phenology (the timing of natural events), including earlier leafing out and flowering of plants and earlier arrival from wintering grounds or nesting of birds. Changes in distribution and phenology are predicted to intensify in coming decades; naturalists can make useful contributions to science and to conservation by documenting them.

ENDEMISM

Endemism may be the purest and most efficient measure of conservation value, if one of our goals is to protect from extinction the greatest number of species possible. A strategic focus on protecting centers of endemism on a variety of spatial scales is wise, because if the endemic taxa in question are not protected in those places, they will be protected nowhere. Moreover, several studies demonstrate that protecting centers of endemism captures total species richness more cost-efficiently than other methods. For example, David Orme and coauthors used a global database on breeding bird distributions to test for congruence across three types of hotspot: total species richness, threatened species richness, and endemic species richness. They found relatively little overlap among these three types of hotspot. Surprisingly, though, the endemism hotspots captured not only a high proportion of endemic species, but contained greater species richness overall than the species richness hotspots and more threatened species than the threat hotspots. A possible reason for this unexpected result is that hotspots of endemism are more widely dispersed than hotspots based on

threatened species or total species richness; hence, they encompass a broader range of biogeographic diversity.

Along the same lines, John Lamoreux and colleagues show that selection of ecoregions based on level of vertebrate endemism and covering only 10 percent of the terrestrial land surface would protect populations of 56.5 percent of the world's terrestrial vertebrate endemics and 61.6 percent of all vertebrate species. With increasing area protected based on the endemism criterion, numbers of endemics and all species captured rise steeply until the curve flattens at approximately 50 percent of the earth's surface, at which point virtually all vertebrates are included. What accounts for this remarkable ability of endemics to serve as surrogates? Consistent with the findings of Orme and colleagues, Lamoreux and coauthors suggest that the likely mechanism is turnover in species composition among areas of high endemism, such that priority areas based on endemism are distinct in species composition. They are therefore "highly complementary" in the language of conservation planning.

In these times of rapid climate change and extinction, an additional advantage of identifying and protecting centers of endemism stands out: these areas are havens of stability in a tumultuous world. Biogeographers have proposed for more than a century that many areas of high endemism are climatic refugia, where species have persisted over long periods of time even as climate changed radically on a broader scale. A 2011 study by B. Sandel and coauthors estimated the velocity of Late Quaternary glacial-interglacial climate change globally and compared velocities with geographic range sizes of amphibians, mammals, and birds. Endemism was highest in areas with low velocities of climate change and lowest in areas with high velocities. They conclude that "low-velocity areas are essential refuges for Earth's many small-ranged species." Peter Kareiva, chief scientist with TNC, is an ardent critic of the hotspots strategy. He comments that hotspots of endemism are just places with "long lists of species" and that "simply counting species often overlooks ecological processes." This conclusion ignores evidence that hotspots are often centers of speciation (an important process!) or refugia within which species persist despite substantial environmental change. These refugia may well provide the seeds for ecological and evolutionary recovery after the current mass extinction event.

The only serious contenders with endemism for conservation value are key ecological processes, such as fire and hydrology, and strongly interactive species that play pivotal roles in maintaining ecological processes, habitat structure, or the integrity of food webs (see chap. 5). Key processes and interactive species help maintain populations of endemics and ultimately most other species in the community. Such critical species include highly flammable plants (e.g., most

grasses), megaherbivores, top carnivores, and ecosystem engineers such as the gopher tortoise, whose burrows and bodies provide habitat for many other species, including several endemics that are obligate commensals—they must live with tortoises (see chap. 5).

By definition, an endemic species (or subspecies, variety, genus, family, etc.) is one that occurs within a defined area and nowhere else. So, a species could be endemic to North America, the United States, the southeastern United States, Alabama, central Alabama, or the Ketona Glades. John Terborgh and Blair Winter attempted to standardize the terminology by suggesting 50,000 square kilometers (ca. 12.4 million acres) as a maximum range size for birds to be considered locally distributed (narrowly endemic). The legendary tropical field botanist Al Gentry, who died in a small airplane crash in 1993 while conducting plant surveys along the coast of Ecuador, followed this 50,000 square kilometers convention for considering plants local endemics. Other authors have used different criteria; for instance, Sandel and coauthors used 250,000 square kilometers for their analysis of the relationship between climate-change velocity and endemism. The narrower the distribution of a species, the greater the concern (all else being equal) to conservationists. A small, endemic-rich site, such as the Ketona Glades, could be eliminated in a single day by a developer and his bulldozers.

Importantly, an endemic species is not necessarily rare in the sense of small population size—it could be abundant within its range, however small that range. Nevertheless, very narrow endemics always have relatively small populations because there are only so many individuals that can be packed into a small area. As suggested by Deborah Rabinowitz, another stellar ecologist who died before her time, a species can be rare in one or more of three basic ways: a restricted distribution (i.e., a local endemic), a small local population size, or high habitat specificity. Combining these traits, Rabinowitz famously defined eight forms of rarity and provided examples from the flora of the British Isles. In the real flora, only seven forms of rarity were apparent—no species fell into the category of narrow geographic distribution, broad habitat specificity, and "everywhere small" population size. Rabinowitz found few species to be rare on all three axes—range size, habitat specialization, and local abundance— but some other studies have found many species rare in all three ways. Earl McCoy and Henry Mushinsky found that 27 percent of plants and 29 percent of amphibians and reptiles of the Florida scrub are triply rare: they have small ranges, high habitat specialization, and low local abundance. Susan Harrison and colleagues identified 939 plant species associated with serpentine habitats in California, of which 29 species in fifteen families were triply rare. The triply

rare plants in this study were associated with relatively stable environmental conditions: moderate temperatures, medium to high rainfall, and large areas of serpentine. Research to identify triply rare species and their habitat requirements in southern grasslands is urgently needed.

In contrast to triply rare species, which may have been that way over their entire evolutionary histories, are species that were once more abundant or widespread and played important ecological roles, but are now rare due to human impacts. An example is the Florida panther (*Puma concolor coryi*), which probably played a key role as a top predator. Despite its name, the panther is not endemic to Florida. The subspecies as originally described occurred nearly throughout the South from the southern tip of Florida to South Carolina, west across southern Tennessee and all of Arkansas, down to extreme eastern Texas and including all of Louisiana and the other Gulf states. So widely dispersing was this animal, it is not surprising that recent molecular genetic studies suggest that all puma in North America belong to a single subspecies.

Conservationists traditionally have been quite concerned with endemics. For instance, the twenty-five global biodiversity hotspots (now numbering thirty-four) identified by Norman Myers and colleagues in 2000 and used by Conservation International to set conservation priorities were defined on the basis of endemic plant richness (at least 1,500 endemic plant species) combined with a high level of habitat loss (at least 70 percent). The number of endemic taxa within a site or region is an indication of the irreplaceability of that area. In the lexicon of conservation planning, irreplaceability refers to the potential contribution of a site to the attainment of conservation goals. A common conservation goal (or target) is to protect at least one (or perhaps two, three, etc.) viable population of each native species within a planning region. A site that contains several species that are found nowhere else or in very few other places leaps to the top in such a prioritization scheme because, for the species in question, that site is the only place, or one of few, where the goal can be met. Barring distributional change (some of which surely will occur as climate changes) or confinement to captivity, if we don't save endemic species in the irreplaceable sites where they occur today, they will go extinct.

The degree of endemism within any region or ecosystem type is a fairly reliable measure of the age of that region or ecosystem. The high number of endemic species associated with longleaf pine ecosystems, for example, suggests that this ecosystem—or something very similar—is ancient. The extreme degree of endemism at the full species or higher (e.g., genus) level in many southern grasslands provides evidence of the antiquity of these ecosystems and supports the argument that they were created and maintained by natural processes—such

as lightning-ignited fires or edaphic (soil) conditions—rather than by human activity, which did not begin in the South until about 14,000 to 15,000 years ago. We will return to this topic, as I am forever amazed by assertions that all grasslands were created and maintained by Indians or other human activity.

Knowledge of patterns of endemism in several regions of the South, especially the Coastal Plain and for plants, has expanded markedly over the last few decades. According to calculations by Bruce Sorrie of the North Carolina Natural Heritage Program and Alan Weakley of the University of North Carolina—updated in 2011 by Sorrie—the Atlantic and Gulf Coastal Plains Floristic Province has ca. 6,170 native plant taxa. This is an extremely rich flora, constituting some 31.8 percent of the flora native to North America. Of the 6,170 native taxa, 1,748 (including 1,628 full species and 120 infraspecific taxa, i.e., subspecies and varieties) are endemic to the Coastal Plain. This yields a respectable rate of endemism of 28.3 percent, very high for a non-tropical continental region. Moreover, fifty-one plant genera are endemic or near-endemic (> 90 percent of occurrences) to the Coastal Plain. Along with high habitat loss (well over 70 percent), this degree of endemism qualifies the Coastal Plain as a global biodiversity hotspot, although it is not recognized as such by Conservation International.

A very high proportion of the Coastal Plain endemics are associated with grasslands. Indeed, Sorrie found that 927 endemic plants of the Coastal Plain are associated with the longleaf pine ecosystem and its embedded communities such as depression wetlands. In comparison, the entire Prairies Floristic Province (the Great Plains) has only 87 endemic plant species and infraspecific taxa and no endemic genera. Only the California Floristic Province in temperate North America—with 2,125 endemic full species and fifty endemic genera—is a slightly more impressive hotspot of endemism for plants than the Coastal Plain. If we look south into Mexico, however, the Mexican Highlands Floristic Province is apparently the most diverse in North America. Approximately 4,900 (70 percent) of an estimated 7,000 plant species are endemic to the province. Patterns of endemism for taxa other than plants have not been thoroughly analyzed in the Coastal Plain or other regions of the South, so quantitative comparisons with other regions are not yet possible.

Endemics have been classified in various ways, but one simple distinction is between old species with long histories versus species that evolved relatively recently. Both types can occur, and probably often do, within a given center of endemism. Two other categories, which overlap these, are insular endemics, which evolved in isolation on islands or island-like habitat patches, and ecological endemics, which evolved strong habitat specificity in a particular

place; the Ketona Glades endemics fit both categories. Ancient endemics are called *paleoendemics*, which include *taxonomic relicts*, survivors of once diverse groups, and *biogeographic relicts*, descendants of taxa that were once widespread and have retreated to restricted areas of favorable conditions in response to climate change. Paleoendemics with primitive characteristics are considered archaic taxa ("living fossils").

Commonly cited examples of southern paleoendemics are mostly from nongrassland habitats, for example Florida yew (*Taxus floridana*), Florida tor-reya (*Torreya taxifolia*), and yellow anise (*Illicium parviflorum*), which are relicts that found refuge within mesic forests in steep ravines of northern Florida during the Pleistocene glaciations. Nevertheless, in 1993 Robert Thorne called attention to a substantial number of "presumably archaic genera" in the Coastal Plain flora, including grassland plants such as *Sarracenia* (pitcher plants), *Dionaea* (Venus fly-trap), and *Taxodium* (bald and pond cypress, which occur in savannas as well as in more closed swamp-forest conditions). Sorrie and Weakley looked more closely at the flora of the Coastal Plain and identified several additional plant genera that are probably archaic, based in part on their being monotypic (represented in the modern flora by only one species with no living close rela-tives). An impressive 72 percent of the genera endemic to the Coastal Plain are monotypic. Besides *Dionaea*, examples of archaic monotypic genera associated (at least in part) with grasslands include the following:

- *Chapmannia* (represented by the Florida alicia, *C. floridana*, found in pine sandhills, flatwoods, and scrub in peninsular Florida)
- *Chrysoma* (represented by bush goldenrod, *C. pauciflosculosa*, which inhab-its scrub, coastal grasslands, and sandhills)
- *Hartwrightia* (represented by *H. floridana*, Florida hartwrightia, found in seepage areas and pine flatwoods)
- *Lophiola* (represented by *L. aurea*, goldencrest, a resident of bogs, marshes, and pine flatwoods)
- *Pyxidanthera* (now recognized as consisting of two species, *P. barbulata* and *P. brevifolia*, common and sandhills pixie-moss, respectively, and inhabiting pine savannas and flatwoods—very xeric in the case of *P. brevifolia*)
- *Schwalbea* (represented by *S. americana*, chaffseed, found in savannas and sandhill-pocosin ecotones and dependent on high fire frequency)
- *Serenoa* (represented by *S. repens*, the well-known saw palmetto of pine flatwoods, dry prairies, and hammocks)
- *Stokesia* (represented by *S. laevis*, Stoke's aster, of wet flatwoods, savannas, bogs, and seepage areas)

• *Zenobia* (represented by *Z. pulverulenta*, honeycup, which inhabits poco-
sins, Carolina bays, and margins of pineland ponds).

Aware of the paradox of ancient taxa occurring on ostensibly young ter-
rain, Sorrie and Weakley point out that portions of the Coastal Plain have been
available for colonization by plants since the Eocene, fifty million years ago.
Moreover, as reviewed in chapter 2, fossil pollen data and vertebrate fossils sug-
gest that the southern portion of the Coastal Plain has been remarkably stable
climatically for tens of thousands to perhaps millions of years.

A neoendemic species, subspecies, or variety may have a limited distribu-
tion because it only recently diverged from its parent species and has not had
sufficient time to expand its range. Endemic taxa at the subspecies or varietal
levels, and some full species, are known in ecosystems that may be only a few
thousand years old. A splendid example of probable neoendemics is the group
of narrow endemic plants and animals associated with pine rocklands and other
habitats in the Florida Keys, especially the Lower Keys. Most of the endemics of
the Florida Keys are classified as subspecies or varieties, rather than full species.
These infraspecific taxa include the Key deer (*Odocoileus virginianus clavium*),
Lower Keys marsh rabbit (*Sylvilagus palustris hefneri*), Key Largo woodrat (*Neo-
toma floridana smalli*), Florida Keys mole skink (*Plestiodon egregius egregius*), Stock
Island tree snail (*Orthalicus reses reses*), Big Pine partridge pea (*Chamaecrista lin-
eata* var. *keyensis*; plate 21), and rockland (deltoid) spurge (*Chamaesyce deltoidea*
ssp. *serpyllum*). The only full-species endemics on the Keys that I am aware
of, given current taxonomy, are the semaphore cactus (*Conseola corallicola*),
Blodgett's wild mercury (*Argythamnia blodgettii*), the Key silverside (*Menidia con-
chorum*), and possibly a rice rat (*Oryzomys*, at various times recognized as a full
species, subspecies, or population). Most of the rare taxa that are restricted to
the Keys in the United States have populations in the West Indies, the Yucatan
peninsula, or in Central and South America.

That the majority of the endemic taxa on the Florida Keys are not full
species suggests recent origin. Full species take time to evolve—how much
time is highly variable and depends on generation length, rate of mutation,
level of gene flow, strength of selection or drift, and other factors. Most of
the endemics of the Keys have not had time to diverge enough from parental
populations to qualify as full species. From geologic evidence we know that
the Keys were completely inundated during the most recent interglacial period
about 125,000 years ago; this is when the massive coral reef, which provides
the foundation for the Keys, developed. The Keys became connected to the
mainland as sea level declined to a low point during the Last Glacial Maximum;

at that time the Florida Peninsula was more than twice its present size (see fig. 2.4). The Keys then gradually became isolated as sea level rose erratically over the last 20,000 years. The endemic subspecies and varieties found in the Lower Keys today may have begun their independent evolutionary trajectories tens of thousands of years ago, but only during the last six thousand years or so have they been isolated enough, with limited or no gene flow with populations on the mainland or on other islands, to develop into distinct taxa. They were able to cope with minor fluctuations in sea level during the last six thousand years, but are unlikely to survive the one- to two-meter rise that they will probably experience by the year 2100.

CENTERS OF ENDEMISM IN THE SOUTH

The best coarse-scale representation of centers of endemism for the United States is a map produced by NatureServe showing rarity-weighted species richness (plate 1). The first version of this map appeared in the marvelous 2000 book on biodiversity in the United States, *Precious Heritage*, edited by Bruce Stein and colleagues. The rarity-weighted richness index weights the richness of species within the categories of critically imperiled globally (G1) and imperiled globally (G2) by the narrowness of their distributions (see table 1.4 for rank definitions). The G1 and G2 categories include all narrow or local endemics, but not all regional endemics. The analysis combines data from all taxonomic groups for which distributional information is available. Distribution maps for the G1 and G2 species are overlaid on a grid of equal-area hexagons, with each hexagon about 160,000 acres in area. The number of imperiled species within each hexagon is computed, with each species weighted according to the narrowness of its range—the smaller the range (i.e., one hexagon being the smallest), the greater the weight. The map thus captures concentrations of limited-range (narrow endemic) species as well as the turnover of species (i.e., change in species composition or "beta diversity") among adjacent grid cells. As Bruce Sorrie points out, however, the rarity-weighted richness index undervalues regions with geographically widespread but "monochromatic" ecosystems, such as longleaf pine. Many taxa are endemic to the longleaf pine region, but are so ubiquitous that they are ranked G3 or lower—hence, they are not included in rarity-weighted richness analyses.

Plate 1 illustrates that centers of rarity-weighted richness in the United States are concentrated in Hawaii, California and portions of neighboring states, and the South. In the South the biologically hottest areas are the south-

ern Appalachians and Ridge and Valley Province from Virginia southwest to central Alabama, the Interior Low Plateaus (especially the Central Basin of Tennessee), and Florida. Isolated hotspots in the South include southeastern North Carolina, the Ouachita Mountains, the Arkansas Valley, and (a surprise to me), southern Indiana along the Ohio River, at the northern margin of my study region. The hotspot in central Texas is on the Edwards Plateau, just to the west of my study region. The areas shown in red and orange in plate 1, though not sufficient for representing biodiversity, are irreplaceable. If we lose these areas to agriculture or urban sprawl, we lose their endemic species. Areas in yellow are also of substantial value and can serve as connectors or buffers for the highest-value areas, as can the intermediate-value areas of green across broader regions.

Several groups of organisms reach their highest richness and endemism globally within the South, particularly within the Tennessee-Cumberland River basin and secondarily the Mobile basin (Alabama River system) of Alabama and portions of Mississippi, Georgia, and Tennessee. As documented in *Precious Heritage*, these taxa include freshwater mussels and snails, crayfishes, caddisflies, mayflies, and stoneflies—indeed, there are more species in each of these groups within the United States (concentrated in the South) than in any other nation on earth. Most of these species are narrow endemics. Thus, the peaks in rarity-weighted richness in western Virginia, eastern Tennessee, Kentucky, and northern Alabama (plate 1) reflect mostly freshwater taxa. Salamanders and plants are also rich in endemics in the southern Appalachians. Subterranean (cave and spring) species are richest in the southern Appalachians, Alabama, Texas, Arkansas, and north and central Florida, and their distributions tend to be extremely narrow. North Florida (especially the Panhandle) has the highest combined richness of reptiles and amphibians in North America north of Mexico, with most of these species narrowly distributed. Hotspots of limited-range species richness in the Coastal Plain can be attributed largely to plants—especially grassland-associated plants.

In 2001 James Estill and Mitchell Cruzan published a geographically extensive treatment of the distribution of endemic plants of the South. Their study area is virtually identical to mine, except they restricted their analysis to the Humid Temperate Domain, thus excluding south Florida, a center of endemism (plate 1) within the Humid Tropical Domain. Estill and Cruzan focused on endemics occurring in twenty-five or fewer counties across the region. The average size of a county in Florida, for example, is 805 square miles (515,200 acres); 25 counties would add up to nearly thirteen million acres. Still, using this criterion, 326 out of 808 potential endemics were removed because they occurred in more than 25 counties. The analyzed endemics totaled 482

taxa, with 60 percent of 1,232 counties in the study region having at least one 25-county endemic present; every county in Florida had at least one.

Estill and Cruzan produced a grid of endemic plant species richness, based on county-level values, and then smoothed the grid to produce contour lines with a density interval of five endemic species. The resulting isocline map (fig. 3.1) delineates six major regions of plant endemism within the South: (1) Central Peninsular Florida (where the narrowest endemics inhabit the Florida scrub ecosystem, followed by longleaf pine sandhills); (2) the Apalachicola Region of the Florida Panhandle and adjacent Georgia and Alabama (where the narrow endemics include species associated with longleaf pine and mesic forest ecosystems); (3) the southern Appalachians, especially in southwestern North Carolina and primarily constituting mesic forest species; (4) the Central Basin of Tennessee, where the endemics are largely associated with cedar glades; (5) the Mid-Atlantic Coastal Plain of southeastern North Carolina and northeastern South Carolina, where the endemics largely occur in longleaf pine ecosystems; and (6) the West Gulf Coastal Plain centered on the border of Louisiana
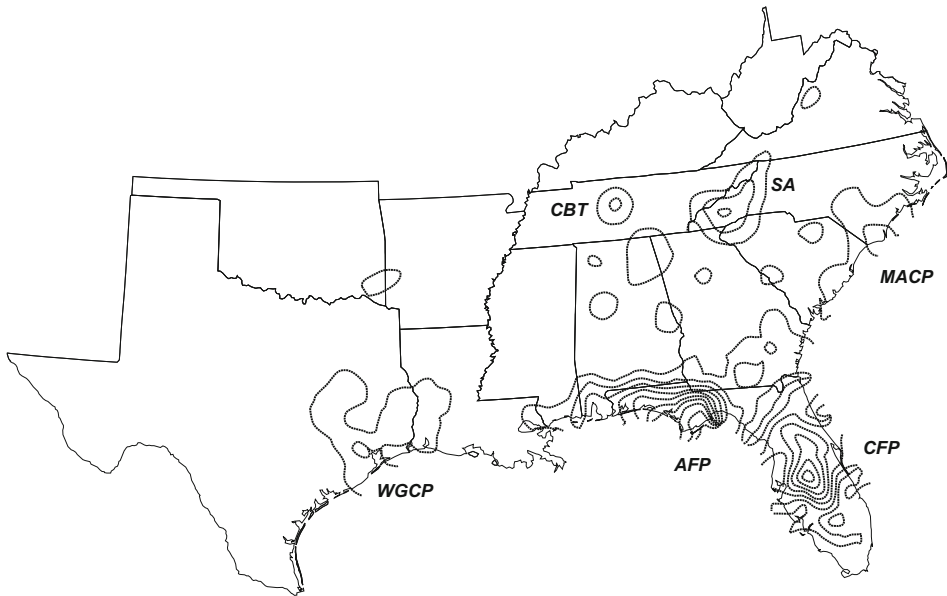
Figure 3.1. Centers of plant endemism in the South, with an endemic defined as a plant species (i.e., not infraspecific taxa) restricted to 25 or fewer counties across the region. WGCP = Western Gulf Coastal Plain; CBT = Central Basin of Tennessee; SA = Southern Appalachians; MACP = Mid-Atlantic Coastal Plain; AFP = Apalachicola region of the Florida Panhandle; CPF = Central Peninsular Florida. South Florida is a center of plant endemism not recognized in this study because it falls outside the temperate zone delineation of the study region. Adapted from Estill and Cruzan (2001).

and Texas, where once again the endemics are associated with longleaf pine ecosystems. Note that these hotspots are generally consistent with the rarity-weighted richness index (plate 1), despite the different taxa and scale of analysis. Estill and Cruzan note that different mechanisms were probably responsible for creating high endemism in these six regions. For example, endemism within the Central Basin of Tennessee probably reflects ecological specialization to limestone glades, whereas endemism in the Coastal Plain reflects climatic stability and Pleistocene refugia, while not ruling out ecological specialization or other mechanisms as contributors.

Sorrie and Weakley, in the same issue of *Castanea* as the Estill and Cruzan paper, identified centers of endemism for plants in the Coastal Plain. Their analysis has been since updated. Based on distributional data obtained from many sources, eight broad regions of the Coastal Plain (one of which extends north of my study region and another south into Mexico) stand out as hotspots of plant endemism:

- Mid-Atlantic Coastal Plain, from southeastern Virginia to southern South Carolina
- South Atlantic Coastal Plain, from central Georgia to northern peninsular Florida
- Temperate Central Florida Peninsula (including the Lake Wales Ridge) [note that I consider this region primarily subtropical]
- East Gulf Coastal Plain, from southwestern Georgia and the Florida Panhandle west to southeastern Louisiana
- West Gulf Coastal Plain, from western Louisiana to eastern Texas, southern Arkansas, and southeastern Oklahoma
- Northeast Coastal Plain, from the Delmarva Peninsula of Delaware, Maryland, Virginia, and northward
- Subtropical southern Florida Peninsula [note that I consider this region subtropical to tropical]
- Southern Texas to eastern Tamaulipas, Mexico (the Tamaulipan Scrub region)

Sorrie and Weakley suggest several factors that might explain high plant species richness and endemism in the Coastal Plain: (1) Soil diversity is high, with eight of the ten soil orders recognized globally, with many soil textures, and with pH ranging from 3 to 8.5. (2) Environmental gradients (especially substrate, nutrient levels, and hydrology) are rich and complex, with community turnover occurring rapidly along these gradients. (3) The "disclimax"

conditions created by the highest lightning fire frequency on the continent favors speciation and coexistence of plant species. (4) The relative stability of the climate and the landscape (periodic inundation of low coastal areas notwithstanding) allowed the region to serve as a refugium for northern taxa and as a template for colonization by species from many regions and for subsequent speciation.

To reiterate, the presence of so many narrow endemics—many of them relicts in southern grasslands—suggests that many of these communities are quite old. High endemism contradicts the commonly held belief, reinforced by popular books such as Charles Mann's *1491*, that these grasslands were created by human activity, such as fires set by Indians. As further support for the antiquity of southern grasslands, other grassland-associated taxa have high rates of endemism in the South, although none has been analyzed as thoroughly as plants. According to the wonderful little book *Grasshoppers of Florida*, by John Capinera and coauthors, eighteen (26 percent) of the seventy grasshopper species known from Florida are strict endemics, and another six species (9 percent) are near-endemics. JoVonn Hill of Mississippi State University tells me that these numbers are conservative, and many distinct taxa are not recognized. Hence, the true percentage of endemic grasshoppers is probably higher. Grasshoppers, as their name implies, are largely grassland associated. It is highly unlikely that many of these full species of grasshoppers evolved during the relatively brief period that humans have occupied this region.

PERIPHERALS AND DISJUNCTS

Peripheral populations are on the edge of the range of their respective species. A disjunct population is a peripheral population that is separated from the rest of its species' distribution by some distance. Barring extinction, today's disjuncts may well become tomorrow's local endemics. The phenomenon of disjunction also include cases where closely related taxa occur in widely separate regions but are absent from the intervening region (see chap. 2). Aside from being exciting finds for the naturalist, peripheral and disjunct populations can be of high conservation value. But is this always so?

In a 1995 article Peter Lesica and Fred Allendorf asked the question, "When are peripheral populations valuable for conservation?" This is a practically relevant question, because state chapters of TNC or government agencies might spend considerable money and effort acquiring sites to protect peripheral pop-

ulations that have widespread distributions and are common elsewhere. Lesica and Allendorf answered their question by concluding that it is often important to protect peripheral populations:

> Peripheral populations are expected to diverge from central populations as a result of the interwoven effects of isolation, genetic drift, and natural selection. Available empirical evidence suggests that peripheral populations are often genetically and morphologically divergent from central populations. The long-term conservation of species is likely to depend upon the protection of genetically distinct populations. In addition, peripheral populations are potentially important sites of future speciation events. Under some circumstances, conservation of peripheral populations may be beneficial to the protection of the evolutionary process.

The only situations in which protection of peripheral populations might be of questionable value, Lesica and Allendorf reasoned, is when they have become isolated only recently, for instance due to recent range contractions, or when they are so close to central populations that strong gene flow precludes genetic differentiation. Due to isolation and the well-documented phenomenon of allopatric speciation (i.e., differentiation and reproductive isolation of geographically isolated populations), we should expect that peripheral and disjunct populations are often on the cutting edge of evolution—on the verge of becoming new species. Disjunctions can be informative of biogeographic history (see chap. 2) and provide insight into the evolutionary trajectories of species and the lineages of which they are branches. Studies of related taxa occurring in widely separated regions can tell us about the types of species and ecological traits that are more or less susceptible to change during evolution, and about how evolution may be constrained by climate, competition with other species, or other factors.

One of my favorite disjunctions occurs on the delightful island of Cayo Costa, off the southwestern coast of Florida and only reachable by boat. I went there twice in 2010 and 2011, not to sunbathe on the white-sand beaches and take in the subtropical scenery, but to see a particular species of grass and the unique coastal grassland in which it occurs. Hairy grama (*Bouteloua hirsuta*) is distributed from Texas through much of the shortgrass prairie and desert grasslands of the Great Plains and the American Southwest, southward into Mexico. Several disjunct occurrences have been reported from the Southeast: in Georgia and South Carolina (which are introduced plants found at wool-combing mills or similar places), and in six counties in the Florida Peninsula.

Most of these records are old, and some populations are extinct. The most intriguing occurrences are from coastal grasslands on a few islands in the Gulf of Mexico off southwestern Florida. Surviving examples of these unique grass-lands are restricted to Cayo Costa—which is almost entirely a state park and one of the most pristine islands in Florida—and a small part of adjacent North Captiva Island. On these islands, *Bouteloua hirsuta* is not just occasional—it is the dominant grass in the coastal grassland/savanna community. There are mil-lions of individuals (plate 22).

How did this grass from the shortgrass prairies and deserts of the West come to dominate a humid subtropical island in southwestern Florida? There are two categories of answers, often argued in the literature of biogeography as competing hypotheses: long-distance dispersal versus vicariance (i.e., geographic isolation of previously connected populations). The vicariance argument would suggest that hairy grama was once distributed continuously or nearly so from Florida to the West, but barriers developed that eliminated central populations and separated populations on either end of the original range. I favor this explanation for hairy grama. Although taxa differ in their biogeographic histories, most grassland taxa in the East that now occur in disjunct locations were probably more widespread during hotter, drier periods of the past and became restricted to extreme and often droughty sites such as sand dunes, glades, powerline corridors, roadsides, and other refugia as climate changed toward more mesic conditions. In this sense, these species and communities are relicts of a past climate. Exceptions to this pattern occur when formerly widespread species become restricted to isolated sites due to conversion and fragmentation of habitat or fire exclusion by humans. Longleaf pine communities, for instance, are not relicts—they are remnants of an extensive distribution that was diminished by human activity.

In the specific case of this little plant with the funny name, I suspect hairy grama was a member of the broad prairie/savanna/woodland ecosystem that stretched across the Gulf of Mexico Coastal Plain in the past (see chap. 2). We ought to conserve disjunct populations, in part, so that future generations will be able to ponder and appreciate the deep history of their homes.

Other interesting disjunctions occur within the South. The pine barrens treefrog (*Hyla andersonii*) has three disjunct areas of occurrence in the Coastal Plain: the Pine Barrens of New Jersey, the upper Coastal Plain and parts of lower Coastal Plain of North and South Carolina (in the vicinity of the Green Swamp), and the western Florida Panhandle and adjacent Alabama. The Flor-ida/Alabama population, first reported in 1970 by biologist Steve Christman, lies some 750 kilometers (466 miles) southwest of the nearest South Carolina population. This frog also was reported in Georgia from an old record of a single

specimen. The current distribution almost certainly reflects vicariance, with the surviving populations being relicts from a broader and perhaps contiguous distribution in the past. The frog is restricted to similar habitats in each of the three regions in which it is extant: localized wetlands such as hillside seepage bogs, pine barrens, and headwater swamps. Nonbreeding habitat is primarily pine-oak areas adjacent to breeding areas. This species is intolerant of closed-canopy conditions; hence, it depends on the frequent fire characteristic of pinelands and seepage bogs. Discontinuous distributions are also characteristic of some grassland plants within my study region, particularly between the Cape Fear Arch uplift (i.e., the Green Swamp and nearby areas) in southeastern North Carolina and adjacent South Carolina, and the Apalachicola lowlands and other areas of Panhandle Florida and adjacent Alabama. These plants include rush-featherling (*Pleea tenuifolia*) and Cooley's meadowrue (*Thalictrum cooleyi*).

SPECIES RICHNESS

Species richness has long been of interest to biogeographers and ecologists. Two of the most publication-generating questions of the last two centuries are these: (1) What accounts for the latitudinal diversity gradient, where species richness increases from the poles to the equator? and (2) What causes the species-area relationship, where the number of species increases with the area of habitat? Entire books have been written on these questions; I briefly review a few points before moving to the topic of species richness in the South, particularly within grasslands. At the outset, it is interesting to note that the two patterns—the latitudinal gradient and the species-area relationship—are connected. As discussed for North American plants by Hong Qian and coauthors, species accumulate faster with increasing area as latitude declines; that is, the slope of the species-area relationship grows steeper, concomitant with the higher level of endemism at lower latitudes. Still, the root causes of these patterns are not entirely understood—there's plenty for naturalists yet to discover!

The latitudinal gradient in diversity has been explained in several ways:

- Extinction rates are reduced at lower latitudes (i.e., less stressful environments, no continental glaciations; low-lying coastal areas subject to inundation by sea-level rise constitute an exception to this pattern).
- Speciation is higher at lower latitudes, and a positive feedback exists between the number of species and the rate of diversification—"diversity begets diversity" as coevolutionary relationships develop.

- Low latitudes have higher primary productivity than high latitudes, due to greater solar radiation and warmth, which supports more plant biomass that can be apportioned into species (with ramifications through the food web).
- Lower latitudes have more contiguous area within a climatic zone, with the largest continuous biome being tropical forest—hence, the species-area effect comes into play.
- Moisture is also important, as many species require abundant water (so, warm rainy places have highest species richness).

For most taxa, climate is the best predictor of species richness over broad spatial extents. In 2003 Bradford Hawkins and coauthors reviewed the empirical literature on the relationship between climate and richness. In eighty-two of eighty-five cases they examined, measures of energy, water, or water-energy balance explained variation in species richness better than other climatic or nonclimatic variables. Water explains most of the variation at low latitudes, whereas energy (for animals) or water-energy (for plants) explains the most variation at high latitudes. Warm, wet places have more species within most taxonomic groups. Why? One hypothesis is that energy constrains richness via bottom-up processes, such that plant richness is limited by solar energy and water, herbivore richness depends on net primary productivity and the richness of plants, and predator richness depends on the secondary production and richness of herbivores and lower-level predators. A competing hypothesis is based on the physiological requirements of organisms for ambient energy (warmth). Support for this hypothesis comes from the frost intolerance of many plants and the susceptibility of many animals to hypothermia and freezing. These hypotheses, as usual, are not mutually exclusive.

Most terrestrial taxa in North America show increasing richness with decreasing latitude (for terrestrial vertebrates, see plate 2). The prominent exception is in the Florida Peninsula, where richness of most taxa declines from north to south. This phenomenon has been explained by the "peninsula effect," where colonization or recolonization of populations is reduced, due to isolation, as one proceeds down a peninsula and away from the mainland species source. Hence, if a species goes extinct locally on a peninsula, like an island, it may not be reestablished. Nevertheless, Bruce Means and Dan Simberloff showed that, for Florida reptiles and amphibians, a decline in habitat diversity down the peninsula better explains this pattern.

Other explanations for the latitudinal gradient also may apply to southern grasslands. As noted, grasslands of the unglaciated South have much higher rich-

ness and endemism than grasslands of the Great Plains, which (except at their southern extent) were glaciated or at least colder than the Southeast during glacial periods. More southern and coastal areas enjoyed relative climatic stability (albeit not sea-level stability) and warmth over long periods of time, whereas areas closer to the glacial margin were boreal or tundra during full-glacial periods. Temperate plants and animals must recolonize northern or interior areas from long distances after each glaciation—unless they inhabited "microrefugia" out of equilibrium with the regional climate, a likely scenario for some edaphic grasslands (those favored by particular soil conditions; see chap. 4).

Within a region, a useful way to consider species richness is to recognize that it represents a balance between speciation and immigration (which add species) versus extinction and emigration (which subtract species). The theory of island biogeography, devised by Robert MacArthur and Ed Wilson, posits that the number of species on an island represents an equilibrium between immigration of new species to the island and extinction of species already present. Larger islands or island-like patches of habitat (such as many grasslands in the South) are predicted to hold more species because, on average, population sizes are larger and large populations are less susceptible to extinction. Islands that are closer to the mainland or a large species source pool should also contain more species at equilibrium because immigration rates will be higher. The "rescue effect" describes how immigration to an island not only leads to recolonization of some extirpated species, but can also bolster (demographically or genetically) small populations that would otherwise be headed toward extinction. Island size should affect immigration rates, as larger islands are bigger targets for dispersing individuals or seeds. For these reasons, all else being equal, we should expect larger patches of grassland to be more species rich.

All else is usually not equal, however, and empirical tests of island biogeographic theory show mixed results. This is to be expected, because many factors other than immigration and extinction, and even patch/island area, influence species richness. Consider habitat diversity. Each species, through natural selection acting primarily on individuals, adapts to a particular set of habitat conditions. Some species are more specialized in their habitat requirements than others, and particularly for specialists, a greater variety of habitats will result in more species coexisting within a given area. Therefore, a small island that is extremely heterogeneous, with high topographic complexity and a diversity of soil types, might contain more species than a larger island that is homogeneous. In general, however, larger islands contain more habitat diversity than smaller islands, and many ecologists suggest this is the primary explanation for the species-area relationship. Although it has shown more restricted predictive

ability than originally hoped, island biogeographic theory played an important role by stimulating ecologists and conservationists to think about how habitat area and isolation affect extinction risk.

SPECIES RICHNESS IN SOUTHERN GRASSLANDS

Southern grasslands are remarkably species rich. The Coastal Plain alone contains nearly one-third of the flora native to North America, with a high proportion of these plants (especially the endemics) associated with longleaf pine communities and other grasslands. These facts bear repeating because they remain an esoteric secret held by a relative handful of botanists and a few other naturalists. When I inform biologists from outside the South that southern grasslands are more species rich (at least in plants) at a fine scale (say, less than 100 square meters) than tropical forests, they are inevitably amazed or incredulous. Admittedly, this comparison is a bit "apples and oranges." Furthermore, tropical grasslands have not been surveyed on a very fine scale. At least some tropical savannas, such as the Cerrado of Brazil, are richer than grasslands of the southern United States on the scale of 1,000 square meters and larger (table 3.2).

Plants

Species richness is very much on my mind as I follow Bob Peet of the University of North Carolina, his PhD student Kyle Palmquist, and Mike Schafale of the North Carolina Heritage Program out into the Big Island Savanna in the Green Swamp Preserve on the first of June 2011 (plate 26). It is midafternoon, and we have already spent a wondrous, though hot, day wandering through a half dozen other pine savannas. The savannas here on the Cape Fear Arch are patches of various size in a matrix of pocosin wetland dominated by a dense thicket of primarily titi (*Cyrilla racemiflora*), fetterbush (*Lyonia lucida*), and pond pine (*Pinus serotina*). Professor Peet took us on one of his notorious "pocosin tours," where we struggled through the tangled, claustrophobic mass of woody stems and vines to get a true feeling of what a pocosin is like. The ecotone between the savanna and pocosin communities is typically very abrupt and does not reflect soil differences between the two communities.

I was eager to enter Big Island Savanna because it has among the highest recorded fine-scale plant species richness of any longleaf pine community and among the highest of any community in the world. In their study here in the early 1980s, Joan Walker and Bob Peet found more than fifty species in some

Table 3.2. Vascular plant species richness within plots, 0.01–1,000 m^2.

	Area (m^2)					
	0.01	**0.1**	**1**	**10**	**100**	**1,000**
Longleaf pine: Xeric sand barrens and uplands						
North Carolina	0.5	1.3	3.2	6.6	12.9	22.5
Florida	1.1	3.2	9.5	20.9	42.6	74.1
Longleaf pine: Subxeric sandy uplands						
North Carolina	0.8	2.7	5.5	10.3	19.1	34.8
Florida	1.1	3.9	11.2	24.4	48.1	84.0
Longleaf pine: Silty and clayey uplands						
North Carolina	2.7	7.5	15.7	27.1	51.7	81.4
Florida	2.1	7.1	17.1	32.8	63.7	107.5
Louisiana (loess plain)	(11)	(21)	(41)	(72)	103 (118)	(170)
Longleaf pine: Flatwoods (spodosol)						
North Carolina	2.3	6.0	11.2	18.7	33.2	54.6
Florida	1.8	5.2	11.7	21.4	40.0	71.2
Florida (Osceola NF)	(8)	(10)	(21)	(31)	(46)	(68)
Longleaf pine: Savannas (ultisols)						
North Carolina	4.4	11.3	22.4	36.0	61.1	94.8
South Carolina	(9)	(27)	(> 50)	(70)	(91)	(128)
Florida	3.1	9.2	18.7 (46)	30.4	54.5	89.8
Florida (Avon Park AFR, wet–mesic alfisol)	(8)	(16)	(29)	(45)	(69)	(109)
Florida dry prairie (average from 4 sites and 6 community types)	—	—	21.6	—	—	—
Florida dry prairie (calcareous wet prairie type)	(8)	(27)	(49)	(69)	(99)	(171–193)
Rockridge pine savanna (pine rockland)						
Florida (Everglades NP)	(15)	(21)	(42)	(61)	(86)	(132)
Rockridge short hydroperiod calcareous prairie ("marl prairie")						
Florida (Everglades NP)	(14)	(27)	(42)	(57)	(84)	(104)
North American tallgrass prairies			18 (28)			
Alvar limestone grassland Öland, Sweden	11.7	—	—	—	—	—
Wooded calcicolous meadow Estonia	(25)	—	(63)	—	—	—
South African fynbos						(103)

(table continues)

Table 3.2. continued

	Area (m²)					
	0.01	**0.1**	**1**	**10**	**100**	**1,000**
Southwestern Australia heath						65 (82)
Australia, West Head woodlands						77 (93)
California woodlands, Carmel						64 (89)
Chile, coastal shrubland						(109)
Israel, disturbed shrubland						(179)
North Carolina, piedmont forest						75 (119)
Sonoran Desert						(70)
Brazil, Cerrado (tropical savanna)						(230)
Australia, Queensland lowland rainforest						140
Ghana, wet evergreen forest						(ca. 212)
Ecuador, dry forest						(173)
Ecuador, moist forest						(169)
Ecuador, wet forest						(365)

Note: Numbers refer to the mean and (maximum) number of species recorded for southern grassland types, with comparisons to other ecosystem types worldwide. In the South, sandy, xeric sites are consistently less diverse, and silty, clayey, or calcareous sites more diverse at all spatial scales. Within longleaf pine communities, savannas have the highest richness at relatively small scales (e.g., 1 m²), whereas the highest richness at the 1,000 m² scale is found in silty and clayey uplands. Across all scales in southern grasslands, richness is usually higher in recently burned plots. Differences among sites may be partially attributable to taxonomic nomenclature. Comparisons with many other communities (especially forests) are not possible because plot sizes were larger (1 hectare [10,000 m²] or greater).

Sources: Adapted from Peet (2006), with additional data from Walker and Peet (1984), Gentry and Dodson (1987), Kull et al. (1991), Wilson et al. (1995), DeCoster et al. (1999), Schmitz et al. (2002), Glitzenstein et al. (2003), Orzell and Bridges (2006a), Orzell and Bridges (2006b), and Platt et al. (2006a).

1-square-meter plots and more than forty in some 0.25-square-meter plots. Plant species richness is high here, in part, because the Cape Fear Arch has been a center of speciation for many taxa. When I ask Bob what factors provided the geographic isolation that is usually necessary for speciation, he explains that the poorly drained, seasonally saturated sandy to silty soils here are isolated from similar edaphic conditions by a large area of different soils; one has to go five hundred miles to the Apalachicola Lowlands of the Florida Panhandle (another richness hotspot) to find similar environmental conditions. With so much speciation, many of the plant taxa here are endemic, with ca. 22 strict endemics and just as many near-endemics, which have at least 75 percent of their global distribution restricted to this area.

Among the strict endemics is one I always wanted to see in the wild—the incredible Venus fly-trap (*Dionaea muscipula*). Charles Darwin considered this

plant "one of the most wonderful in the world." As a narrow endemic in a monotypic genus (and formerly a monotypic family, but now included within the sundew family, Droseraceae), this plant is about as phylogenetically distinct as you can find. Its trap leaves, which vary in size, capture insects about five millimeters smaller than the length of the trap. As an adaptation to minimize false alarms, the trap leaf closes when an arthropod contacts at least two trigger hairs inside the trap leaf within a twenty- to forty-second interval, at which point the leaf snaps shut in about one-tenth of a second. Over a period of a day or two, the arthropod body is digested. Other strict endemics of the Cape Fear Arch we observed include the savanna indigo-bush (*Amorpha confusa*), pocosin loosestrife (*Lysimachia asperulifolia*), and Carolina goldenrod (*Solidago pulchra*). The near-endemic Carolina dropseed (*Sporobolus pinetorum*), a "wiregrass" that superficially resembles the better known wiregrass (*Aristida stricta*), dominates the groundcover over much of these savannas.

As we ambled farther into Big Island Savanna, I began to notice features of the habitat that might partially account for the extraordinary richness. In many places it was difficult to walk without twisting an ankle due to the pronounced microtopography created by the grass clumps and intervening hollows. Such microtopography can produce a variety of "regeneration niches" for plants, in which seeds of many species with slightly different requirements can germinate and grow. Soils are also quite heterogeneous in these savannas. Richard LeBlond points out that most of the narrow endemics are associated with ultisols (acidic silty or clay-rich soils, often reddish), but others are found on both ultisols and spodosols (ashy gray acidic sandy soils with a strongly leached surface layer), and still others only on entisols (well-drained sandy soils with little or no soil horizon development). In his 2006 chapter on ecological classification of longleaf pine communities, Peet notes that the siltier sites—and we saw these as distinct "microsites" within the Big Island Savanna—are dominated by the grasses *Aristida stricta*, *Schizachyrium scoparium*, and *Sporobolus pinetorum*. The *Aristida* drops out in wetter pockets and is replaced by greater cover of toothache grass (*Ctenium aromaticum*), cutover muhly (*Muhlenbergia expansa*), and other grasses. The most fertile areas often have abundant switch cane and lower plant species richness.

Other environmental factors contribute to this heterogeneity. For instance, subtle differences in the timing of rainfall or fire from year to year will favor some species over others. In a review of the effects of season of burn on plants in longleaf pine communities, which included an original study in northern Florida flatwoods, Donna Streng and coauthors showed that virtually all the dominant grasses flower more abundantly after growing-season fires (i.e., the

natural lightning fire season) than after dormant-season fires. The same was true for narrowleaf silkgrass (*Pityopsis graminifolia*), a goldenaster. The timing of fire within the growing season is also influential. Some species, such as tooth-ache grass, flower most profusely after fire early in the season, whereas others, such as bluestems (*Andropogon* spp.), flower more after later burns. In Streng's study, plant species composition in pine flatwoods did not change with season of burn, but in pine sandhills, a couple of species (wiregrass and a blazing-star, *Liatris*) increased following growing-season burns, whereas needleleaf pani-cum (*Dichanthelium aciculare*) increased after dormant-season burns. In another study, Douglas Goldman and Steve Orzell found that manyflower grasspink (*Calopogon multiflorus*) contradicts the usual trend by showing a strong flower-ing response to dormant-season (January to early March) fire, flowering rarely in years without fire or after fires later in the spring in peninsular Florida. This response may be an adaptation to escape competition from the multitude of species that flower within the main fire season. An implication from these studies is that even slight differences in timing of fire from year to year may promote coexistence of a larger number of species, whereas identical fire tim-ing would favor species that prosper under those particular conditions at the expense of others.

　　As we walked through Big Island, identifying and admiring the plants, Bob showed us the patchiness of the plant associations. As we went "uphill" (rela-tively speaking in this flat landscape) into more mesic or dry-mesic patches, we lost the yellow meadowbeauty (*Rhexia lutea*), but the abundance of legumes increased and we gained tall meadowbeauty (*R. alifanus*), the tallest and showi-est of the meadowbeauties; Mohr's eupatorium (*Eupatorium mohrii*); and com-mon roundleaf eupatorium (*E. rotundifolium*). Proceeding back downhill, orchids increased with the siltier, wetter conditions, and *Rhexia lutea* returned. This rich, fine-scale mosaic of soil moisture, soil particle size, microtopogra-phy, and other environmental conditions—such as annual variation in fire and rainfall—surely explains, in large part, the high richness at the site level in this savanna. Still, I am left wondering, in the most positive sense of that term, how this observable heterogeneity at the scale of several meters can explain the pres-ence of forty to fifty plant species in one square meter.

　　Table 3.2 provides examples of plant species richness values from various southern grasslands within plots ranging from 0.01 square meter to 1,000 square meters in size. Values from other species-rich grasslands and other communities elsewhere in the world are included for comparison. Comparisons are most informative when studies use the same plot sizes; richness values derived from other sampling methods, such as points along transects or whole-site invento-

ries, are not directly comparable. Differences in taxonomic nomenclature can also frustrate comparisons. For example, the sites in table 3.2 from south-central and south Florida were inventoried using a conservative taxonomy, in which some taxa recognized by other authorities are not recognized or are considered synonymous with referenced taxa, whereas species numbers for other sites reflect the more speciose taxonomy of Alan Weakley.

An interesting phenomenon is the variety of spatial scales at which different communities stand out as most diverse. This is a reflection of different rates of species accumulation with increasing area, in turn a consequence of complex and poorly understood abiotic (e.g., substrate heterogeneity) and biotic (e.g., competition or herbivory) mechanisms operating somewhat differently in various communities at different spatial extents. Peet found that the highest plant richness at relatively fine scales is in savannas, such as Big Island, whereas silty or clayey uplands have the highest richness at the 1,000-square-meter scale. At all spatial scales, silty, clayey, or calcareous sites are more diverse than dry, sandy sites, and richness increases with fire frequency. Walker and Peet found that annually burned savannas in the Green Swamp average 26 percent more plant species per square meter than less frequently burned sites. Similarly, in European grasslands and many prairies of the North American Prairie Region, moderately to intensively grazed sites are typically more diverse than ungrazed sites, likely reflecting coevolution of grasses and other prairie plants with large herbivores.

How do species richness figures from grasslands compare to the most species-rich terrestrial communities in the world—tropical forests? Below 100 square meters, the richest temperate grasslands (and very likely some tropical grasslands) surpass tropical forests. Somewhere between 100 square meters and 1,000 square meters, wet tropical forests begin to take the lead. Comparisons are challenging because most surveys of plant species richness in tropical forests have been limited to trees (i.e., woody stems greater than ten centimeters in diameter at breast height [dbh]). Al Gentry, in a 1988 paper, reported values of woody plant species richness up to three hundred species per hectare (10,000 square meters or 2.47 acres: 283 trees > 10 centimeters dbh and seventeen lianas [woody vines]) in upper Amazonian forests of Peru, which may be the highest woody plant species richness globally. A year earlier, Al Gentry and Calaway Dodson published the first account of species richness of "nontrees," as well as trees, in tropical forests and compared these richness values at the 1,000-square-meter (0.1-hectare) scale with other plant communities globally. They found an incredible 365 species in their richest site, a wet forest (Rio Palenque) in Ecuador. Life-forms other than trees composed most of this richness, with more than one-third of the species being epiphytes.

Of the site-level factors associated with species-rich grasslands, four stand out:

Nutrient limitation

One might expect the most nutrient-rich and productive sites to support the greatest diversity of plants, but in fact such sites usually are dominated by a relatively small suite of species that are able to best take advantage of those nutrients (for example, nitrogen), grow rapidly, and shade out others. In general, southern grasslands occur on rather poor soils with low organic and nutrient content. Other species-rich grasslands worldwide tend to be oligotrophic (nutrient poor) rather than eutrophic (nutrient rich). A shortage of nutrients in the soil prevents superior nutrient-users from monopolizing the sites, hence enhancing species richness. Some southern grasslands, such as longleaf pine communities, are found on virtually pure sand and are quite species rich, although as noted above, the richest sites have wetter silty, clayey, or calcareous soils (see table 3.2). Peet and colleagues further suggest that chronic disturbance, such as by fire or grazing, allows richness to increase farther across a fertility gradient before competition for light begins to reduce richness (fig. 3.2).
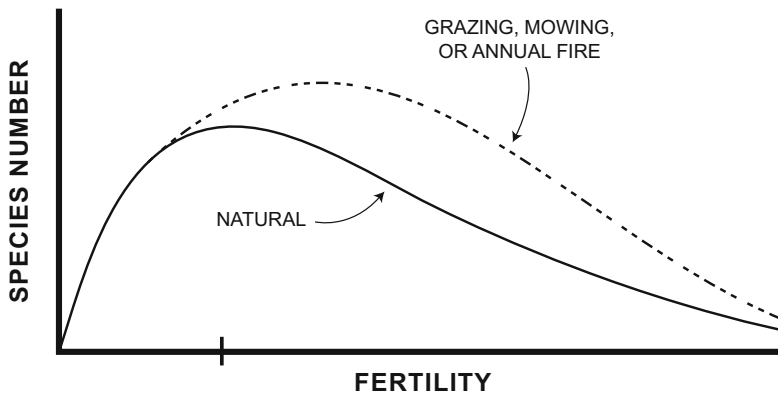
Figure 3.2. Species richness of plants often peaks at low to intermediate levels of soil fertility or productivity in grasslands, after which competition for light limits some species and reduces richness. A chronic disturbance such as fire, grazing, or mowing allows richness to increase further along a fertility gradient, peaking at somewhat higher levels of fertility. This is the pattern often seen in southern grasslands. Adapted from Peet et al. (forthcoming).

Substrate heterogeneity and microtopography

If soils and exposed rock vary in their properties, there are more niches, with plant species able to specialize on particular microenvironments where they outperform others. On a site level, barely visible and seemingly trivial vari-

ability in elevation, soil texture, soil moisture, hydroperiod (the length of time inundated each year), and other conditions allow more species to coexist than under more uniform conditions. A detailed study by Susan Carr and colleagues of 271 plots in north and central Florida found that local edaphic factors and topographic gradients had the largest influence on plant species composition and richness. In a remnant coastal prairie in Louisiana, James Grace and coauthors determined that variability in microtopography and soils best explained variation in species richness. Martin Schmitz and coauthors looked at the relationship between substrate heterogeneity and plant species richness in pine savannas (rocklands) and marl prairies (plate 20) in Everglades National Park. In the pine rocklands, variability in elevation was associated with higher richness at scales of one to ten square meters. No such relationship was evident in these particular marl prairies, which lacked fine-scale topographic variation; nevertheless, the prairies had higher small-scale richness. Schmitz and coauthors reasoned that richness should increase more rapidly with area in communities with greater microtopography.

Disturbance

The intermediate disturbance hypothesis, proposed in various forms by several ecologists, is attributed most commonly to Joe Connell due to the influence of his 1978 paper on the role of hurricanes in maintaining high species richness in tropical forests and coral reefs. The hypothesis proposes that species richness peaks at some intermediate frequency or intensity of disturbance. The logic is that at low frequencies of disturbance, superior competitors exclude many other species, but at very high frequencies, populations of many species cannot rebound quickly enough between disturbances. Severity (or intensity), which unfortunately is often conflated with frequency in this hypothesis, might have similar effects—at low severity, superior competitors drive out other species (as in high-nutrient habitats); at high severity, only the toughest, most disturbance-tolerant or best-colonizing species persist. Hence, intermediate disturbance promotes coexistence of the greatest diversity of species, including good competitors, good colonizers, and disturbance specialists.

Like many appealing general hypotheses, the intermediate disturbance hypothesis has numerous exceptions, with most studies showing nonsignificant relationships (see the 2001 paper in *Ecology* by Robin Mackey and David Currie). The hypothesis does not apply well to grasslands such as pine savannas. Brian Beckage and Jack Stout found no relationship between species richness and fire frequency in a Florida pine sandhill community. Broader comparative studies generally show highest plant species richness with the highest—not

intermediate—frequency of fire in pine savannas. Frequent fire appears to prevent competitive exclusion by exposing bare soil for colonization and growth of a diverse assortment of plant species. Intriguingly, this positive relationship between fire frequency and plant species richness is precisely opposite that in tallgrass prairie. Scott Collins and colleagues found that "there was a significant monotonic decline in species richness with increasing disturbance [fire] frequency" in the Konza Prairie in Kansas. I suspect this difference reflects the much higher lightning frequency in the South and the older and stronger evolutionary relationship between southern grassland plants and fire, compared to the Great Plains. Hence, species richness may be maximized when the current disturbance regime is most similar to the regime that the species present experienced over their evolutionary histories.

Seed availability

No matter how heterogeneous the physical environment or how optimal the nutrient and disturbance regime, a community will remain species-poor if seeds are lacking in the seed bank (i.e., a store of seeds in the soil produced by earlier residents) or are not dispersed to the site. Dispersal limitation is a well-documented phenomenon in plant ecology, where certain species are missing from sites because they are poor dispersers or the sites in question are isolated. In dry calcareous grasslands in northern Europe, M. Zobel and colleagues found through seed-sowing experiments that seed availability is the key limiting factor for species richness; as they increased "seed rain," the richness of plants in small plots increased and there was no evidence of the community becoming saturated with species. They speculated that the presence or absence of pathogens, mycorrhizal fungi (which have mutualistic relationships with the roots of many vascular plants), and herbivores have more of an impact on the colonization success of arriving seeds than does the number of functionally similar plant species in the community. A meta-analysis of the effects of seed arrival in plant communities, published by Jonathan Myers and Kyle Harms in *Ecology Letters* and involving twenty-eight studies with sixty-two experiments, found that seed arrival increases species richness in a wide variety of plant communities, but that disturbance increases the opportunities for recruitment of arriving species.

A paper that considers many of the above factors in a longleaf pine community, at the evocative Camp Whispering Pines in Louisiana, was published by Myers and Harms in 2011 in *Ecology*. The authors set out to test two competing models that have been much debated: (1) the niche assembly model, in which species composition and richness are controlled by relatively deterministic local environmental conditions and biotic interactions such as competition; and

(2) the dispersal assembly model, generally associated with the "neutral theory" of biodiversity championed by ecologist Stephen Hubbell, in which species composition and richness are determined by the size of the source species pool and chance events in species colonization and demography. I was encouraged to see this study demonstrate that both "immigration from the species pool and niche-based ecological filters interactively structure species-rich plant communities." The authors found through field experiments that seed rain was important in determining species richness; however, seed rain interacted with fire intensity and soil moisture ("ecological filters") to determine local species membership. Localized variation in fire intensity, produced by variability in prefire fine fuel (e.g., grass thatch) loads, appears to promote coexistence of dominant and rare species and to increase recruitment opportunities for arriving seeds.

Animals

I dwell on plants throughout this book, but not because I prefer plants to animals. Indeed, I was trained as an animal ecologist; ethically, I see no reason to believe that any species is fundamentally superior to any other. I emphasize plants because they have been better studied than animals in southern grasslands—even more so than birds, which are generally the best-studied organisms besides humans. What do we know about vertebrate and invertebrate species richness in southern grasslands? One thing we know is that species richness of large vertebrates in the grasslands of North America was much higher for most of the past few million years than it has been for the last 13,000 years, after the end-Pleistocene extinctions. The richness of grazing and browsing ungulates continent-wide peaked in the mid-Miocene, approximately sixteen to fourteen million years ago, when it may have been higher in North America than in any other continent at any time in history. Judging from the adaptations and diets of these animals, as reflected in their bones and teeth (including stable isotopes of carbon that tell us what they ate; see chap. 2), the dominant vegetation across much of the continent, including the South, at this time was savanna and woodland. Today, the species richness of vertebrates (plate 2) and invertebrates generally parallels plant species richness, being higher at southern latitudes. The association is fickle, however; as noted earlier, many animal groups peak in richness in the southern Appalachians, not in the Coastal Plain, where plant richness reaches its zenith east of California.

Within southern grasslands, some animal groups are very rich and others not so rich, but surveys are few and geographically restricted. Insect species richness would be expected to track plant species richness, since many insects are specialized herbivores, pollinators, or seed dispersers of particular plant species.

Hence, the high plant species richness of southern grasslands should promote high insect richness. Unfortunately, the literature on terrestrial insect distributions and diversity is too sparse to form many general conclusions. For example, when I searched for papers that might address insect richness in longleaf pine ecosystems, I came up primarily with reports of pests of longleaf pine trees.

Ants, which are very species rich in the Coastal Plain, have received a fair amount of study. A paper by David Lubertazzi and Walter Tschinkel in 2003 reported seventy-two ant species representing twenty-five genera and five subfamilies in longleaf pine flatwoods in the Florida Panhandle. This is the highest within-habitat ant species richness ever reported for North America. Within-plot richness (fifty-five) is also the highest yet reported; plots were 5,600 square meters in size. This extreme species richness is not surprising, since Florida is known to contain more ant species (218) than any other eastern state. Indeed, the highest site-level species richness of ants in the United States is 102 species, reported by Mark Deyrup and James Trager for Archbold Biological Station on the Lake Wales Ridge of the central Florida Peninsula. Most of these ants inhabit scrub and pine sandhill communities.

Aside from ants, few invertebrate groups have received much study in southern grasslands. A partial exception is moths, which are very diverse in at least some southern grasslands. A survey of moths by Deborah Landau and Dorothy Prowell in longleaf pine savannas in two parishes of Louisiana yielded 208 species. Surveys in longleaf pine ecosystems in the Carolinas are coming up with high numbers of moth species as well. In the Black Belt of Mississippi, Richard Brown reports 1,021 species of moths, plus many undescribed species, in the small remnant mosaic of grassland and forest there; 780 of those species were collected in prairie sites, including 50 of the 59 uncommon and geographically restricted species. Two species of moths and two species of beetles, so far, are strictly endemic to Black Belt prairies and adjacent forest in Mississippi and Alabama.

As noted earlier, the combined species richness of amphibians and reptiles (herpetofauna) in North America peaks in the lower Coastal Plain, centered on the Florida Panhandle and adjacent Alabama, and then declines southward and northward from there. Many reptiles are heliotherms—obtaining body heat by basking in the sun—hence, reptiles tend to be species rich and abundant in open-canopy environments such as pine savannas and other grasslands. The historic range of the eastern diamondback rattlesnake, my personal favorite snake, coincides closely with the historic distribution of longleaf pine ecosystems. William Martin and Bruce Means, noting that eastern diamondback fossils date from 1 to 1.5 million years ago, propose that this snake was always associated

with open-canopy habitats. A recent study by Jayme Waldron and coauthors confirms that the diamondback is closely associated with pine savannas and that its decline coincides with fire exclusion and other factors that led to a greater than 97 percent loss of this ecosystem.

The longleaf pine ecosystem, with its embedded wetlands and abundant gopher tortoise burrows, also is essential for many amphibians. Again, open, grassy habitat is a key factor in this richness. In his review of vertebrate diversity in longleaf pine ecosystems, Means found that amphibians are more diverse here than reptiles. Of the nine salamander and twenty-six frog species found in longleaf pine savannas, six species of salamanders and eleven species of frogs, as adults, are specialists in these ecosystems; this compares to thirteen specialist reptiles—nine snakes, two lizards, one worm lizard, and one turtle.

In contrast to herpetofauna, breeding birds and mammals become less species rich at lower latitudes in the South, that is, the Coastal Plain and especially the Florida Peninsula. Jack Stout and Wayne Marion, in their 1993 chapter in *Biodiversity of the Southeastern United States*, suggest that the peninsula effect—for example, limited recolonization of extirpated populations from the mainland—may partially explain lower richness of birds and mammals in peninsular Florida, but not across the Coastal Plain; the full explanation remains elusive. Interestingly, reduced species richness of breeding birds is not a phenomenon restricted to the Coastal Plain. Breeding bird richness in eastern North America increases steadily from Florida to New England and adjacent Canada. Kerry Rabenold, in 1979, hypothesized that the brief but dramatic pulse in insect activity at northern latitudes (and also at high elevations in the Appalachians) may allow more bird species to coexist without competitive exclusion. That is, there are more than enough insects to go around during the compressed breeding season. In the South, insect activity is less pulsed, with higher consumer biomass relative to food abundance during the breeding season. Southern birds must compete more strenuously for insects, and some species are outdone by others: hence, a reversed latitudinal diversity gradient. This explanation remains hypothetical, but I have not heard a better one.

Birds and mammals are expected to be less species rich in grasslands, especially treeless grasslands, than in forests, due to reduced vertical structure for partitioning of niches. Beginning with the seminal work of ecologist Robert H. MacArthur in the late 1950s, many studies have shown that the number of bird species in a forest increases markedly with foliage height diversity. Diversity of foliage heights on a scale meaningful to territorial birds is distinctly low in grasslands; presumably, this should matter less to mammals, fewer of which are arboreal. Todd Engstrom, in his review of mammals and birds of longleaf

pine ecosystems, found 36 mammal species and 86 bird species (35 permanent residents, 29 breeding season only, and 22 winter visitors) characteristic of this ecosystem. Engstrom noted that this unexpectedly high diversity—for birds, as high as in virtually any hardwood forest in the region—is dependent on a fire-maintained, grassy groundcover, as 69 percent of the mammals and 36 percent of the birds forage primarily on or near the ground. Again, the familiar refrain: diversity in this ecosystem is tied to the open, frequently burned, grass-dominated herbaceous layer.

Another key consideration is the size of the grassland. Recall the species-area relationship: larger patches tend to have more species. This rule is well established for grassland birds, which have declined more than any other group of birds in North America over the past several decades. Many studies (albeit few in the South) show that some species of grassland birds are not found during the breeding season in patches of otherwise appropriate habitat below a certain size; with increasing patch area, their probability of occupancy increases. This is likely due both to habitat selection factors (birds prefer not to settle in small areas) and extinction risk (small populations in small patches are more likely to go extinct). A large study by James Herkert and coauthors of four grassland bird species in 39 prairie fragments in five states, ranging from 60 to more than 100,000 acres in size, found nest-predation rates highest in small (< 250 acres) and lowest in large (> 2,500 acres) fragments. Another regional study of grassland birds, in eastern Wyoming, by Tammy Hamer and colleagues, found that habitat area explained 17 percent of the variation in species richness, which is good explanatory power for a single variable in ecological research. Bird species richness in this study also was positively related to grasshopper diversity (major prey) and negatively related to habitat dispersion (i.e., patches spread farther apart), grassland edge (where nest predators often concentrate), and attributes of the landscape matrix that restrict movement. The weight of evidence from decades of research suggests that most grassland birds require patches of grassland that are large and unfragmented by human-created habitats and infrastructure.

PEOPLE CARE ABOUT DIVERSITY, ENDEMISM, AND DISJUNCTIONS

I have been told many times by colleagues that it is foolish to promote conservation actions to the public on the basis of such arcane concepts as endemism, disjunction, and species richness. But my own experience and the small

but growing literature on the topic indicate that with very little introduction, people care about these phenomena because they are inherently fascinating.

It is a universal human trait to value diversity and to classify nature. Natural selection would have favored individuals who recognized and sampled a variety of food items, versus a monotonous diet, and thereby avoided nutrient deficiencies. Anthropological evidence shows that our primate relatives use a large variety of plants, not just for food, but for medicinal purposes; I have read that gorillas have a pharmacopeia consisting of dozens of plants. Those plants have to be identified correctly, or poisoning could result.

My experiences working with young children as an environmental educator and as a parent persuade me of the basic correctness of Ed Wilson's biophilia hypothesis, which examines "the connections that human beings subconsciously seek with the rest of life" and suggests that an affiliation with nature is at least partially innate. An attraction to diversity persists, despite discouragement at an early age by many parents and teachers.

A recent study in Switzerland by Petra Lindemann-Mathiess and coauthors reported on a series of experiments and field studies designed to evaluate the influence of plant diversity on laypeoples' perception and appreciation of grasslands. As species richness increases both in experimental arrays and natural meadows, people's aesthetic appreciation of those arrays and meadows increases significantly. The authors speculate that "psychologically, the increase in visual complexity with increasing species richness might explain the higher aesthetic appreciation of high-diversity communities," citing other studies that have found human preference for visually complex pictures and landscapes. They conclude that "plant diversity in itself is attractive to humans." Diversity of animals is also preferred over low species richness. Based on analysis of interview data, Richard Fuller and colleagues report that the psychological well-being of urban residents increases with the species richness of plants, butterflies, and birds in urban greenspace. Similarly, Susannah Lerman and Paige Warren documented that urban residents notice varying levels of bird species richness in their yards and that their satisfaction with their yards increases with increasing bird species richness.

There are some caveats to these reported biophilic trends. Lerman and Warren expressed concern about "environmental inequities" in their Phoenix, Arizona, study landscape. Specifically, Hispanic and lower-income neighborhoods, which tended to be closer to the urban core, had few to no native desert birds and were generally noisier, so that people had less opportunity to hear birds. Thus, the opportunity for appreciating bird species richness was reduced in the urban core.

Though I do not dwell on them in this book, practical reasons for valuing species richness also exist. There is an old idea in ecology that more diverse ecosystems are more stable. Ecosystem stability, in turn, benefits people by assuring reliable delivery of ecosystem services such as protection from floods, provision of clean water, and pollination of crops. The diversity-stability hypothesis has been debated by ecologists for decades, with some theoretical and empirical studies suggesting that more diverse ecosystems are actually more prone to disruption. Modern ecological theory and experimental evidence, however, provide increasing support for the idea that species richness—or, alternately, richness of "functional groups" of species, which perform particular roles in an ecosystem—promotes some forms of ecosystem stability. The type of stability emphasized in recent studies is "resilience," the ability to maintain or rapidly recover essential functions after disturbance.

A decade-long experiment by David Tilman and colleagues shows that higher species richness of perennial prairie plants increases temporal stability of aboveground plant production. Tilman and coauthors concluded in 2006 that "our results indicate that the reliable, efficient and sustainable supply of some foods (for example, livestock fodder), biofuels and ecosystem services can be enhanced by the use of biodiversity." A review by Anthony Ives and Stephen Carpenter the following year similarly concluded that "a growing number of empirical studies demonstrate positive diversity-stability relationships." They noted, however, that existing studies have examined only a few types of stability and have seldom identified the mechanisms responsible. Diversity per se may not be the stabilizing factor; that is, "The presence of one or a handful of species, rather than the overall diversity of an ecosystem, is often the determinant of stability against different perturbations…depending on the types of stability and perturbation, different species may play key roles." In contrast, a 2011 synthesis of grassland biodiversity experiments by Forest Isbell and coauthors shows that high plant species richness is needed to maintain ecosystem services. They concluded that "although species may appear functionally redundant when one function is considered under one set of environmental conditions, many species are needed to maintain multiple functions at multiple times and places in a changing world."

Despite lingering questions about what ultimately determines how resilient an ecosystem will be to environmental change, some commonsense lessons emerge from recent research on the diversity-stability relationship: (1) it is wise to maintain the full natural diversity of functional groups in ecosystems; (2) it is wise to maintain high species richness within and among functional groups; and (3) it is useful to identify keystone species (or ecologically pivotal and

strongly interactive species generally) and keep them in ecologically effective, not just minimally viable, populations. Allowing continued erosion of native species richness and loss of key species is just plain foolish.

Endemism and disjunction are also interesting to people. A study in British Columbia by Emily Meuser and colleagues sought to determine what kinds of species people value. Although I would expect such attributes as large body size, furriness, and overall charisma to be most valued, Meuser and colleagues determined that endemism (e.g., "species only or mainly occurring in British Columbia" and "species that exist in British Columbia and no other area of Canada") is the species attribute on which people placed highest value. Valuing endemism makes sense psychologically—if a species is found in your area and nowhere else, that distinction makes the place you live more special; you have something to be proud of.

All of us who are biologists, naturalists, and conservationists have a responsibility to be educators, specifically to help awaken intuitive biophilia and help people discover or rediscover the real world outside their doors. This can be challenging in an urban setting, but we can make it easier by saving and restoring native vegetation and associated species everywhere, from big wilderness landscapes to every untamed nook and cranny in the cities. Although protecting relatively pristine, endemic-rich hotspots and intact wild areas is essential, highly altered or "novel" ecosystems, which may be dominated by nonnative species, can also have considerable conservation value. I live, for example, near the edge of the big red hotspot in east-central peninsular Florida (plate 1), known as the Wekiva Basin, and it is far from pristine. Yet a tremendous amount of biodiversity and a surprising degree of wildness lie at my doorstep.

THE DECLINE OF SOUTHERN GRASSLANDS

Although the joy of natural history is an incentive for caring, awareness of what biodiversity and wildness we've lost and are still losing remains essential for setting goals and priorities for conservation and restoration. The decline of southern grasslands is emblematic of the decline of ecosystems, biodiversity, and ecological integrity—however one defines these things—worldwide. Grasslands are among the most endangered of the world's ecosystems because (1) they are the most densely inhabited by people; (2) many of them (but fortunately not all) are highly suitable for agriculture and thus were quickly converted to cropland, pine plantations, or intensive livestock grazing; and (3) they are acutely sensitive to the disruption of ecological processes such as fire,

hydrology, and the activities of large herbivores. Some southern grasslands also have proven susceptible to invasion by nonnative species, but thankfully, many types (for example, species-rich pine savannas) have, so far, been surprisingly resistant to invasion.

The greatest proximate threat to southern grasslands, like most other terrestrial ecosystems, is the loss, fragmentation, and degradation of habitat for native species, driven by the ultimate threats of human population growth and overconsumption of resources. Habitat fragmentation and degradation disrupt fundamental ecological processes, such as fire and hydrologic regimes (see chaps. 4 and 5), which then degrades the ecosystem further. Although addressing proximate threats quickly, such as through habitat protection and management, is essential, these threats will never go away until we—or nature—find a way to reduce the human population to a sustainable level. Although I do not have space to discuss this challenge here, another responsibility of a naturalist is to remind people regularly of the root causes of the extinction crisis.

Southern Grasslands as Endangered Ecosystems

A global analysis in 2005 by Jonathan Hoekstra and colleagues showed that temperate grasslands, savannas, and shrublands are the most highly imperiled biomes in terms of the proportion of their area that has been converted to other land uses and the proportion that is represented in protected areas. Hoekstra and coauthors cleverly combined these two criteria, conversion and protection, into a Conservation Risk Index (CRI) that represents a ratio of percent converted to percent protected. With a CRI of 10.1, temperate grasslands and associated ecosystems top the list (fig. 3.3).

Unfortunately, because a conventional biome classification was used in this study, the southeastern United States fell into neither the Temperate Grasslands, Savannas and Shrublands category nor the Tropical/Subtropical Grasslands, Savannas and Shrublands category. Rather, the entire South, and north to southeastern Canada, fell into the Temperate Broadleaf and Mixed Forests category, which is perilously misleading, especially for the Coastal Plain. Thus, the decline of southern grasslands since EuroAmerican settlement, their poor representation in conservation areas, and continuing threats to their existence were masked by this classification. On an ecoregion scale, the South was classified by Hoekstra and coauthors as Vulnerable, whereas the Prairie Region was considered Critically Endangered—even though the South has already lost more grassland than the Great Plains and has much more to lose biologically (e.g., endemic taxa). Nevertheless, a conclusion of Hoekstra and colleagues' paper rings true: "Identification of biomes at risk—e.g. temperate grasslands

Habitat converted		Habitat protected		CRI
45.8	Temperate Grasslands, Savannas & Shrublands	4.6		10.1
41.4	Mediterranean Forests, Woodlands & Scrub	5.0		8.2
48.5	Tropical/Subtropical Dry Broadleaf Forests	7.6		6.4
46.6	Temperate Broadleaf & Mixed Forests	9.8		4.7
27.3	Tropical/Subtropical Coniferous Forests	6.7		4.1
32.2	Tropical/Subtropical Moist Broadleaf Forests	16.0		2.0
23.6	Tropical/Subtropical Grasslands, Savannas & Shrublands	11.9		2.0
26.6	Flooded Grasslands & Savannas	18.1		1.5
6.8	Deserts & Xeric Shrublands	9.9		0.7
12.7	Montane Grasslands & Shrublands	24.7		0.5
12.6	Temperate Conifer Forests	26.3		0.5
2.4	Boreal Forests/Taiga	8.9		0.3
0.4	Tundra	16.0		0.0

60   40   20   0   0   10   20   30

% biome area   % biome area

Figure 3.3. A biome-scale prioritization of ecosystems for conservation based on the extent of conversion relative to the extent of protection. The Conservation Risk Index (CRI) was calculated as the ratio of percent area converted to percent area protected as an index of relative risk of biome-wide biodiversity loss. Unfortunately, southern grasslands were not captured in these biome categories (see text). Adapted from Hoekstra et al. (2005).

and Mediterranean scrub—underscores the global magnitude of the biome crisis and points to high-level priorities around which international funding agencies, governments and conservation organizations can coordinate."

The report on *Endangered Ecosystems of the United States* that my colleagues and I published in 1995 took a more qualitative, but detailed, look at the status

of vegetation types and other recognizable ecosystems by reviewing the published and unpublished literature that addresses the extent of decline and degradation of natural communities nationwide. Because, at the time, no consistent nationwide classification of vegetation or ecosystem types existed, we had to use classifications developed by original authors in the literature and in the various states and regions of the country. Much of the unpublished literature that we reviewed constituted internal reports and estimates by experts, the bulk of them ecologists or botanists with the state natural heritage programs. Our review showed that grasslands, most of them fire-dependent, dominated the list of the most reduced and degraded ecosystems. Estimates of decline of southern grassland types, from our 1995 report and updated where new and better estimates were available, are provided in table 3.3.

Does it matter that grasslands and related communities are imperiled? For human purposes, it could matter a lot. Every major cereal crop, including wheat, corn, rice, barely, millet, and many others, is a grass whose predomestication ancestors evolved in grasslands, as is also true for the most economically important livestock, including cattle and sheep. Wild grasses and ungulates remain critical sources of genetic material to enrich our domesticated species. Moreover, despite all the attention given to forests as carbon sinks, on a global scale grasslands store nearly as much carbon: 34 percent of total terrestrial carbon compared to 39 percent for forests, according to a report by Robin White and coauthors for the World Resources Institute. In contrast to forests, most of the carbon stored in grasslands is belowground, including living carbon in roots and dead carbon in charcoal; therefore, it is more securely sequestered. And although the idea remains controversial, some studies suggest that frequent fire actually enhances the ability of grasslands to store carbon. Frequent low-severity fires burn less biomass and stimulate grasslands to sequester more carbon than high-severity fires; the latter release a tremendous amount of carbon following long periods of fire exclusion. Protecting intact grasslands, with their natural fire regimes and carbon-storage mechanisms, will help reduce the magnitude of climate change and its impacts to humans and nonhumans alike.

More meaningful to me and perhaps most naturalists are the noneconomic, nonquantifiable values of grasslands: call them intrinsic, inherent, spiritual, scientific, "for their own sake," or whatever—each of these terms incites philosophical debate—yet these values are shared by many people. A major 2010 poll, commissioned by TNC, found that people generally do not understand or like the term *ecosystem services*; they prefer a broader concept of *nature's value* or *nature's benefits*. Moreover, nearly half of those polled feel that the most signifi-

Table 3.3. Estimates of decline for southern grasslands, organized according to the categories introduced in chapter 1 (table 1.2).

Grassland type	Estimates of decline
Prairies	> 99.99% loss of native prairies in Kentucky, from 1.05 million ha to < 81 ha
	99.999% loss of tallgrass prairie in Grand Prairie area of Mississippi Alluvial Plain in Arkansas
	Loss to agriculture of all but a few small remnants (> 99%) of Black Belt prairie in Alabama and Mississippi and Jackson Prairie in Mississippi
	> 99.9% loss of all prairie types in Texas
	> 99% loss of wet and mesic coastal prairies in Louisiana
	95%–99% loss of Mississippi terrace prairie in Louisiana
	90%–95% loss of calcareous prairies (all types) in Louisiana
	ca. 90% loss of Florida dry prairie (from > 1.2 million acres to ca. 100,000 acres)
	25%–50% loss of coastal dune grassland in Louisiana
Grassy Balds	No quantitative information on losses
Savannas and Woodlands	100% loss of intact bluegrass savanna–woodland in Kentucky
	> 99.5% loss of pine rocklands on the Miami Rock Ridge
	Almost complete loss of the loblolly–shortleaf pine–hardwood woodland of West Gulf Coastal Plain
	97%–98% loss of longleaf pine savanna/woodland across its historic range
	95%–99% loss of wet longleaf pine savanna and eastern upland longleaf pine woodland in Louisiana
	90%–95% loss of eastern xeric sandhill woodland in Louisiana
	75%–90% loss of western upland longleaf pine woodland in Louisiana
	88% loss of longleaf pine ecosystems in Florida from 1936 to 1987
	85% loss of slash pine savannas in southwestern Florida from 1900 to 1989
	74.4% loss or degradation of scrub, scrubby flatwoods, and sandhills on southern Lake Wales Ridge, Florida, as of 1985
	50% loss of cedar woodlands in Louisiana
Barrens, Glades, and Outcrops	90%–95% loss of Fleming glades in Louisiana
	90% loss of ecologically intact limestone cedar glades in Tennessee and ca. 50% loss of total cedar glade area by 1993
	75%–90% loss of saline barrens in Louisiana
	25%–50% loss of sandstone glades in Louisiana
Canebrakes	Over 99% loss of large, tall canebrakes throughout range

Note: Decline includes reduction in area (direct conversion to an anthropogenic habitat) and significant degradation of structure, function, or composition since EuroAmerican settlement, as documented in the literature or estimated by experts.
Source: Noss et al. (1995; see original sources cited there), with updates from other sources.

cant value of nature is not what it does for people, but rather its intrinsic value: "Roughly equal proportions of American voters believe that the best reason to conserve nature is for its own sake (42 percent) and for the benefits it provides to people (45 percent)." It seems to me that conservationists should encourage both kinds of values. To paraphrase John F. Kennedy, let's not ask only what nature can do for us, but also what we can do for nature.

REFERENCES

Ketona glades: Allison and Stevens 2001, Garland 2008, http://jimbotany.com/01a-Title -Abstract-Intro-PhysChar.htm, Lawless et al. 2006

Cane: Triplett et al. 2006

Pine barrens tree frog: Christman 1970, Means and Longden 1976, Means 1983

Endemics, endemism, rarity, and hotspots: Harper 1907, Neill 1957, James 1961, Axelrod 1985, Gentry 1986, Rabinowitz et al. 1986, McCoy and Mushinsky 1992, Myers et al. 2000, Stein et al. 2000, Estill and Cruzan 2001, LeBlond 2001, Sorrie and Weakley 2001, Orme et al. 2005, Lamoreux et al. 2006, Peet 2006, Sorrie and Weakley 2006, Harrison et al. 2008, Bond and Parr 2010, Sandel et al. 2011

Conservation International hotspots: http://www.biodiversityhotspots.org/

Kareiva interview: http://www.nature.org/ourscience/ourscientists/q.xml

Sea-level rise: Pilkey and Young 2009, Noss 2011, Zhang et al. 2011

Florida panther and puma distribution and genetics: Culver 2010

Irreplaceability: Pressey et al. 1994, Noss et al. 2002

Peripheral and disjunct populations: Lesica and Allendorf 1995, Lomolino et al. 2006

Species richness: MacArthur and MacArthur 1961, MacArthur and Wilson 1967, MacArthur 1972, Connell 1978, Shmida and Wilson 1985, Means and Simberloff 1987, Engstrom 1993, Platt 1999, Grace et al. 2000, Zobel et al. 2000, Mackey and Currie 2001, Schmitz et al. 2002, Hawkins et al. 2003, Orzell and Bridges 2006a and 2006b, Peet 2006, Platt, Carr, et al. 2006, Qian et al. 2007, Weakley 2008, Carr et al. 2009, Myers and Harms 2009, Carr et al. 2010, Isbell et al. 2011, Myers and Harms 2011, Peet et al., forthcoming

Fire effects on species richness: Walker and Peet 1984, Streng et al. 1993, Collins et al. 1995, Beckage and Stout 2000, Goldman and Orzell 2000, Peet 2006, Myers and Harms 2011, Gagnon et al. 2012

Species richness in tropical forests: Gentry and Dodson 1987, Gentry 1988, Phillips et al. 1994

Venus fly-trap: Forterre et al. 2005

Island biogeography, habitat fragmentation: MacArthur and Wilson 1967, Noss and Cooperrider 1994, Duncan and Schmalzer 2004, Noss et al. 2006, Laurance 2008

Ants and other invertebrates: Deyrup and Trager 1986, Deyrup 1989, Deyrup 1990, Landau and Prowell 1999, Capinera et al. 2001, Brown 2003, Deyrup 2003, Lubertazzi and Tschinkel 2003, Provencher et al. 2003

Vertebrates: Engstrom 1993, Stout and Marion 1993, Helzer and Jelinski 1999, Martin and Means 2000, Herkert et al. 2003, Hamer et al. 2006, Means 2006, Waldron et al. 2008

Human response to species richness and endemism: Wilson 1984, Fuller et al. 2007, Meuser et al. 2009, Fairbank, Maslin, Maullin, Metz & Associates 2010, Lindemann-Mathiess et al. 2010, Lerman and Warren 2011, Luck et al. 2011

Diversity and stability: May 1974, Pimm 1984, Loreau et al. 2002, Tilman et al. 2006, Ives and Carpenter 2007, Isbell et al. 2011

Ultimate and proximate threats, endangered ecosystems: Means and Grow 1985, Noss 1988, Noss and Cooperrider 1994, Noss et al. 1995, Noss and Peters 1995, Samson and Knopf 1996, White et al. 2000, Hoekstra et al. 2005, Dietz et al. 2007

TNC poll on ecosystem services: Fairbank, Maslin, Maullin, Metz & Associates 2010

CHAPTER 4

❧

Physical Factors: Rock, Soil, Landform, Water, and Wind

The most satisfactory system of geographical classification of the vegetation of temperate Eastern North America is one based on geology.

Roland Harper (1906a)

With this chapter we begin a more detailed exploration of the origin and maintenance of grasslands in the South. As reviewed in chapter 2, prolonged periods of drier climate or increased seasonality can convert forest to grassland. This process has occurred periodically in the past. Positive feedback loops involving megaherbivores and fire further contribute to grassland formation and can maintain grassland after climatic conditions favorable for its development have ended. The long sequence of grassland-adapted vertebrates in the fossil record, patterns of disjunction in plant and animal taxa between the semiarid West and the Southeast, and positive responses to fire in the flora and fauna provide evidence of this history.

Other factors that maintain grassland in a relatively rainy region are physical. Although southern grasslands occur on a variety of bedrock and soil types, certain physical conditions can allow grassland to persist with few other conducive influences, for instance sometimes with little or no fire. Remnant grasslands often occur on soils that are shallow, alkaline, toxic, infertile, coarse-textured (e.g., deep sands, through which water drains quickly), or fine-textured (e.g., "shrink-swell" clay soils). Soils with any of these properties tend to favor grasses and associated plants in competition with trees. As noted earlier, grasslands associated with particular soils and associated physical conditions are called "edaphic grasslands." One notable attribute of edaphic communities is that they may

persist relatively unaltered despite changes in regional climate. Because edaphic communities are often isolated and tend to accumulate endemic taxa, they often represent long-term hotspots of biodiversity and centers of creative evolutionary processes. Many southern grasslands are edaphic to some degree, in that properties of their geologic substrates or soils distinguish them from surrounding vegetation. Landform often plays a role, too, with steep, erosive slopes and relatively hot and dry south- and southwest-facing slopes less favorable to forest.

Also important to grassland development is hydrology. Scouring by river waters or inundation or saturation for prolonged periods can favor grassland over woody vegetation. High winds from hurricanes, tornados, or other stormy conditions break open tree canopies and promote grassy understories; with fire or other positive feedback, these grassy openings may convert to more extensive grasslands. Acting alone or in combination, these various physical factors can prevent closed-canopy forests from developing within a regional climatic regime that would otherwise favor them.

Some sites, such as exposed rock outcrops, are so harsh physically that the sparseness of vegetation is easy to understand. If there is any soil, it is limited to cracks, crevices, and hollows in the bedrock. Edaphic grasslands are not always so extreme or obvious, however. Highly calcareous soils, often quite fertile, are typical of many grasslands of the South. Although sometimes shallow, the soils that support blackland prairies, such as in the Black Belt of Alabama and Mississippi, include some types (at least formerly) that are relatively deep and fertile. The most favorable soils, however, are now or were formerly in agriculture. With rare exceptions, native prairie vegetation remains on only the poorest, thinnest, droughtiest, or most eroded soils. These rigorous sites, and frequently disturbed places such as roadsides and powerline rights-of-way, serve as refugia for grassland species during periods of climate that favor forest and where large-scale, grassland-maintaining agents, especially fire and megaherbivores, have been excluded from the landscape by humans. Such is the case today across virtually the entire South.

A problem with classifying edaphic grasslands, or any community, is that terminology has been used in inconsistent and confusing ways. Prairie, barren, and glade have been applied by different authors to describe the same communities or sites, and what some people call glades, others call outcrops. I view these communities as a continuum from deep-soiled prairies on the one end, to thin-soiled prairies (best called barrens), through a spectrum of sparse herbaceous communities with exposed rock (glades), to sites with predominantly rock (outcrops) at the other end. If scattered trees or open-canopied "forests" occur along the gradient, those areas may be classified as savanna or wood-

land. The grassland continuum is real—you can see virtually the entire gradient displayed on some individual sites. Therefore, I consider the whole open and sunny gradient within my definition of grasslands. As an ecologist, I find it more interesting to recognize the changing combinations of species along environmental gradients and mosaics than to draw boundaries around a segment of a complex gradient and study it as a discrete association.

A primary goal of conservation is representation, within protected areas, of the full range of biodiversity in each region. Wherever possible, these areas should be large enough to maintain complete food webs and natural processes such as fire and hydrologic regimes. At the community or ecosystem level of organization, representation requires the identification of a series of sites that collectively capture the entire environmental gradient over which each defined ecosystem type occurs—this is the "coarse-filter" approach to conservation described in chapter 1. Even if one accepts, as I do, the "individualistic concept of the plant association," promoted by Henry Gleason in the early twentieth century and later by such influential ecologists as Robert Whittaker and John Curtis, classifying nature in order to represent all features relevant to biodiversity makes good sense. A representative series of sites would include all geographical subregions, bedrock and soil types, elevations, slope aspects, and hydrologic conditions across which ecosystems intergrade. Maintaining habitat connectivity among sites will promote movement and re-sorting of species assemblages in response to climate change.

Because humans preferentially settled rich lowland areas close to rivers and other navigation routes, and farmed soils that were most fertile or easiest to till, some types of communities and physical environments were more thoroughly converted to human uses, with remaining undeveloped areas not representative of the original diversity. Grasslands were generally the first and biggest losers in this chain of events, but some types suffered more than others. The extreme and infertile sites where we find most southern grasslands today do not reflect the distribution of grasslands prior to EuroAmerican settlement. Nevertheless, these unusual sites have been critical in maintaining grassland vegetation in the South out of equilibrium with the regional climate and dominant vegetation.

THE PURPOSE OF MY JOURNEYS

In this chapter I describe grasslands associated with the many regions, bedrock types, landforms, soils, and hydrologic regimes of the South through the medium of my personal travels. For portions of four years I wandered

through my study region, seeking out exemplars of grasslands associated with a range of physical environments, as broad a range as my time and travel budget allowed. I chose sites to visit based on the ecological literature and recommendations from local and regional biologists and naturalists. My goal was to obtain representative samples of knowledge, in the form of direct experiences, photographs, and written and oral information from experts, from a comprehensive spectrum of grassland types. I was especially interested in sites with high species richness and populations of endemic species, but I also sought characteristic examples of natural communities and sites that have been damaged and are in the process of restoration. Even roadsides and powerline corridors were informative places for me, as these are often the last homes for grassland species that have lost their natural habitats. On most sites I was guided by experts who know these places as well as, or better than, anyone else. This was the most gratifying aspect of this project. These folks absolutely loved to show me around their favorite spots. Not only is their knowledge amazing, but their respect and affection for these places are clear.

Inevitably, some regions were undersampled in my peregrinations. Despite good intentions, I never made it to Oklahoma, West Virginia, or Delaware for this project, and managed only one trip to each of Texas, Louisiana, and Maryland. Every other state I visited two or more times. Florida, my home state, was overrepresented in my sample, but I can easily defend this apparent bias with the reminder that Florida has the highest species richness and endemism of grassland-associated plants and animals in the South and probably in all of North America. That's a major reason why I choose to live here.

The questions that drove my travels and discussions are the prominent themes of this book and include, for each site: (1) How does the physical environment of this place influence its habitat structure, species composition, and richness? (2) How do fire and other components of the disturbance regime influence this site and its structure, composition, and richness? (3) What is the history of this site, from deep time through the immediate past? (4) If endemic species and disjunct populations occur here, what are their likely histories? (5) What are the threats to this site, and how are they being addressed? The experts who led me in the field helped me find at least tentative answers to these questions. As much as possible, I visited sites during times when endemic or imperiled plants were in bloom or when the natural community in question displayed its distinguishing features most vividly. I was rarely disappointed.

ROCK, SOIL, AND LANDFORM

The *zonal* (most characteristic) soils of grassland biomes, such as the Great Plains, are deep loams with good internal drainage and a dark-colored, humus-rich surface layer. The grasslands of the South, prior to settlement, occurred across a broad range of soils. Some were on deep loams, but these types are almost entirely gone. Doug Zollner and coauthors describe a cherrybark oak-(pecan)/deciduous holly/Cherokee sedge–whitegrass mesic blackland woodland in Arkansas, which occurs on fertile loams and silty clay loams. They note that "this is a very rare community type. Few examples are known because these rich sites were cleared for cotton in the early 1900s and later converted to pasture." This is a familiar story. By 1901, Charles Mohr, in *Plant Life of Alabama*, commented that all the prairies in the Alabama Black Belt with deep soils had been brought into cultivation and that "only the poorest spots remain in the original state."

Blackland Prairies

Blackland prairies are among the most widespread edaphic grasslands of the South. Within my study region, NatureServe recognizes one blackland prairie ecological system, the Southern Coastal Plain Blackland Prairie and Woodland, occurring primarily in the Jackson Prairie and Black Belt of the East Gulf Coastal Plain, with an outlier in the Atlantic Coastal Plain of Georgia. NatureServe also recognizes the Texas Blackland Tallgrass Prairie in Texas and part of southern Oklahoma, just to the west of my study region. In *Blackland Prairies of the Gulf Coastal Plain*, Evan Peacock and Timothy Schauwecker more liberally include calcareous grasslands of Texas, Arkansas, Louisiana, Mississippi, Alabama, and Georgia, all of which occur on limestone or other calcareous formations of Late Cretaceous to Eocene age, in contrast to most other grasslands of the South, which occur on later Tertiary or Quaternary sediments. "Blackland" and "Black Belt" refer to the dark soils, rich in organic matter, once characteristic of these prairies. Visiting remnant sites today (plate 9) one sees mostly eroded chalky or marly clays, light gray in color. Not only were the most fertile sites converted to agriculture, but intensive livestock grazing led to erosion and loss of the upper organic soil layer on other sites.

The calcareous, relatively high pH, shrink-swell clay soils typical of blackland prairies are alternately sticky wet or crusty dry—tough conditions for woody vegetation. Philip Henry Gosse, an English naturalist who served as a schoolteacher for the children of cotton plantation owners near present-day

Pleasant Hill, Alabama (Dallas County), reported prairies and their harsh soil properties in the Black Belt in 1838:

> There are in my neighborhood many prairies…little ones, varying in extent from an acre to a square mile. They are generally so well defined, that the woods environ them on every side like an abrupt wall…. The soil is a very tough and hard clay, and in wet weather the roads running through them are almost impassable, so adhesive are they to the feet of the passengers and the wheels of carriages…. There are prairies not very far distant of many miles in extent…. There are no springs in the prairies, and the inhabitants depend on the rain-water, which, owing to the tenacity of the soil, does not soak into the ground, but accumulates in the hollows until evaporated by the sun.

Blackland prairies are typically patchy, but become progressively larger and more contiguous toward the west. In addition to fire, and perhaps herbivores, drought limits woody vegetation on these grasslands. Interestingly, warm-season grasses on blackland soils tend to decline during drought relative to perennial forbs, which benefit more from drought and disturbance and contribute to the high species richness characteristic of these grasslands.

Arkansas

In Arkansas, blackland prairies, savannas, and woodlands are distributed along gradients of soil moisture and soil depth, as illustrated in a model by Doug Zollner and coauthors (fig. 4.1). The deep-soil communities have been largely replaced by agriculture. Remaining prairies occur mostly on shallow soils over chalk (calcium carbonate) ridges or marl (a mud or mudstone rich in calcium carbonate and often clay) slopes, commonly on the steep sides of asymmetrical ridges known as "cuestas" (fig. 4.2). With Tom Foti and Theo Witsell of the Arkansas Natural Heritage Commission, I visited these landforms and observed how they influence vegetation. Tom is a master of interpreting the effects of landform and substrate on vegetation. Figures 4.1 and 4.2 portray the landscape we traveled through, though the real experience is more revealing than the models.

I stood at the top of the abrupt one hundred-foot cliff at White Cliffs Natural Area, above the Little River. This site represents the lower left corner of figure 4.1: an outcrop of Annona Chalk of Late Cretaceous age. Southern Arkansas was an estuary and offshore reef of the Cretaceous Sea/Mississippi Embayment back then. This is a strange, xeric site for the Coastal Plain, more like the Edwards Plateau of Texas. Post oak (*Quercus stellata*), blackjack oak (*Q.*
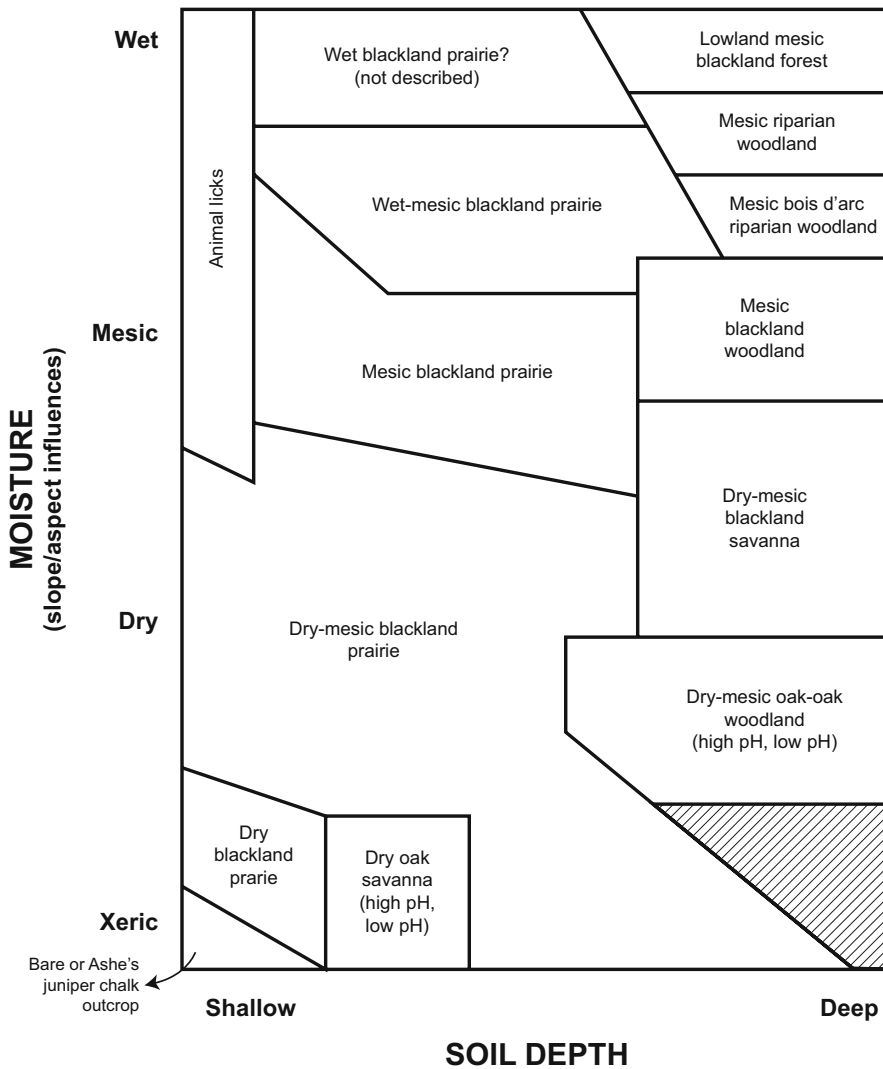
Figure 4.1. Hypothesized blackland community distribution along soil–moisture and soil–depth gradients in Arkansas. Adapted from Zollner et al. (2003).

marilandica), southern red oak (*Q. falcata*), bastard oak (*Q. sinuata*), Carolina holly (*Ilex ambigua*), and black locust (*Robinia pseudoacacia*) are the common trees in this woodland, accompanied by many plants—and collared lizards (*Crotaphytus collaris*)—derived from the West. As another odd juxtaposition, alligators (*Alligator mississippiensis*) swim in the Little River below. As we traveled around southern Arkansas that week in May 2008, we crossed several times the Cretaceous/Tertiary boundary. This boundary marks the last mass extinction event
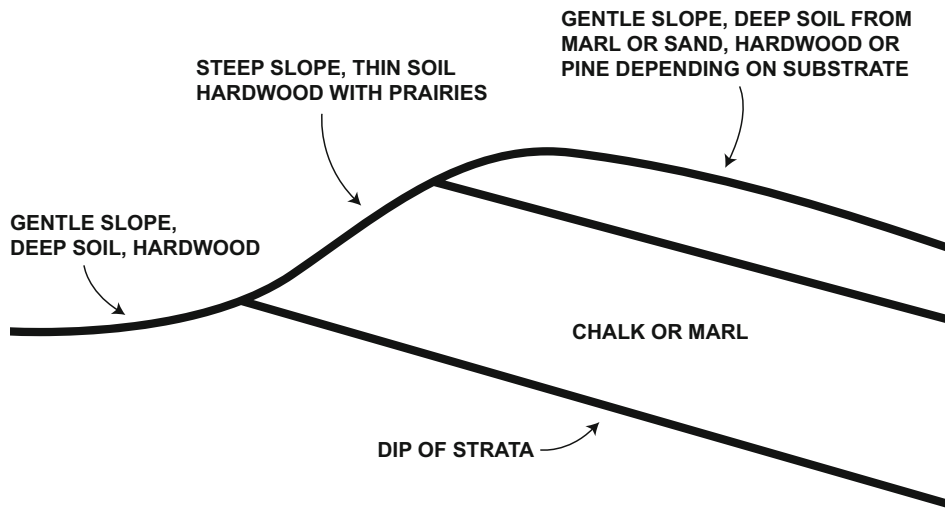
Figure 4.2. Model of the geology, soil, and vegetation of a cuesta (an asymmetrical ridge) in southwestern Arkansas. Grasslands occur mostly on steep slopes with thin soils derived from chalk or marl. Adapted from Foti et al. (2003).

(before the present one), caused by a meteorite about 10 kilometers (6.2 miles) in diameter slamming into the Gulf of Mexico along the northern coast of Yucatan. Reading a landscape is seeing time in space.

Black Belt and Jackson Prairies

The crescent-shaped Black Belt of Alabama and Mississippi (see figs. 1.6 and 1.7) is the best-known blackland prairie. In a 1957 paper packed with historical anecdotes going back to the de Soto expedition of 1539–43, Erhard Rostland created a stir by claiming that the Black Belt is a "myth." In support of his claim, Rostlund marshaled early vegetation maps and historical accounts and concluded that "the Alabama Black Belt, as a distinct and unique vegetation zone would disappear from [a vegetation map of the historic South], not because there was no open country in that region but because open country was common almost everywhere in the Southeast." Rostland's point that grasslands were abundant across the South is valid. On the other hand, many authors take issue with his conclusion that the Black Belt is not distinct as a concentration of grassland patches. Richard Brown, in the *Blackland Prairies* book, notes that prairie vegetation in the region was historically restricted to certain soils. Prairies of the Black Belt occur on soils derived from the Late Cretaceous Demopolis chalk of the Selma group, which was formed through deposition of sediments along the eastern edge of the Mississippi Embayment during the

Late Cretaceous. Fossil pollen and plant macrofossils from Goshen Springs, Alabama, only twenty miles south of the Demopolis chalk, show no evidence of prairie from 33,000 years ago to the present. No fossil pollen sites exist within the Black Belt. Pleistocene vertebrate fossils, however, indicate a rich community of browsers and grazers, including six species of horses (*Equus*), three known only from the Black Belt and the Great Plains.

John Barone refutes Rostland in a 2005 paper that reexamines the historical evidence for a distinct Black Belt prairie region. Citing early literature and General Land Office (GLO) surveys, Barone shows that Rostlund made many editorial errors, misquoting some sources, misstating the locations of certain observations, and misinterpreting historical reports from an ecological standpoint—for example, by citing observations of people traveling by boat, who would have seen forest along watercourses, as evidence that the region was forest rather than prairie. Barone's review shows that, although forest (or woodland) dominated the presettlement Black Belt, nearly 350,000 acres of prairies were present as late as the 1830s, forming an "arc of islands" across the Black Belt. Indians probably expanded grassland in the Black Belt through burning and other activities. By increasing mortality of trees, Indians could have gradually transformed woodlands or grassy openings into savannas and prairies. As is documented for EuroAmerican settlers, Indians would have preferentially located their agricultural fields within existing grasslands and forest openings, rather than in dense forests, where they would need to manually remove trees. Physical factors and human activities can work in synergy to maintain or expand grasslands. Yet today, less than 1 percent of all presettlement Black Belt prairies remain.

That the Black Belt and other blackland prairies have an origin that predates the arrival of humans to the area is suggested by the presence of local endemics. These grasslands are not as endemic rich as the Ketona Glades, the cedar glades of central Tennessee, or parts of the longleaf pine region, but they contain species found nowhere else. One interesting endemic is the Old Cahaba rosinweed (*Silphium perplexum*), which occurs in the Old Cahaba prairies in Dallas County, Alabama, near Selma (plate 10). Cahawba (a variant of "Cahaba") was the state capital of Alabama from 1820 to 1826 and a prosperous antebellum river town. It became a ghost town after the Civil War, and many of the abandoned buildings remain today. There are numerous small prairie patches in this area, mostly on hills and bluffs above the Cahaba River.

Jim Allison, whose discovery of the Ketona Glades was highlighted in chapter 3, recognized *Silphium perplexum* as a new species. Because *S. perplexum* is intermediate between *S. glutinosum* (one of the Ketona Glades endemics)

and *S. integrifolium* (a much more widespread species) for some characters, and resembles one or the other species for other characters, Allison hypothesizes that *S. perplexum* arose as a hybrid between these two species. In plants, speciation frequently occurs through hybridization (and animal examples of hybrid origin are now commonly recognized as well). All populations of *S. perplexum* have consistent morphology, are readily identifiable, and do not overlap in distribution with the likely parental taxa. On his website, Allison proposes a plausible scenario for the hybridization event:

> All of the known *Silphium perplexum* populations are within 13.5 km of the Cahaba River … about 76 km south of and downstream from a riverside population of the Bibb County endemic, *S. glutinosum*.… It is easy to envision propagules of the latter being transported downstream by flood waters at a time when the range of *S. integrifolium* extended somewhat eastward of its present known extent, facilitating hybridization between two formerly allopatric species. The fact that *S. perplexum* extends over a greater geographic area than one of its putative ancestors, *S. glutinosum* (ca. 32.4 km across versus 11.5 km), argues against its formation in the immediate past.

Animal species endemic to blackland prairies in Alabama and Mississippi include the Jackson Prairie crayfish (*Procambarus barbiger*). This attractive copper-blue crayfish rarely occurs in prairies, but rather in people's yards. (I hate it when endangered species behave like this.) Other endemics are two species of beetles (a large flightless ground beetle, *Cyclotrechus hypherpiformis*, and a May beetle, *Phyllophaga davisi*); and two species of moths (an undescribed large *Neodactria* and a grass-miner moth, *Elachista ciligera*—all known species of *Elachista* feed on grasses and sedges).

I first visited Black Belt prairies at Old Cahaba in early March 2008 (plate 9). If I had not known that prairies were in this area and was driving quickly through, I might have assumed that the openings along the road were old pastures or fields invaded by redcedars (*Juniperus virginianus*). Getting out of my car and wandering through these openings, however, I saw their prairie character. Little bluestem (*Schizachyrium scoparium*) is the dominant grass, with others including big bluestem (*Andropogon gerardii*), Indiangrass (*Sorghastrum nutans*), and side-oats grama (*Bouteloua curtipendula*). These species sometimes colonize old fields or pastures, but to find them together suggests a natural community. I found just one wildflower in bloom in the prairies on this cool March day—eastern prairie anemone (*Anemone berlandieri*). I returned to Old Cahaba in July 2008 and saw many prairie plants blooming, including the endemic

Silphium perplexum and the more widespread gray-headed coneflower (*Ratibida pinnata*), bitterweed (*Helenium amarum*), white prairie-clover (*Dalea candida*), and rosepink (*Sabatia angularis*).

In August 2009 I drove to Mississippi to visit the Jackson Prairie and several Black Belt sites with Toby Gray, who at the time was finishing his master's thesis at Mississippi State University on the use of historical records and geographic information systems for identifying opportunities for prairie restoration. Toby spent many months checking out sites that were recorded as prairies during the surveys of the General Land Office (GLO), which in this area were conducted from 1810 through 1836. Toby also evaluated the efficacy of various vegetation treatments (e.g., herbicides versus cutting and burning) for restoring prairies on the Bienville National Forest, where some seventy-two prairie patches have been discovered.

Toby's research led him to conclude that edaphic factors—in particular, chalky, shrink-swell clay soils—play the dominant role in blackland prairie formation; fire and drought provide reinforcement. Most other experts with whom I've spoken (for example, Al Schotz at the Alabama Natural Heritage Program) express a similar view. The Jackson Prairie, unlike most blackland prairies, developed on Eocene rather than Cretaceous sediments, deposited in a deep marine environment of the Mississippi Embayment approximately 38 million years ago. Most trees do not grow well on these chalky soils. Nevertheless, cedars are invading after farming and abandonment. Other trees that germinate in prairie soils here include redbud (*Cercis canadensis*), gray dogwood (*Cornus drummondi*), persimmon (*Diospyros virginiana*), ash (*Fraxinus* spp.), hawthorns (*Crataegus* spp.—including two rare taxa that favor partial sunlight in prairie edges), post oak, hickory (*Carya* spp.), and sweetgum (*Liquidambar styraciflua*), but the trees usually do not grow large. Fire and drought thin the trees and knock them back to prairie edges. In the absence of fire, trees slowly reinvade. Also found on the edges of these prairies is Oglethorpe oak (*Quercus oglethorpensis*), an uncommon tree of western South Carolina and adjacent Georgia, with disjunct populations in Mississippi and Louisiana.

Toby and I first visited the Harrell Prairie, a Jackson Prairie site in the Bienville National Forest. The Forest Service had just burned the northern portion of this prairie in March of this year; most of the rest was burned the previous year. Toby pointed out that small post oaks had been killed by fire, but those taller than about twelve feet had survived with their lower limbs killed—a phenomenon my friend Johnny Stowe calls "thermal pruning." We observed purple coneflower (*Echinacea purpurea*, a predominantly midwestern species), biennial gaura (*Gaura biennis*), cup plant (*Silphium perfoliatum*), gray-headed coneflower,

rattlesnake-master (*Eryngium yuccifolium*), partridge pea (*Chamaecrista fasciculata*), and other grassland plants in bloom. I learned that whale bones have been found in these prairies, so commonly that local farmers claim that these bones are what made the soils so chalky.

We next visited Second Prairie, which is in an earlier phase of restoration and is less diverse than Harrell Prairie. Fire was excluded so long at Second Prairie that it was under forest for forty years. Still, a number of prairie plants survived in small openings or in the soil seed bank. We visited a variety of other Jackson Prairie sites that had been marked as prairie in the GLO surveys. Most have been destroyed by conversion to pine plantations or pastures planted with nonnative grasses, yet some had surviving prairie indicator plants, such as big bluestem, bushy bluestem (*Andropogon glomeratus*), rosinweeds (*Silphium integrifolium*, *S. trifoliatum* var. *latifolium*), milkweeds (*Asclepias* spp.), partridge pea, false aloe (*Manfreda virginica*), and soft hair marbleseed (*Onosmodium molle*).

Then we proceeded to the remnant Black Belt prairies, northeast of the smaller Jackson Prairie belt. Our first stop was Osborn Prairie, also known as Sixteenth Section Prairie. In Mississippi, Section 16 in each county is owned by the county and is intended to generate income for schools. In this case, Friends of Osborn Prairie lease the prairie, now up to 150 acres, from the school district. Virtually the entire site had been farmed, with the prairie community persisting in a refugium in the powerline right-of-way. Redcedar invasion is a serious management issue here, but there is a concern that heavy erosion could occur and that nonnative plants such as privet (*Ligustrum* sp.) and Japanese honeysuckle (*Lonicera japonica*) will take over if the cedars are logged aggressively; instead, Friends of Osborn Prairie is removing cedars slowly using volunteer labor. The cut trees are placed in gullies to reduce erosion.

Here and in other edaphic grasslands, I wonder how much gulley erosion is natural (i.e., these are highly erodible soils) and how much can be traced to past or present land uses such as farming, livestock grazing, or off-road vehicle use. I suspect both inherent site qualities and human land uses are responsible. A certain amount of erosion may help maintain suitable open habitat; this might be especially important for rare forbs that do not compete well with grasses. We observed a diversity of prairie plants at Osborn, including side-oats grama, yucca or Adam's needle (*Yucca filamentosa*), two species of blazing-star (*Liatris aspera* and *L. spicata*), gray-headed coneflower, some very robust yellow puff (*Neptunia lutea*), palespike lobelia (*Lobelia spicata*), lots of compass plant (*Silphium laciniatum*), and prairie dock (*S. terebinthinaceum*). Also present is the osage orange or Bois d' Arc (*Maclura pomifera*), whose original distribution was ostensibly the Red River drainage of Oklahoma, Texas, and Arkansas and in the

blackland prairies, post oak savannas, and Chisos Mountains of Texas; however, some ecologists suspect that the Black Belt and nearby grasslands served as refugia for this species during glacial periods. The large fruits ("hedge apples"), which my friends and I heaved at one another as kids, were likely consumed, and their seeds dispersed, by Pleistocene megaherbivores. Later, this tree was widely naturalized and planted by Indians for its wood (excellent for bows) and by white settlers to create living fences for livestock.

Our next stop was Chickasaw Wildlife Management Area (WMA), southwest of Tupelo, the birthplace of Elvis Presley. While driving to Chickasaw, we observed along the roadside many tiny remnants of the once magnificent Black Belt prairie. Chickasaw WMA is a moderate-sized prairie with many typical blackland plants, including palespike lobelia, purple prairie-clover (*Dalea purpurea*) still barely in bloom, narrow-leaved mountain-mint (*Pcynanthemum tenuifolium*), blazing-stars, the exotic *Lespedeza bicolor* (a bad sign—this aggressive species is widely and foolishly planted as a wildlife food), switchgrass (*Panicum virgatum*), little and big bluestem, yucca, and rattlesnake-master. The diversity of insects, especially grasshoppers and butterflies, was impressive. Our final site visit was to the Chickasaw Village Site, a village of the Chickasaw tribe before their eviction to Oklahoma between 1837 and 1847. The site is on the edge of Tupelo and is managed by the National Park Service as part of the Natchez Trace Parkway. The prairie is in the process of restoration. Grass cover is low here compared to forbs, most of which are somewhat weedy (e.g., goldenrods [*Solidago* spp.] and poison ivy [*Toxicodendron radicans*]). In blackland prairies and other grasslands everywhere, restored sites typically have lower species richness and less characteristic flora than relict sites—but perhaps we just need to give them a few centuries.

Georgia and Florida

The easternmost blackland prairies occur in a narrow band along the Fort Valley Plateau in central Georgia, directly east of the southeastern tip of the Black Belt in Alabama. The best remaining examples are a series of chalk prairies within Oaky Woods Wildlife Management Area, 10,000 acres of which were protected by the Georgia Department of Natural Resources in 2010. I have not yet visited here, but Lee Echols and Wendy Zomlefer provide an account of the flora of Oaky Woods in a 2010 paper. They document twelve plant associations (and a new natural community: Georgia Eocene Chalk Prairie), high species richness (315 native plant species), and 23 rare plant species on the site, including four species new to Georgia, one federally endangered species (fringed campion, *Silene catesbaei*), and one candidate for federal listing (Georgia aster,

Symphyotrichum georgianum). Like other blackland prairies, the grassland char-acter and unusual flora of Oaky Woods can be explained by the shrink-swell, chalky clay soil. Echols and Zomlefer make a good point about conservation of relict grasslands: "It is not only the prairies per se but also the unique mosaic of associated vegetation that comprise the exceptional diversity of blackland prairie landscapes." We need to do more than protect tiny relict prairies in "vest-pocket" preserves. Wherever possible, we must conserve and restore the landscape mosaic in which these grasslands were embedded.

Florida upland glade is endemic to a small area in the Florida Panhan-dle and ranked as critically imperiled globally (G1); I describe my visit to these glades in chapter 6. Ten plant species on these glades, most of them more common in calcareous grasslands to the north and west, are tracked by the Florida Natural Areas Inventory (FNAI). Side-oats grama and littletooth sedge (*Carex microdonta*) make their only known Florida appearances here. An endemic species of tickseed (*Coreopsis*) has yet to be described. Two types of upland glade have been defined: Jackson glades in Jackson County and Gads-den glades, a separate constellation of small sites in adjacent Gadsden County. The two types can be distinguished by a few species replacements, that is, with some species found only in Jackson glades, other species only in Gads-den glades. Florida upland glades might be considered an outlier of blackland prairie. The soil is calcareous, shrink-swell clay. Ann Johnson, an FNAI ecolo-gist, analyzed the species composition of these glades and their similarity to blackland prairies and other calcareous grasslands. She found that the flora of Florida upland glades is most similar to that of the blackland prairie at Oaky Woods, with 169 shared species, followed by the Ketona Glades, with 134 shared species; other blackland prairies and limestone glades also have similar floras. Among the bizarre features of Florida upland glades is that some are dominated by black bogrush (*Schoenus nigricans*), which everywhere else is a wetland plant, as its common name implies. This species occurs in the United States only in California, Nevada, Texas, and Florida; but then also in Eurasia (for example, in the fens of Scotland and Ireland); and in parts of Africa, Aus-tralia, and Mexico.

Other Calcareous Grasslands

Calcareous prairies, woodlands, barrens, and glades occur as small-to-moderate-sized patches in a forest matrix throughout the South. Besides blackland prairies, they include many community types in Louisiana, Texas, Kentucky, southern Ohio and Indiana, Tennessee (with the Central Basin cedar glades especially significant biologically), Virginia, West Virginia, the Carolinas, Alabama, and

Georgia. As noted by Elsie Quarterman and colleagues, most glades east of the Mississippi River occur within an unusual climatic zone in which winter precipitation exceeds summer precipitation (i.e., summer drought is characteristic). This seasonality enhances the hydroxeric and shrink-swell properties of clay soils. Soil fertility is low on most calcareous grasslands, despite moderate (i.e., circumneutral, 6.0–8.0) pH; a low level of soil phosphorus may explain the low fertility.

Louisiana

In Louisiana I visited several small but rich grasslands with Chris Reid and Patti Faulkner of the Louisiana Natural Heritage program. Interior Louisiana grasslands are similar to blackland prairies, but their soils have not been well studied. Among the calcareous types we visited was Carpenter Road Prairie in the Kisatchie National Forest, where we found a profusion of plants blooming in mid-May 2008, including pale purple coneflower (*Echinacea pallida*), groove-stem Indian plantain (*Arnoglossum plantagineum*), pineland milkweed (*Asclepias obovata*), prairie redroot (*Ceanothus herbaceus*), blue larkspur (*Delphinium carolinianum* ssp. *carolinianum*), woodland poppymallow (*Callirhoe papaver*), showy evening primrose or pinkladies (*Oenothera speciosa*—a white flower with bright pink veins and a yellow center), hairy fimbry (*Fimbristylis puberula*—a sedge), woodland pinkroot (*Spigelia marilandica*), prairie Junegrass (*Koeleria macrantha*), compass plant, rattlesnake master, and many others. Among my favorites were the hairiest eastern prairie marbleseed (*Onosmodium hispidissimum*) plants I've ever seen. We also observed prairie acacia (*Acacia angustissima* var. *hirta* = *Acaciella hirta*), which occurs in grasslands west of the Mississippi River and as a disjunct in north Florida.

Copenhagen Hills is a preserve managed by The Nature Conservancy (TNC) on calcareous clays of the Jackson Formation, along the Ouachita River. The preserve hosts another disjunct population of Oglethorpe oak and more than twenty other rare plant species tracked by the Louisiana Natural Heritage Program. The prairie (known as "Prairie du Cote") was described by S. H. Lockett in 1869 as "gently undulating, covered with a luxuriant growth of grass and thousands of bright wild flowers, and is free from trees, except for a few clumps of thick-growing hawthorns. Large herds of cattle and sheep graze here." Chris explained an interesting phenomenon: species composition on these small, isolated prairies is not highly predictable. Certain plants that might be expected—such as pale purple coneflower—are missing from Copenhagen Hills, which, however, has many northern disjuncts. A pattern of inconsistent community membership is common for small, isolated sites, where chance

colonization and extinction events are influential. We also found here coral bean (*Erythrina herbacea*), a common species in Florida, whose relatives in the same genus are tree-sized plants in the West Indies and Neotropics.

Texas

In Texas I was guided by expert field botanist Jason Singhurst of the Texas Natural Heritage Program. The calcareous prairies we visited are the Weyerhaeuser Fleming Prairies. Our hosts were Dan Jones and Chris Gregory of Weyerhaeuser, who have put considerable effort into restoring these prairies (Dan said he keeps his restoration work "under the radar"). The calcareous Fleming Formation overlays the Catahoula Formation (sands and sandstones), with some Catahoula outcrops; both formations are of Miocene age. The calcareous nature of the soil was evident by the abundant snail shells on the ground and live snails on the underside of Indian plantain leaves. Dan has noticed a positive correlation between the density of snails and the floristic quality of the prairie. Like many other calcareous prairies, much of this site is highly eroded. The gulleying is probably natural to a large degree, given these friable soils.

We found an impressive diversity of plants in this Fleming prairie, including weird admixtures of out-of-range taxa and rarities such as the Texas lady's tresses (*Spiranthes brevilabris*), which has disjunct populations east to Florida and Georgia. Particularly gorgeous plants in bloom were Topeka purple coneflower (*Echinacea atrorubens*, endemic to Texas, Oklahoma, and Kansas; plate 23), Engelmann's daisy (*Engelmannia peristenia*), and Cobaea beardtongue (*Penstemon cobaea*). We also saw hairy grama (*Bouteloua hirsuta*), here near the eastern edge of its main range. This is the grass that, as a disjunct, dominates the coastal prairie on Cayo Costa in southwest Florida (see chap. 3). Like most southern grasslands, Fleming prairies are being lost rapidly to development. One of the highest quality sites is now a Target store. As Dan put it, "People just don't recognize the significance of these sites."

Alabama and Georgia

The Coosa Prairies of northwestern Georgia and adjacent Alabama also are characterized by heavy, shrink-swell clay soils. In *Plant Life of Alabama*, Mohr provides a classic description that could apply to most any calcareous prairie: "The perfectly level tracts of cold, gray, impervious soil, a perfect mire during the season of rain and a hard crusty mass torn by many fissures while taking in the summer sun, form a peculiar feature in the topography and flora of the Coosa Valley." Longleaf pine (the community known as montane or mountain longleaf) is in the hills surrounding the Coosa Valley in Georgia and Alabama,

and in the valley itself; however, longleaf seems to have been absent from the Coosa Prairies proper. I visited this complex of prairies, woodlands, and pine plantations in August 2009 with Johnny Stowe, Malcolm Hodges, Philip Juras, and Bill Garland. This is far from a pristine ecosystem. Much of the site was plowed with a "soil ripper," which fractures impermeable clay layers to allow for row-planting of loblolly pines (*Pinus taeda*). Fortunately, the foresters mostly avoided patches of prairie with this treatment. A timber company donated a 929-acre conservation easement to TNC in 1992. The area is managed by prescribed fire every two to three years, with woody vegetation in prairie patches manually removed. Some forestry activities, however, are not so benign. Loggers often use prairie openings as loading decks and parking areas. With each timber harvest, substantial scarring occurs from skid trails. During rainy periods, the price of timber goes up at the mills due to shortage, encouraging logging when the most erosion will occur. Meanwhile, trespassers in ATVs regularly tear up the area.

Still, the prairies that remain are of high conservation value. Species of conservation concern here include the whorled sunflower (*Helianthus verticillatus*), which was discovered in 1892 but thought to be extinct until rediscovered in 1994. Today, it is documented in only four locations in west Tennessee, Alabama, and Georgia; recent genetic studies suggest that the Coosa population might be distinct enough to warrant recognition as a new species. Other rare species here are Coosa Barbara's-buttons (*Marshallia mohrii*), Little River black-eyed Susan (*Rudbeckia heliopsidis*), Cumberland rose gentian (*Sabatia capitata*), and Tennessee yellow-eyed grass (*Xyris tennesseensis*). After visiting several prairie patches on this not-too-hot August morning, we entered Indigo Prairie. We noted that the glade wild indigo (*Baptisia australis* var. *aberrans*) had been heavily browsed by deer. We found big bluestem, the quintessential grass of the tallgrass prairie, in bloom for the first time we'd seen this year. We also found New Jersey tea (*Ceanothus americanus*), swamp rose (*Rosa palustris*), and black-seed speargrass (*Piptochaetium avenaceum*). You do not want to get speargrass in your socks—the long, sharp awns can work their way into flesh and have been known to kill sheep.

We noticed a faint, pleasant odor—slightly soapy, or a bit like cilantro. Finally we found the source: a patch of prairie dropseed (*Sporobolus heterolepis*), whose primary distribution is in the Great Plains. When we picked some leaves of this grass and sniffed them in the sun, the odor became more intense. Could this be the southernmost occurrence of this species? Little things like this get naturalists excited. After later consulting NatureServe Explorer and Weakley's Flora, I discovered that we had likely stumbled upon the southeastern-most

occurrence of prairie dropseed, recorded from Floyd County, Georgia, where we were. Tantalizingly, Indigo Prairie is near the Georgia–Alabama line, and this species has not been reported from Alabama.

Tennessee

Limestone glades (often called cedar glades) are prominent in Tennessee and portions of adjacent states (fig. 4.3, plate 25). Thanks to the work of many fine botanists, beginning with the pioneer Tennessee botanist, Augustin Gattinger, in the nineteenth century, and continued by Elsie Quarterman of Vanderbilt University and her students Jerry and Carol Baskin of the University of Kentucky, among others, these glades have been well explored botanically. As a summary of their importance for conservation, southeastern cedar glades contain 448 native plant taxa, including 21 endemic/near-endemic plants and many disjunct and peripheral species with centers of distribution mostly to the west. The largest and biologically hottest collection of cedar glades is on Ordovician limestone in the Inner Central Basin of the Interior Low Plateaus of Tennessee, in the vicinity of Nashville.

The edaphic factor that promotes grassland (perhaps better called rockland) on limestone glades is thin soil and consequent xeric conditions for much of the year. Like the shrink-swell clays of calcareous prairies, glade soils are saturated for a period of time before drying out. Species of glades and outcrops of various types have been described as "obligate heliophytes," because they thrive in high-sunlight environments. Winter annuals, such as the several species of gladecress (*Leavenworthia* spp.) characteristic of limestone glades, escape competition by germinating in autumn, overwintering as a rosette, flowering in early spring while conditions are wet, and then setting seed and withering away as warmer, drier weather prevails. Because few pollinators are active during the early spring flowering period, many winter-annual glades plants have evolved self-compatibility, the ability to pollinate themselves and set seed. Given the high tolerance of glades plants to drought and solar radiation, it is not surprising that Edwin Bridges and Steve Orzell found that 19 percent of the nonendemic plants in Central Basin glades are extraneous (i.e., from elsewhere), with centers of distribution in drier regions to the west and northwest.

Quarterman and colleagues note that glades vary in soil depth, but depth "is never great enough to allow growth of shrubs and trees that would shade the surface." Nevertheless, shrubs and trees can be observed invading glades from the edges and germinating in cracks in the limestone, where deeper soil accumulates. The Baskins present a model of vegetation development on cedar glades and limestone prairies in the Central Basin (fig. 4.4), to which I would add climate change/
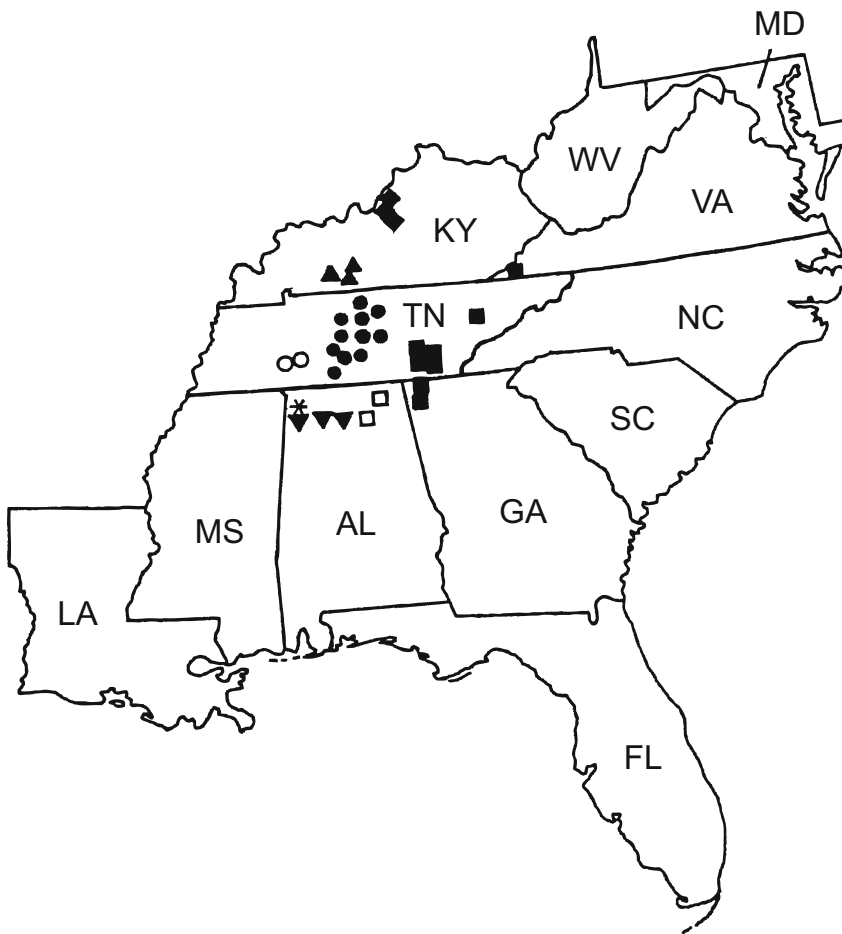
Figure 4.3. Distribution of limestone (cedar) glades in the southeastern United States. Each symbol represents all cedar glades in a county. Diamond: Outer Bluegrass; triangle: Pennyroyal Plain; closed circle: Central Basin; open circle: Western Valley; star: Tennessee Valley and Little Mountain; inverted triangle: Moulton Valley; open square: Sequatchie Valley; closed square: Ridge and Valley. © 1999 Cambridge University Press. Reprinted from Baskin and Baskin (1999) with the permission of Cambridge University Press.

drought as a factor, in addition to management, that may retard woody invasion. Quarterman describes "grassy glades" as having somewhat deeper soil than "gravel glades," with poverty dropseed (*Sporobolus vaginiflorus*) and witchgrass (*Panicum capillare*) usually the dominant grasses, with occasional slimspike threeawn (*Aristida longespica*) and, on deeper soils, little bluestem. Where little bluestem is dominant and dense, the glade is better considered a barren or prairie. Again, plant communities change in membership and dominance along environmental gradients in space and time, with species responding individualistically to physical factors.
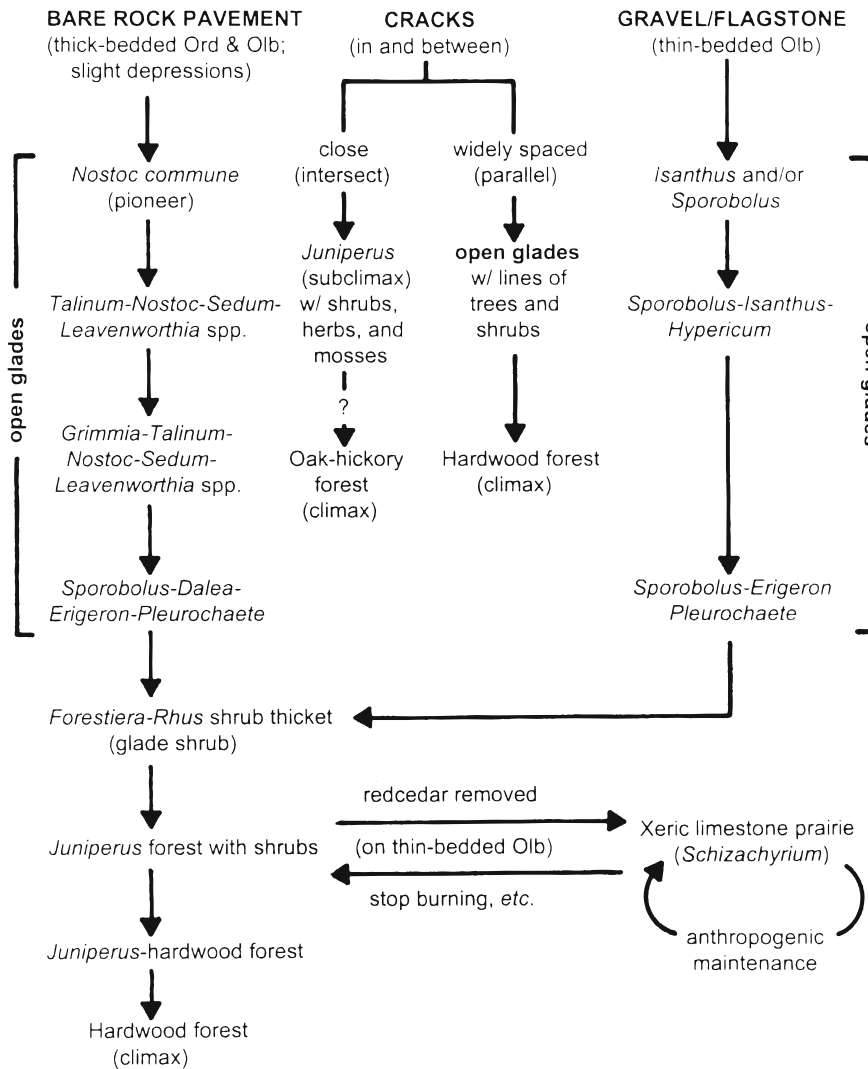
Figure 4.4. A conceptual model of vegetation development on cedar glades in the Inner Central Basin of Tennessee. Ord = Ridley limestone, Olb = Lebanon limestone. Complete names for taxa shown in diagram are *Dalea gatteringi, Erigeron strigosus, Forestiera ligustrina, Grimmia apacarpa* (a moss), *Hypericum sphaerocarpum, Isanthus brachiatus, Juniperus virginiana, Leavenworthia exigua* var. *exigua, L. stylosa, Nostoc commune* (a cyanobacterium), *Pleurochaete squarrosa* (a moss), *Rhus aromaticum, Schizachyrium scoparium, Sedum pulchellum, Sporobolus vaginiflorus,* and *Talinum (Phemeranthus) calcaricum.* From Baskin and Baskin (2004). I would add "or climate change/drought" at the lower right of the figure to reflect the hypothesis that climate could substitute for anthropogenic maintenance of edaphic grasslands. Vegetation development of glades on substrates other than limestone shows somewhat analogous patterns, but with different taxa involved. © 2004 The New York Botanical Garden Press. Reproduced from Baskin and Baskin (2004) with permission of the publisher.

I visited Central Basin cedar glades in mid–May 2008 with Brian Bowen, David Lincicome, and Andrea Bishop of the Tennessee Department of Environment and Conservation. We toured several glades in three counties near Nashville. Among the soil types typical of glades in this region is the Gladeville flaggy, silty, clay loam, about three to twelve inches deep over Lebanon Limestone; the "flags" are thin fragments of limestone found throughout the soil profile and scattered about on the surface. This region has horrendous human population growth and development, which have destroyed many of the glades. We drove by housing subdivisions that sit on top of former high-quality glades, a sickening sight all too reminiscent of Florida. These glades are endangered ecosystems, but we have no "Endangered Ecosystems Act" or similar law to protect them. We have an Endangered Species Act, but the federally listed species here are plants, and in contrast to animals, the act offers no protection to plants on private land. This quirk reflects the legal heritage of our country, where plants belong to the landowner but wildlife belongs to the state. Lacking effective legal tools for protecting imperiled plants outside public lands, we must rely on the environmental ethics of landowners. Such ethics are often lacking.

We were lucky to find an individual of one of those endangered plants, Tennessee coneflower (*Echinacea tennesseensis*) in bloom at Couchville Cedar Glade State Natural Area. This species normally blooms in June and July, so this flower on May 12th was unusual; it was close to the ground, where conditions are warmer. The Tennessee coneflower, legally an endangered species when I observed it, was delisted by the US Fish and Wildlife Service on August 3, 2011, based on a finding that the species has recovered and no longer meets the legal definition of threatened or endangered under the Endangered Species Act. I am always suspicious when the government delists a species, because the basis for delisting is often more political than biological; an example is the Rocky Mountain population of gray wolf, which was delisted in May 2011 under pressure from ranchers and hunters. In the case of the Tennessee coneflower, however, delisting represents a true improvement of conditions for the species. As described by Brian Bowen in the *Natural Areas Journal*, the recovery of the Tennessee coneflower, achieved through land protection, management, and population reintroduction, is a success story that demonstrates how the Endangered Species Act was intended to function.

Two other endangered plants associated with the cedar glades of the Central Basin are Pyne's ground plum (*Astralagus bibullatus*) and leafy prairie-clover (*Dalea foliosa*). We did not find any *D. foliosa* during my tour of the Central Basin, but we found *A. bibullatus* in fruit at a couple of sites. The reddish plum-like fruits are ridiculously large for the size of the plants. Among other memorable plants in

flower were the long-styled or cedar gladecress (*Leavenworthia stylosa*), which has the largest flowers in the genus, and bigfruit evening primrose (*Oenothera macrocarpa*), whose impressive yellow flowers, four inches wide, dominated the scene in some areas (plate 25). We observed them blooming in the afternoon, when they open, but the flowers remain open at night; during full moons they are pollinated by sphinx moths. At Flat Rock Cedar Glades and Barrens State Natural Area, I lifted one of the flat rocks to find a large spider, which I thought might be a tube-dwelling tarantula. Spider authority Susan Riechert at the University of Tennessee identified it, from a photo I sent her, as the Carolina wolf spider (*Hogna carolinensis*), probably the largest of the wolf spiders in North America.

Cedar glades superficially resemble human-disturbed sites undergoing succession to forest. They are not; these are endemic communities of ancient origin. Jerry and Carol Baskin noted in 1986 that the southeastern cedar glade near-endemics, Tennessee milkvetch (*Astragalus tennesseensis*) and leafy prairie clover—both of which have disjunct populations in the Midwest—and the narrow endemic Pyne's ground plum are not closely related to any living species within their respective genera. This evidence, along with the determination that the endemic genus *Leavenworthia* (gladecress) is not closely related to any extant genus, "suggest[s] that these taxa evolved in the distant geological past." The Baskins make a compelling case that the herbaceous flora of cedar glades remained essentially intact during the glacial episodes of the Pleistocene, when the regional vegetation was boreal jack pine-spruce-fir forest during the Last Glacial Maximum (23,000 to 16,500 years ago) and a mixed coniferous-deciduous forest during the late glacial period. Some other glades endemics, however, including Tennessee coneflower, are closely related to living taxa, which suggests they evolved more recently. Moreover, as pointed out by the Baskins in 2003:

> The southeastern cedar glades … are different from the so-called "cedar glades" described in the Ozarks and in the Midwestern United States, which appear to be secondary successional communities.… In the absence of fire, grazing, or other disturbances, succession to a redcedar and/or hardwood forest may occur relatively quickly in the rocky glades of the Ozarks and Midwest, but not in the true cedar glades such as those in the Southeast.

Kentucky and Ohio

My first acquaintance with native grasslands was in Ohio, where I spent my boyhood and was later employed by Ohio State Parks and the Ohio Natural Heritage Program. The most abundant (albeit still rare and tiny) relict prairies

in Ohio are in the flat central portion of the state on rich glacial till of Wisconsinan age (i.e., the most recent glaciation). According to Edgar Transeau and interpretations since, these prairies spread into Ohio during the Holocene Climatic Optimum (Hypsithermal Interval) about nine to five thousand years ago. They clearly have a close affinity to tallgrass prairies farther west, with the same dominant and characteristic species of plants. Relict prairies persist today in pioneer graveyards, along old railroad rights-of-way, and in other odd sites that were fortunate to remain unplowed. In Adams County, adjacent to the Ohio River, however, prairies occur on droughty slopes and promontories of Peebles (Cedarville) dolomite of Silurian age. These prairies fall within the unglaciated Outer Bluegrass physiographic region, which extends from Kentucky across the Ohio River only in this area. Similar dry prairies and glades occur on the Kentucky side of the river, in Lewis County. Four types of prairie have been described in Adams County: promontory, hanging (on slopes), riverscour, and oldfield (on abandoned agricultural land).

One of the ecologists I respect most, E. Lucy Braun from the University of Cincinnati, who became the first female president of the Ecological Society of America and was a staunch defender of natural areas, studied these unusual Adams County prairies. She first published articles about them in 1928. Braun noted differences between these prairies and those in the glaciated till plains to the north. The Bluegrass Prairies are mostly dominated by little bluestem and side oats grama, with Indiangrass and big bluestem usually present. Their distinctive southern and western xeric-adapted taxa include limestone adderstongue (*Ophioglossum engelmannii*), false aloe (*Manfreda virginica*), and downy milkpea (*Galactia volubilis*). Braun concluded that these prairies are not part of the Prairie Peninsula, which is of Holocene age, but are of Pleistocene origin, "pre-Wisconsin or even earlier." Transeau and other ecologists disagreed with Braun and included the Bluegrass Prairies within the Prairie Peninsula, but the weight of opinion is shifting back to support Braun's hypothesis, at least to the extent that these prairies are distinct from the Prairie Peninsula.

My former colleague at the Ohio Natural Heritage Program, Dennis Anderson, in *Plant Communities of Ohio*, concluded that the prairies of the Bluegrass region are strongly edaphic and are relatively stable in the absence of fire, although woody species eventually invade many sites without fire. Jerry and Carol Baskin suggest that these prairies are better lumped with xeric limestone prairies than with the Prairie Peninsula grasslands to the north. A study by Susan Boettcher and Paul Kalisz of phytoliths (plant opal, which is abundant and of a characteristic dumbbell shape in prairie grasses) in soils in Adams

County confirmed that grassland vegetation here was historically more promi-
nent on soils derived from dolomite, as opposed to shale. Prairie and forest
(redcedar-hardwood) vegetation alternated over time on these sites, apparently
in response to climate change, and the distinction between primary and sec-
ondary prairie was unclear. Forbs seem to have contributed more phytoliths
than grasses to soils in the prairie openings, suggesting that forbs are important
components of the community. However, Boettcher and Kalisz restricted their
sampling "to soil areas judged to be free of severe erosion," thus avoiding the
promontories and steepest slopes, which may provide the most stable long-
term refugia for grassland species. Boettcher and Kalisz surmised that "prairies
may have been most important in the vegetation history on southerly slopes
and areas of shallow soil, and least important on protected slopes and areas of
deep soil."

How old are these prairies, not far south of the glacial boundary? Lucy
Braun was probably incorrect in her conclusion that the mixed mesophytic
forests of this region have changed little since the Pleistocene or earlier. Nev-
ertheless, edaphic grasslands—such as the cedar glades of Middle Tennessee
(as suggested by the Baskins) or promontory prairies of the Outer Bluegrass
region—could have persisted through glacial cycles. Indeed, recent research
related to climate change shows that species assemblages on unusual sites can
persist for long periods of time in disequilibrium with the regional climate.
These sites serve as climatic refugia (in this case, for species adapted to xeric
warm-temperate conditions) and help explain how northern sites were col-
onized so rapidly by some species after glaciation, much faster than can be
explained by their known dispersal rates.

The Cincinnati Museum of Natural History and TNC have worked jointly
for many years to create and manage the nearly 16,000-acre Richard and Lucile
Durrell Edge of Appalachia Preserve system, which today consists of eleven
sites. Although awfully far north for my subtropical-acclimated phenotype,
this landscape remains one of my favorites. This is where I first designed and
mapped a "regional reserve network," which schematically connected these
preserves with broad corridors and linked them to the nearby Shawnee Wil-
derness in Shawnee State Forest and beyond to other state, federal, and private
conservation areas across southern Ohio. In one version I expanded the system
southeastward to the Daniel Boone National Forest of Kentucky, including
the spectacular Red River Gorge area. This region is the heart of the mixed
mesophytic forest, as recognized by Lucy Braun, one of the biologically richest
temperate forests on earth. Francois André Michaux, son of the famous botanist
André Michaux, had this to say about the forests of the Ohio River Valley in

1804: "In more than a thousand places of the territory I have passed over at different periods in North America I do not recollect to have seen one which can be compared to the vegetative power of its forests." That these magnificent forests are sprinkled with dry prairies, outcrops, glades, rivers, gorges, caves, and other nonforest communities makes them all the more interesting to the naturalist and deserving of full ecological recovery.

It was nostalgic to revisit Adams County in late September 2008 with Chris Bedel of the Cincinnati Museum and Rich McCarty of TNC. This is a perfect season in southern Ohio, with usually dry and mild weather and leaves of all sorts changing color. I had just crossed the river from Kentucky, where I observed similar prairies in Lewis County. Edaphic control of the promontory and some hanging prairies is glaringly obvious—these are thin and droughty soils, with high rates of erosion, upon which trees tread lightly. I learned that primary prairies in Adams County host twelve to thirteen species of grasshoppers, compared to only one or two in oldfields, suggesting antiquity of the primary prairies. Some of the dry prairies and promontories host arborvitae—also known as northern whitecedar (*Thuja occidentalis*)—which is more typical of the mesic limestone gorges of this region, of calcareous fens from Ohio northward, and of the edges of the Niagara Escarpment of Ontario, where individuals exceed a thousand years in age. Bruce Sorrie informed me that arborvitae also occurs on dry rocky escarpments in West Virginia, Virginia, Pennsylvania, and New Jersey. A more expected xeric-adapted species on the promontories and hanging prairies of Adams County is dwarf hackberry (*Celtis tenuifolia*), which is rare north of the Ohio River.

One of the largest grassland regions of Kentucky was the Big Barrens, which occupied much of the Kentucky Karst Plain in the central to southwestern portion of the state, extending into northwestern Middle Tennessee. Some two to three million acres of prairie were described here by early white settlers. Lucy Braun, in her monumental *Deciduous Forests of Eastern North America*, examined the Big Barrens and concluded that these grasslands did not arise during the Hypsithermal Interval (then called the "xerothemic period"), despite their depiction by Transeau as part of the Prairie Peninsula. In contrast to her hypothesis about the history of Bluegrass Prairies in Ohio, Braun concluded that the Big Barrens were recent in origin, with a "short period of dominance of prairie vegetation." Jerry and Carol Baskin, with Edward Chester, studied this region extensively and agreed with Braun. Analyzing fossil pollen data, they found no dramatic increase in grass or prairie forb pollen during the Hypsithermal; rather, a rapid shift in vegetation from dry oak-hickory woodland to oak-grass barrens occurred only about two thousand years ago.

They attribute this shift to widespread burning by Native Americans at that time. This is a reasonable conclusion. It should not imply, however, that Indians created barrens out of closed forest. They had something to work with. Flammable grasses and grassland plant seed sources probably were present in the dry oak-hickory woodlands that preceded the transition to barrens, as indicated by the rapid increase in grass pollen two thousand years ago. Here, as in many places, Indians apparently converted woodlands into barrens/prairie and oak savanna through their use of fire.

I visited grasslands in Kentucky twice in 2008. My guides were Marc Evans and Joyce Bender from the Kentucky State Nature Preserves Commission. Joyce is a colleague from Ohio; we worked together at the Ohio Natural Heritage Program in the early 1980s. Marc and I got along immediately, as we have a similarly twisted sense of humor (Marc has since retired, so I can insult him freely). Pine Creek Barrens, on dolomite, was the first calcareous glade we visited. It was a chilly and rainy morning in early May, and the hydric phase of these hydroxeric glades was quite evident. The cyanobacteria ("blue-green algae") *Nostoc commune*, characteristic of glades, was plump and conspicuous on exposed dolomite. The gladecress here, *Leavenworthia exigua* var. *laciniata*, is endemic to Kentucky and confined to dolomite, whereas the more widespread variety *exigua* (Tennessee gladecress) occurs on limestone glades in Tennessee and northern Georgia. The *Leavenworthia* were already in fruit, whereas shooting star (*Dodecatheon meadia*) was in full bloom. Marc pointed out that redbud is a troublesome invader on these glades. We next visited Panther Glade (Jim Scudder Preserve), a slope glade (or xeric prairie) on the edge of the Elizabethtown Karst Plain, where we were lucky to find white lady's slipper (*Cypripedium candidum*) and enjoy its delightful odor. It was strange for me to see this orchid on a glade, as I was familiar with it on blacksoil wet prairies in Ohio and elsewhere in the Midwest. Greater yellow lady's slipper (*C. parviflorum* var. *pubescens*) was in the adjacent woods at Panther Glade, with apparent hybrid plants growing in between.

The most edaphically controlled calcareous glades I visited in Kentucky were the Thompson Creek Glades, a set of small limestone hill glades on thin-bedded Salem limestone. Redbud is not invading these glades, and there has been no need to use fire to suppress other woody plants, although some cedars were manually "worked back from the edges." At Flatrock Glade, in the middle of the Big Barrens region of the Kentucky Karst Plain, we observed several rare plants, most notably necklace gladecress (*Leavenworthia torulosa*), limestone fameflower (*Phemeranthus calcaricus*), and limestone quillwort (*Isoetes butleri*). Michaux's gladecress (*Leavenworthia uniflora*) was also present. I captured a large,

iridescent purple–blue ground beetle (family Carabidae, probably genus *Amara*), which none of us had observed before and which may be the most beautiful beetle I've seen outside the tropics. No one yet has been able to identify it from my photograph. As Richard White writes in his beetle field guide, *Amara* includes over two hundred species, and "it is extremely difficult for even the practiced taxonomist to identify species."

Raymond Athey Barrens, named in honor of the self-taught botanist who discovered the site, was our next stop. This natural area includes an open woodland with post oak and blackjack oak, with scattered open glades. The rarest plant residing here is the prairie (downy) gentian (*Gentiana puberulenta*), which occurs at only one other site in Kentucky and is patchy across its substantial range. Returning to northern Kentucky in late September, the main calcareous barren/glade complex I visited with Marc and Joyce was Crooked Creek Barrens State Nature Preserve. This barrens is on the edge of the Outer Bluegrass region, in Lewis County, right across the river from Adams County, Ohio. The openings here are highly erosive with thin, shaly clay soils that, at this time of year, are exceedingly dry and dusty. Among the treats were four species of blazing-star in bloom—tall (*Liatris aspera*), cylindrical (*L. cylindracea*), scaly (*L. squarrosa*), and dense (*L. spicata*)—plus obedient plant (*Physostegia virginiana*) and earleaf foxglove (*Agalinis auriculata*) scattered among the dominant little bluestem, side-oats grama, and super-abundant Lucy Braun prairie dock (a small form of prairie dock, sometimes classified as *Silphium terebinthinaceum* var. *lucy-brauniae*).

Virginia

Calcareous prairies, glades, and barrens also occur in Virginia. I'll briefly recount some experiences from a couple of sites that I visited with Chris Ludwig and Larry Smith of the Virginia Natural Heritage Program. Chris was my gracious host, and Larry and I go back to graduate school at the University of Tennessee–Knoxville in the 1970s, when we hiked and drank a considerable amount of beer together (not necessarily at the same time).

As described on the Virginia Natural Heritage Program website—which features the best vegetation descriptions of any state heritage program with which I'm familiar—limestone and dolomite barrens in Virginia are scattered throughout the western Ridge and Valley Province, mostly on steep, south- to west-facing slopes. The thin soils typically have relatively high pH (> 7.0) and calcium; dolomitic soils are also high in magnesium. One significant site we visited, reminiscent of the Adams County prairies of southern Ohio, was Sweet Springs State Natural Area in the Ridge and Valley Province. The site is

private land, on which the state has an easement. The bedrock is dolomite of the Elbrook Formation, which is exposed in only six counties in Virginia. The shallow, rocky soils on dry southwest-facing slopes support a rare natural community known as montane dry calcareous forest/woodland. Redcedar, redbud, and several species of oaks are the major trees, and little and big bluestem, Indiangrass, and side-oats grama the dominant grasses.

The rarest plant at Sweet Springs is Addison's leatherflower (*Clematis addisonii*), found in only four Virginia counties and nowhere else in the world. Like many narrow endemics, it is not listed under the US Endangered Species Act. The more widespread smooth purple coneflower (*Echinacea laevigata*) is federally listed as endangered and makes an unexpected appearance here, disjunct from the Piedmont. Chris pointed out the scarcity of calcareous barrens in this region—only about 100 to 500 limestone barrens exist in Virginia, West Virginia, Maryland, and Pennsylvania combined, compared to some 5,000 to 10,000 shale barrens within the same region, including thousands in Virginia alone. Limestone is underrepresented in conservation areas because it grows crops and cows well; the farmers give their sandstone lands to conservation. Of 1.6 million acres of national forests in Virginia, only 15,000 acres are on limestone. Although the barrens at Sweet Springs are clearly edaphic, Chris, Larry, and I agreed that the woods are closing in and that fire is needed, although it will be challenging to apply it here on private land.

The other significant calcareous barrens we visited is Cleveland Barrens Natural Area Preserve, the second largest limestone/dolomite barren in Virginia. This site is in on the very edge of the Ridge and Valley Province, in the Clinch River Valley (a biodiversity hotspot) in the southwestern sliver of the state; the Cumberland Plateau is just one ridge to the west. The series of dolomite barrens here feature thirteen rare plant species and three rare insect species. One of the rare insects is the Olympia marble butterfly (*Euchloe olympia*), which oviposits (lays its eggs) on hairy rockcress (*Arabis hirsuta*). Chris watched a female tasting every *Arabis* on one barren; he discovered a lot more *Arabis* than he had noticed without the expert guidance of the butterfly. We observed a number of prairie plants in the adjacent woods, "hanging out" with little or no reproduction, waiting for a canopy opening. How long can these populations persist, vegetatively or in the soil seed bank, without fire or other disturbance to provide sunlight and stimulate growth and flowering? This question usually cannot be answered definitively. On one site in Virginia, only three individuals of Peter's mountain mallow (*Iliamna corei* or *I. rivularis*), a rare plant disjunct from the West, could be located; however, 50,000 seeds were found in the seedbank! Rounding out our day in early September 2009, we found bar-

rens silky aster (*Symphyotrichum pratense*), a lovely plant disjunct here (and also in Florida upland glades and a few other southern sites) from the West, plus another calciphile (calcium-lover), eastern leatherwood (*Dirca palustris*).

Sandstone Glades and Barrens

Sandstone glades occur in most southern states, but have not been as well studied as calcareous grasslands. This may be because sandstone glades and barrens typically have lower species richness and far fewer endemics. A salient question is why sandstone glades are less rich in endemics than glades on other substrates. I discussed this question with Alan Weakley of the University of North Carolina and Jerry Baskin of the University of Kentucky, two impeccable botanists. Both independently reasoned that the endemics of calcareous glades, such as in Middle Tennessee and Bibb County, Alabama, are derived from taxa of limestone prairies and glades of the Midwest (e.g., the Ozarks of Missouri) or farther west, which moved east during dry times, got stranded on glades by moister regional climates, and then speciated in isolation. Such a process didn't happen often with sandstone-associated species, presumably because the source pool of species associated with open sandstone habitats is smaller than the pool of species associated with open limestone habitats.

The "sandstone" (really a mix of sediments) barrens I visited in Texas, with Jason Singhurst, were Catahoula Barrens on the Oligocene/Miocene Catahoula Formation. About a dozen Catahoula barrens with vernal pools and a strongly prairie flora are known on the Angelina National Forest. The shallow, nutrient-poor soils, high aluminum content, low pH, and fluctuating extractable water indicate stressful environmental conditions. Tuffaceous ash was deposited here about twenty million years ago from volcanoes in Trans-Pecos Texas and northern Mexico, and volcanic glass shards are present in the sediments. Characteristic plants include little bluestem, Nuttall's rayless goldenrod (*Bigelowia nuttallii*), and *Cladonia* lichens. Species richness is high, with up to 150 species of plants in a single small opening, comparable to seepage pitcher plant bogs (one of the most species-rich communities in the South). Among the rare plants here are a federally listed Texas endemic, Navasota lady's tresses (*Spiranthes parksii*), and San Saba pinweed (*Lechea san-sabeana*), which was endemic to Texas until Chris Reid recently found a population in Louisiana. Four species of pinweed (*Lechea*) are known from the Catahoula Barrens. Especially attractive in the early morning was velvet panicum (*Dichanthelium scoparium*), with dewdrops clinging to its dense hairs. To the northeast, sandstone glades of Paleozoic (probably Mississippian) age occur in Arkansas in the Ouachita Mountains. They are especially prominent at Petit

Jean State Park. The thin soils support grassy patches amidst the exposed rock; it is easy to see how trees are limited here.

Two kinds of sandstone glade occur in Kentucky, distinguished geographically, geologically, and floristically. One type is on the Shawnee Hills, a subregion of the Interior Low Plateaus Province in western Kentucky, of Mississippian age; the other is on the Cumberland Plateau in eastern Kentucky, of younger Pennsylvanian age. The Mississippian and Pennsylvanian epochs, usually distinguished only in the United States, constitute the Carboniferous Period of the Paleozoic Era. Mississippian and Pennsylvanian sandstones weather differently, creating distinct microhabitats for plants. On my May 2008 trip I visited just two sandstone glades on the Shawnee Hills. It was a drizzly gray morning at the Macy Highway Barrens and Sandstone Glades (also known as Sunset Barrens). The site is a xeric (although not particularly so that day) post oak–blackjack oak woodland with a series of charming open glades. Mosses were thick on the exposed rocks, with interspersed devil's-tongue (prickly pear) cactus (*Opuntia humifusa*); the patches of grass were primarily broomsedge bluestem (*Andropogon virginicus*) and Elliott's bluestem (*A. gyrans*). Of all the glades I visited, the effects of the previous summer's drought were most conspicuous here: redcedars were healthy and green in the surrounding woodland, but those that had colonized the thin soils of the glade were dead and brown.

I next visited Mantle Rock, a TNC preserve in western Kentucky, just south of the Ohio River and the Shawnee National Forest in Illinois. The centerpiece of Mantle Rock Preserve is a 30-foot-high natural bridge spanning 188 feet and reminiscent of the natural bridges in the Red River Gorge area on the Cumberland Plateau. This is the only site in Kentucky for prairie Junegrass. The glade and woodland had been thinned and burned just a couple weeks before my visit, with the open glades burned in fingers of grasses extending down from the woodland of post oak, white oak (*Quercus alba*), and northern red oak (*Q. rubra*). In places, the fire burned downslope through beech-maple (*Fagus grandifolia–Acer saccharum*) forest to the creeks and beneath the sandstone cliffs. I noted that May apple (*Podophyllum peltatum*) was the first herb to emerge above the ashes in the burned bottomland. This site has an eerie, melancholy feel to it, as I knew it to be a place of great tragedy for the Cherokee people along the "Trail of Tears." After being evicted from their lands in the Appalachians and marched westward toward Oklahoma, approximately 1,766 Cherokee were forced to spend two weeks under Mantle Rock and the shallow rock shelters here during the hard winter of 1838–39 while waiting for the Ohio River to thaw and become passable. Many died from exposure.

At Walker Mountain/Sinking Creek in Virginia, sandstone barrens occur

on southward slopes of northeast-southwest trending parallel ridges. I visited these with Chris Ludwig, Gary Fleming, and Karen Patterson of the Virginia Natural Heritage Program in September 2009. My hosts pointed out that some openings support warm-season grasses, such as big and little bluestem, with white ash (*Fraxinus americana*) and redcedar characteristic of calcareous habitats, while more acidic sandstones on the same ridge support pitch pine (*Pinus rigida*) and heaths such as American barberry (*Berberis canadensis*). Here and elsewhere, plants of the heath family (Ericaceae) are indicative of acidic soils. These sandstones are actually calcareous, but calcium weathers out quickly in the thin soils, producing strongly acidic (pH ca. 3.8) conditions. The calciphile plants here, such as ash and cedar, may get the calcium they need directly from the rock.

Among the most unique sandstone sites I visited are longleaf pine–wiregrass (*Pinus palustris–Aristida beyrichiana*) communities associated with the Altamaha Formation and Citronelle Formation in Georgia and Florida, respectively. The former, commonly known as Altamaha Grit, is of mid-Miocene age and occupies some 15,000 square miles in the Atlantic Coastal Plain of Georgia and a small part of Alabama. It is composed of fluvial and upper estuarine sediments, as opposed to marine sediments. The sandstone was probably not available to colonization by plants until the Early Pleistocene, after being exposed by erosion. The largest outcrop is Broxton Rocks, a 1,650-acre preserve owned by TNC and nestled within a 13,466-acre conservation area managed by multiple partners. Roland Harper published his dissertation, "A Phytogeographical Sketch of the Altamaha Grit Region of the Coastal Plain of Georgia," in 1906. In a follow-up paper that same year, he noted the unusual admixture of geology and vegetation at "The Rocks": "In fact the whole appearance of the place, barring its surroundings of open pine-barrens, is much like that of some places in the sandstone plateaus of Alabama with which I had recently become acquainted, and this similarity extends also to the flora."

I visited Broxton Rocks with Frankie Snow, a TNC land steward who teaches at South Georgia College in nearby Douglas. Frankie knows this place better than anyone and was the key person behind its protection. This is an amazing place: a rocky longleaf pine savanna. Of all the sandstone outcrops in the Coastal Plain, Broxton Rocks has the largest acreage and shows the most extensive weathering. Rocky Creek has cut through the sandstone, forming outcrops, cliffs, and a 10-foot waterfall. As Dana Griffin and Frankie Snow note in a 1998 paper, the result of this heterogeneity is "an increase in the number of microenvironments, which translates directly into increased biodiversity." As of 1998, seventy-five species of mosses and thirty-six species of liverworts had

been catalogued at Broxton Rocks. TNC is restoring longleaf pine to what was mostly loblolly pine (*Pinus taeda*) plantation with some slash pine (*P. elliottii*) at the time of acquisition. A few old longleafs remain, along with abundant tur‐ key oaks (*Quercus laevis*). The groundcover restoration is coming along nicely. Gallberry (*Ilex glabra*) is thick on this perched water table, but in better drained areas, wiregrass dominates.

Among the rare species we observed were dissected (grit) beardtongue (*Penstemon dissectus*), a Georgia endemic. We saw leaves of Menges' fameflower (*Phemeranthus mengesii*), which were much more robust on fire ant mounds, perhaps due to aeration of soil on the mounds. We also observed sporophytes ("adults") of the shoestring fern (*Vittaria lineata*), a neotropical fern that occurs as a sporophyte in the United States only in Florida and Georgia. In Florida it grows on the bark of cabbage palm (*Sabal palmetto*), but at Broxton Rocks it grows on mineral deposits from water dripping through mudstone beneath the sandstone. Also growing on rocks here is the green fly orchid (*Epiden‐ drum magnoliae*), which too is usually an epiphyte (on hardwoods). Southern Barbara's‐buttons (*Marshallia ramosa*), endemic to Georgia except two disjunct occurrences in the Florida Panhandle, is here, as is Georgia plume (*Elliottia racemosa*), in the Ericaceae. This species is extant only in Georgia; a disjunct population in South Carolina is now extinct. One of the more outlandish plant occurrences here is grit portulaca (*Portulaca biloba*), a species previously known only from Cuba, but recently discovered here and on a handful of other Alta‐ maha Formation outcrops in Georgia. How on earth did it get here?

Broxton Rocks is an important haven for imperiled animals as well, with apparently healthy populations of gopher tortoise and the federally threatened eastern indigo snake. The southeastern American kestrel (*Falco sparverius paulus*), which has declined sharply due to loss of its longleaf pine sandhills habitat, is nesting here and across much of southern Georgia in the hollow tube arms of powerline poles, demonstrating its adaptability. Still, they have disappeared from much of their former range, and I have not observed adaptation to poles as nesting sites in Florida.

The only sandstone outcrop in Florida is in the Panhandle, near Chipley, at TNC's Rock Hill Preserve (plate 19). Harper surmised that this outcrop is an extension of the Altamaha Grit, which is still common belief. However, it has been shown to represent the Citronelle Formation of Pliocene age, formed from sediments washed down from the southern Appalachians. I was guided at Rock Hill by preserve manager David Printiss. Rock Hill does not look like Florida. Everything seems normal as the eye takes in the longleaf pine savanna and the pitcherplants on seepage slopes, but then there are those big blocks of

sandstone and the bare gravelly patches, which just don't fit in. David explained that Rock Hill is something of a "red-headed stepchild"—it is isolated from other TNC preserves and a hassle to manage. It was supposed to be a state park, but the state backed out. Rare plants here include two that also occur at Broxton Rocks: southern Barbara's-buttons and Nuttall's rayless goldenrod (the latter I also saw in the Catahoula barrens of Texas). A third is southern milkweed (*Asclepias viridula*), endemic to two small, disjunct areas: the Florida Panhandle (i.e., Rock Hill and barely into adjacent Georgia and Alabama) and northeastern Florida. Dana Griffin and coauthors discovered that the bryophyte flora at Rock Hill overlaps strongly with that of the Altamaha Grit. Several lithophilous ("rock-loving") mosses and lichens have their only known Florida populations at Rock Hill.

Similar sandstone outcrops and glades in a longleaf pine setting occur within the Kisatchie National Forest of northwestern Louisiana. This site is on the northwestern range margin of longleaf pine and contains a substantial population of the endangered red-cockaded woodpecker. A female banded in the Ouachita National Forest, in a shortleaf pine–bluestem woodland, dispersed 210 miles to the Kisatchie; later, her great-granddaughter flew back to the Ouachita! Only two decades ago, no records of long-distance dispersal existed for this species. Especially in the Longleaf Vista area, the Kisatchie has considerable topographic relief, with large sandstone outcrops, cliffs, and panoramic views. The sandstone is of the Catahoula Formation, the same Oligocene/Miocene rock that I observed in the Catahoula barrens in Texas. The terms *mesa* and *butte* are used locally for these features, suggesting that, culturally, we are on the edge of the West. This site is reminiscent of the Altamaha Grit, but hillier, in this respect similar to the montane longleaf community of northeastern Alabama and northwestern Georgia.

Igneous and Metamorphic Glades and Outcrops

My first close encounter with igneous/metamorphic outcrop communities in the South was in mid-April 2008, near the beginning of my intensive field work for this book. I traveled to north-central Georgia, bypassing as much as possible the monstrosity of Atlanta, to the community of Lithonia, named after the Greek *lithos* for stone, as this is the heart of Georgia's granite-quarrying region. The next morning I met Jim Allison at Mt. Arabia, a preserve managed by DeKalb County Parks and Recreation, for which Jim works as a naturalist, after retiring from the Georgia Natural Heritage Program. The morning was cool and foggy, but the rain had stopped and it ended up with ideal conditions for glade plants and photography alike (plate 13). Mt. Arabia is one of the

highest quality granitic outcrops remaining. Better known is Stone Mountain to the north, which is overused and now totally enveloped in suburbs. From the top of Mt. Arabia, one can see only one ugly development in the distance.

Granitic outcrops (often called flatrocks) are scattered across the Piedmont Plateau for nearly 750 miles from eastern Alabama to Virginia, with the greatest concentration in Georgia, east of Atlanta. Flatrocks are made of several igneous and metamorphic rock types. Mt. Arabia is Precambrian metamorphic rock, specifically granitic schists and gneisses. Like other glades and outcrops, flatrocks are characterized by widely fluctuating and often extreme temperatures and high levels of solar radiation. They form incredibly beautiful rock gardens and vernal pools, the plants often arranged in roughly concentric circles from deeper soil (competitive) species in the centers of patches to species more tolerant of shallow soils and drier conditions on the margins. The predictable sequence of species appears planted by a gardener. Here, in a wet spring, near the peak of vernal blooming, the community is fresh and vibrant. Yet in the summer this will become a hot, dry, rock desert, the spring plants having died back.

Granitic flatrocks are rich in endemic species—at least twelve full species and several subspecies and varieties are strict endemics. They appear to be ancient taxa that evolved in isolation through adaptation to the extreme habitat, as opposed to remnant populations of species that were once more widespread. Several characteristic but nonendemic plants of granitic flatrocks also occur on sandstone glades. Jim Allison showed me two federally endangered endemic plants in the vernal pools on Mt. Arabia: blackspore quillwort (*Isoetes melanospora*, endemic to Georgia) and pool sprite (*Amphianthus pusillus*). The pool sprite, which also occurs in Alabama and South Carolina, has tiny floating leaves, like a miniature water lily. It produces exposed and submerged flowers, enabling both self- and cross-pollination; judging from its low genetic diversity, self-pollination is probably more common. Among the common and lovely plants blooming in the herbaceous patches were Canada toadflax (*Nuttallanthus canadensis*), oneflower stitchwort (*Minuartia uniflora*), elf orpine (*Diamorpha smallii*), wooly ragwort (*Packera tomentosa*), and yellow sunnybells (*Schoenolirion croceum*). The elf orpine, a stonecrop with bright red-pink succulent leaves, usually occupies the outer, most stressful zone of each patch. Common graminoids in these patches, sometimes forming pure stands, are broomsedge bluestem (not a weedy plant here), Elliott's bentgrass (*Agrostis elliottiana*), and Georgia rush (*Juncus georgianus*). Stunted individuals of crossvine (*Bignonia capreolata*) grow out of cracks in the gneiss. We also saw the regional endemic Georgia oak (*Quercus georgiana*). One of my favorite hardwoods, white fringetree (*Chionanthus virginicus*), was just coming into bloom in the adjacent woods.
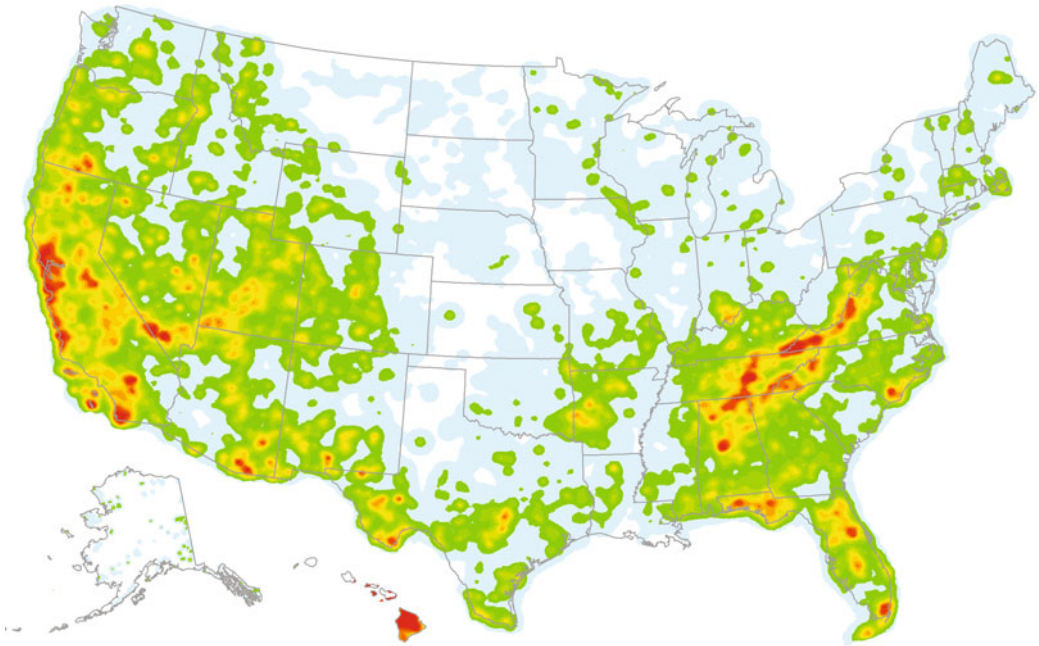
Plate 1. Hotspots of rarity-weighted richness for globally critically imperiled (G1) and imperiled (G2) species in the United States. The index weights species richness of imperiled taxa by the narrowness of their geographical distributions. The index is a measure of irreplaceability, with red spots most irreplaceable, followed by orange, yellow, green, and blue, respectively. Map courtesy of NatureServe.
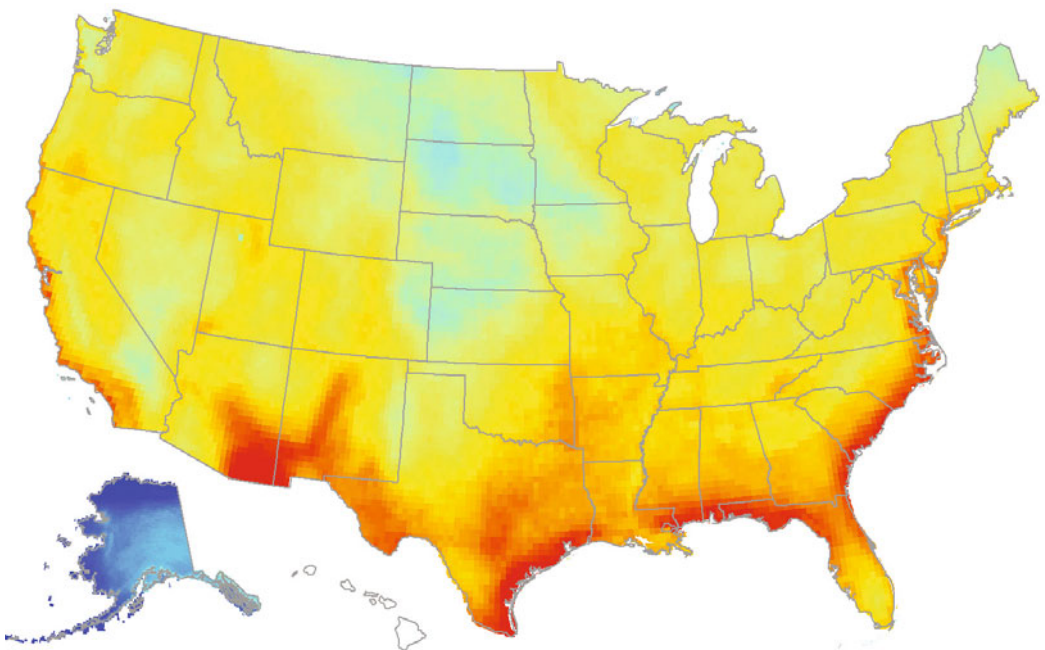
Plate 2. Species richness of vertebrates year-round in the United States. The latitudinal gradient in richness is apparent, as is a striking increase in richness near the coasts, except in the southern two-thirds of the Florida Peninsula. Map courtesy of NatureServe.
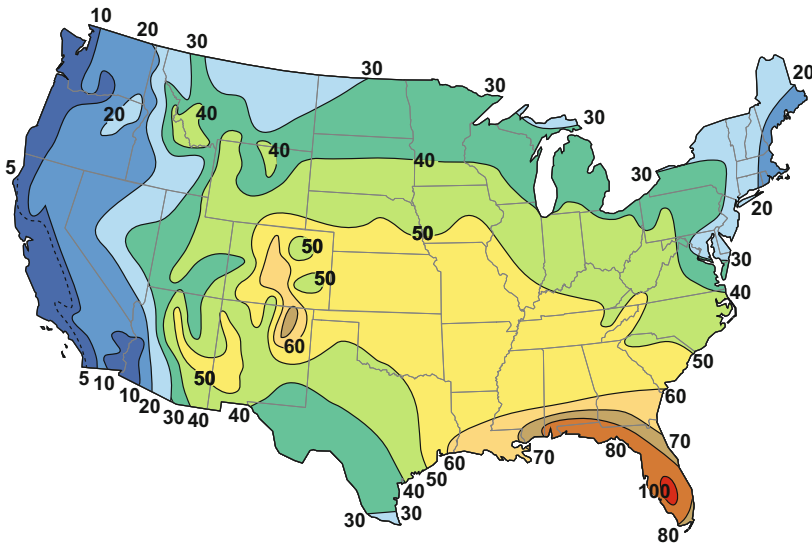
Plate 3. Average number of thunderstorm days per year in the 48 contiguous states. The highest frequency is in the southern Coastal Plain, especially Florida. In the Southeast, warm, moist air from the Gulf of Mexico and Atlantic Ocean fuels thunderstorm development. From NOAA/National Weather Service.
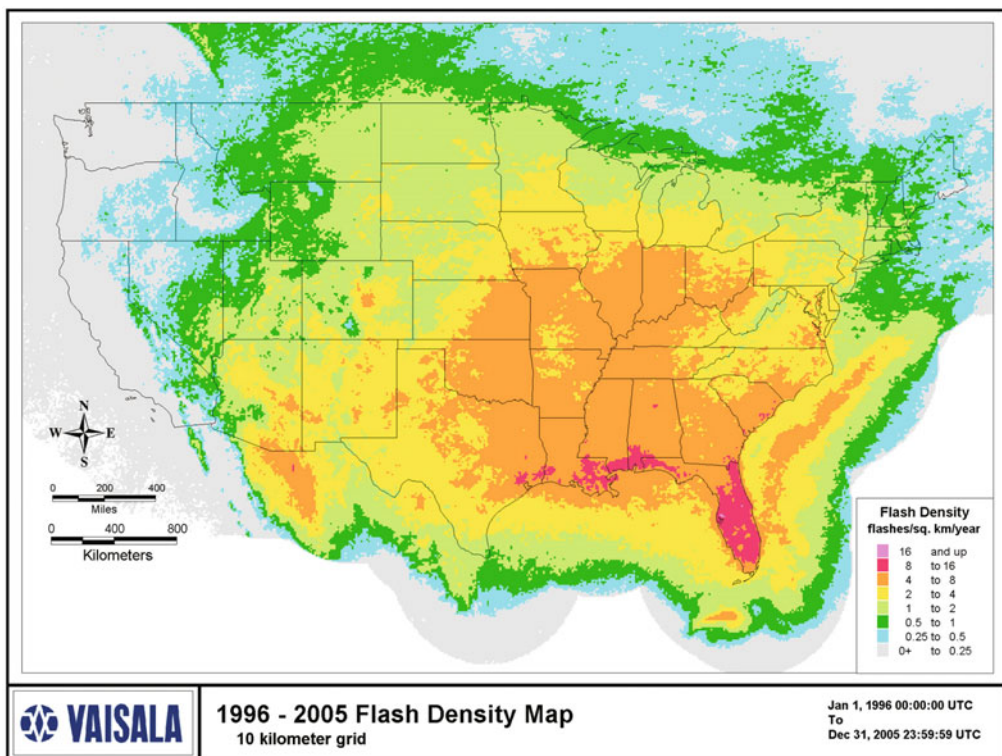
Plate 4. Lightning flash density in the 48 contiguous states, 1996–2005. The highest density (16 and more flashes per square kilometer per year, in violet), difficult to see at this scale, is just northeast of Tampa Bay and a smaller area in east-central Florida. From NOAA/National Weather Service.
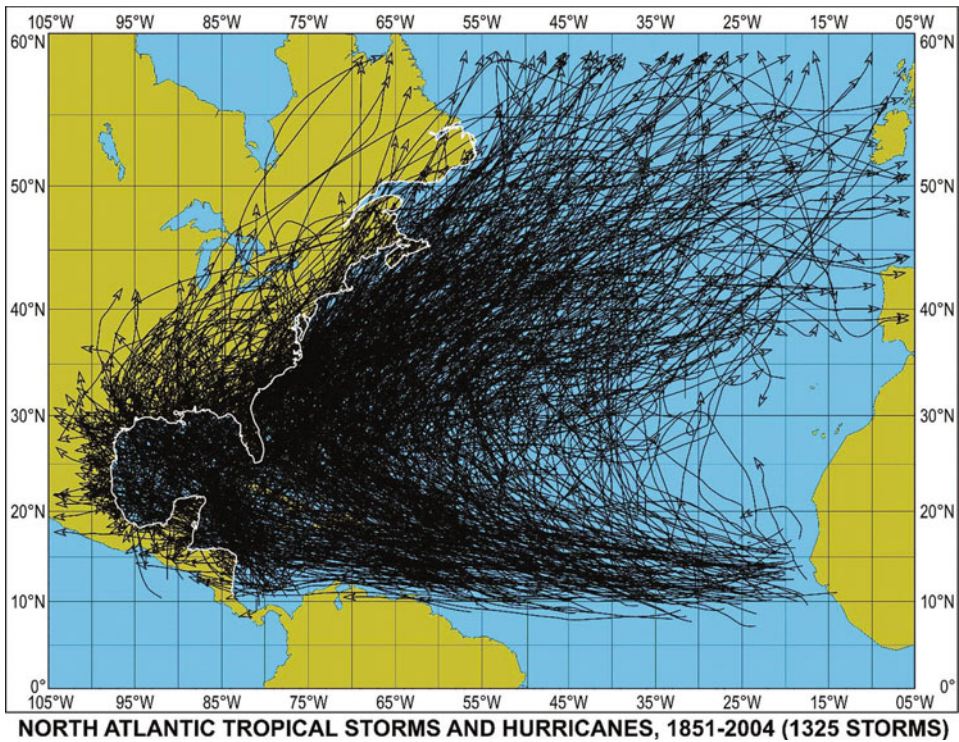
Plate 5. Tracks of tropical storms and hurricanes in the North Atlantic from 1851 through 2004. No wonder tree canopies are generally open in the Coastal Plain! Florida, which is entirely black in this figure, also has the highest frequency of tornados nationwide. From NOAA.

Plate 6. Celestial lily (*Nemastylis floridana*), a Florida endemic, Joshua Creek Tract, Charles H. Bronson State Forest, Florida. The flowers open during a brief period of the fall between ca. 4:00 p.m. and dusk.

Plate 7. Florida dry prairie at Kissimmee Prairie Preserve State Park. Once covering more than 1.2 million acres, the dry prairie has been reduced by around 90%, mostly due to conversion to "improved" pasture. Still, tens of thousands of acres remain in relatively large blocks, making this one of the most extensive grasslands in the South.

Plate 8. The Florida grasshopper sparrow (*Ammodramus savannarum floridanus*), endemic to the Florida dry prairie, federally listed as endangered, and declining rapidly for reasons that are not entirely under–stood. This is probably the most highly imperiled bird in the continental United States.

Plate 9. Old Cahaba Prairie, Dallas County, Alabama. This Black Belt Prairie might appear to be just an abandoned pasture being invaded by cedars, but a close look reveals dominance by several classic prairie grasses and associated forbs.

Plate 10. Old Cahaba rosinweed (*Silphium perplexum*), endemic to the Old Cahaba Prairie. Endemics provide evidence of antiquity.

Plate 11. The Ketona Glades of Bibb County, Alabama, where botanist Jim Allison discovered eight plant taxa new to science in the 1990s. The Ketona Dolomite here is extremely high in magnesium, which limits plant growth and helps maintain open conditions.

Plate 12. Alabama gentian–pinkroot (*Spigelia gentianoides* var. *alabamensis*), one of the plants endemic to the Ketona Glades. The endemics described so far include five full species and three varieties.

Plate 13. Mt. Arabia, Dekalb County, Georgia. This is a granitic flatrock community just east of Atlanta. At least twelve full species and several subspecies and varieties of plants are strict endemics on these igneous and metamorphic outcrops in the Piedmont.

Plate 14. A shale ridge bald in the Ridge and Valley Province, George Washington National Forest, Virginia. These barrens face ca. 200° southwest (range 160°–290°), placing them in direct sun around 2:00 p.m. The relatively hot and dry conditions and thin soils favor grassland over forest.

Plate 15. Woodland also develops on shale ridges of the Ridge and Valley Province of Virginia, yet the groundcover is grass dominated (George Washington National Forest).

Plate 16. Warren Prairie Natural Area, a saline barren in the Coastal Plain of Arkansas. The alkali or "natric" soils of saline barrens are so extreme that fire is not necessary to maintain open grassland.

Plate 17. Craft Prairie, Arkansas, in the Arkansas River Valley. This is on the northwestern edge of my study region, yet the prairies here have more southern affinities than those on the Ozark Plateau and other midwestern regions to the north.

Plate 18. A shortleaf pine–bluestem (*Pinus echinata–Andropogon gerardii–Schizachyrium scoparium*) woodland in the Ouachita National Forest of Arkansas. These woodlands are reminiscent of longleaf pine (*P. palustris*) savannas in the Coastal Plain and have many of the same characteristic bird species.

Plate 19. Rock Hill Preserve in the Florida Panhandle. This longleaf pine site requires fire, but the sparseness of the vegetation also reflects shallow soils over sandstone, which outcrops in Florida only at this site.

Plate 20. A marl prairie and dwarf cypress savanna in the Big Cypress National Preserve, Florida.

Plate 21. Big Pine partridge pea (*Chamaecrista lineata* var. *keyensis*) on Big Pine Key, Florida. This narrow endemic plant and many other species of pine rocklands and other communities in the Florida Keys are severely threatened by sea-level rise over the next century.

Plate 22. Coastal grassland on Cayo Costa, off the southwest coast of Florida. The dominant grass is hairy grama (*Bouteloua hirsuta*), disjunct here from Texas, the Great Plains, and semiarid grasslands of the southwestern United States and northern Mexico.

Plate 23. Topeka purple coneflower (*Echinacea atrorubens*) at Weyerhaeuser Fleming Prairies, a calcareous grassland in eastern Texas. This plant is endemic to Texas, Oklahoma, and Kansas.

Plate 24. A Barbara's-button new to science (*Marshallia* sp. *nova*) at Difficult Creek Natural Area Preserve, in the Piedmont of Virginia.

Plate 25. A limestone glade in Couchville Cedar Glade State Natural Area in the Central Basin of Tennessee. In bloom is bigfruit evening primrose (*Oenothera macrocarpa*), whose impressive yellow flowers are four inches wide. During full moon nights they are pollinated by sphinx moths.

Plate 26. Big Island Savanna, Green Swamp Preserve, North Carolina. This longleaf pine savanna has one of the highest measured levels of fine-scale plant species richness worldwide.

Plate 27. Eglin Air Force Base in the Florida Panhandle: the largest remaining tract of virgin longleaf pine savanna.

Plate 28. Bison (*Bison bison*), as well as elk (*Cervus canadensis*), have been reintroduced to a portion of Land Between the Lakes National Recreation Area in Kentucky and Tennessee. These are the most recent of a long chain of native megaherbivores that inhabited and influenced the dynamics of south-ern grasslands.

Plate 29. The trails of megaherbivores, which led among salt licks from Pleistocene to modern times, spread throughout much of the South and were most abundant in Kentucky. A brand of bourbon commemorates these trails, known as "buffalo traces."

Plate 30. One of the rarest plants in the world, Short's goldenrod *(Solidago shortii)* is closely associated with ancient megaherbivore trails (buffalo traces) at Blue Licks Battlefield State Park in Kentucky and a recently discovered site in Indiana.

Plate 31. A grassy bald on Roan Mountain, on the Tennessee–North Carolina border.

Plate 32. Northern copperhead (*Agkistrodon contortrix mokasen*) seeking refuge with a family of timber rattlesnakes (*Crotalus horridus*, not shown) in a mafic amphibolite barren on Buffalo Mountain State Natural Area Preserve, Virginia.

I visited a few other granitic flatrocks, the most memorable being Heggie's Rock, in Columbia County, Georgia, which I toured in mid-April 2009 with Malcolm Hodges (TNC) and Philip Juras. This site is a TNC preserve and may be the most pristine large granitic flatrock remaining. The outcrop here is of Appling granite, at 294 million years old (Late Carboniferous Period) much younger than Mt. Arabia. It is an attractive rock with abundant xenoliths (chunks of older rock that floated to the top in an igneous flow and didn't melt) and dikes (stripes formed when cracks in the granite filled with molten minerals). You can lift up the mats of moss and spikemoss (*Selaginella*—three species here) from the granite like a rug, exposing the brilliant pink, wet granite underneath. Twelve plant taxa endemic to granitic flatrocks occur on Heggie's Rock. Unfortunately, one fascinating little plant, dwarf hatpins (*Eriocaulon koernickianum*), is not found here. Of perhaps eighteen populations of this species in Georgia, only one occurs within a protected area. The Georgia populations are separated by more than six hundred miles from the nearest population in Arkansas. I was able to see this plant in Arkansas with Theo Witsell, in an infertile Coastal Plain wet prairie. A less distant disjunct on Heggie's Rock is cockspur pricklypear cactus (*Opuntia pusilla*), a coastal species normally found on sand dunes.

Many of the same plants that I observed on Mt. Arabia a year earlier are on Heggie's Rock, but with some differences. The pool sprite is here, along with elf orpine in bloom. Instead of the blackspot quillwort, Heggie's Rock has Piedmont quillwort (*Isoetes piedmontanum*), which is not a narrow endemic, but has the very narrow endemic Merlin's grass or mat-forming quillwort (*I. tegetiformans*); this is the type locality, and only a handful of populations survive. Heggie's Rock is also the type locality for a microscopic crustacean— the free-living copepod, *Stolonicyclops heggiensis*, a new species and new genus described from here in 1998. This copepod is now known from several other sites, including within Great Smoky Mountains National Park, where it was discovered during the All Taxa Biodiversity Inventory that Ed Wilson refers to in the foreword to this book. An undescribed midge (in the fly order, Diptera), which emerges in November and disappears by January, has been found only at Heggie's Rock and a few nearby outcrops of Appling granite. One year, I am going to make a special trip up here just to see this little midge, and my family will be all the more certain that I am insane.

Biologically significant igneous and metamorphic glades occur in other parts of the South, but I cannot do them justice here. I must mention, however, an unusual igneous glade of Cretaceous age just south of Little Rock, Arkansas. This intrusion of nepheline syenite is within the Coastal Plain, just

off the fall line of the Ouachitas. TNC has a preserve on these glades, Dry Lost Creek, where Tom Foti and Theo Whitsell led me around. This is a species-rich site consisting of seeps around a dry glade, with much exposed rock and grass-dominated patches and a flora similar to Arkansas shale barrens. Grasses and sedges are especially diverse, with hairyawn muhly (*Muhlenbergia capillaris*) most common. Among the imperiled plants is Nuttall's cornsalad (*Valerianella nuttallii*), endemic to Arkansas and Oklahoma. Also here is Pelton's rose-gentian (*Sabatia arkansana*), endemic to Saline County and found on just two sites: a shale glade and these nepheline syenite glades. The species was discovered in 2001 by John Pelton, a retired mechanic turned amateur photographer and naturalist, recognized as distinct by Theo, and formally described in 2005. Another local endemic is an undescribed species of fameflower (*Phemeranthus* sp. nova). Largeflower fameflower (*Phemeranthus calycinus*) is also here; both fameflowers grow out of cracks in the syenite.

Shale Barrens and Glades

Shale is a fine-grained, clastic (fragmenting) sedimentary rock composed of mud that is a mix of clay minerals and silt-sized particles of other minerals, especially quartz and calcite. Shale typically shows parallel bedding less than one centimeter thick, which breaks into thin fragments and weathers to a droughty clay soil. This soil usually lacks an organic (O) horizon and has little available nitrogen, which restricts the range of plants that can grow on shale barrens. In the South layers of shale are interbedded with other sedimentary rocks, including limestones, dolomites, and sandstones, of Paleozoic age (usually Ordovician, Silurian, or Devonian). Shale barrens occur as isolated patches in a belt running from south-central Pennsylvania to southern West Virginia and south-central Virginia, with another concentration in the Ouachita Mountains of central and western Arkansas and adjacent Oklahoma. I focus here on shale barrens and glades in Virginia and Arkansas, which are exceptionally rich in rare plants.

I visited two adjacent shale barrens/glades in Arkansas with Theo Witsell and Tom Foti. These sites are owned by the Ross Foundation, formerly the Ross Timber Company, which seems to be managing them well. Although occupying only around 1,000 to 1,500 acres, shale barrens and glades in the Ouachitas are the most significant natural communities in Arkansas in terms of narrow endemic plants and other imperiled species. At last count, these communities support 630 vascular plants, including 35 taxa of state conservation concern, 19 of which are of global concern (G1–G3). The communities include open and semi-open habitats with shale on or very close to the surface. Besides conspicuous areas of exposed shale with little plant cover, the glade

mosaic includes seepage meadows, prairie-like grasslands, shrub thickets, and, on deeper soils, open woodlands. The xeric-adapted flora is considered relict from the Hypsithermal or other warm, dry climatic periods, and is maintained by edaphic factors, supplemented by fire. Several of the shale formations that form barrens also contain thin interbedded limestones and support calciphile species, which are uncommon or rare in the Ouachitas, including limestone adderstongue, purple cliffbrake (*Pellaea atropurpurea*), pinnate prairie coneflower (*Ratibida pinnata*), composite dropseed (*Sporobolus compositus* var. *compositus*), and Nuttall's pleatleaf (*Nemastylis nuttallii*, in the same genus as the celestial lily I found near my home in Florida).

Among the shale-associated plants of greatest conservation concern are Pelton's rose-gentian and Nuttall's cornsalad (both mentioned earlier in connection with syenite glades), Ouachita false indigo (*Amorpha ouachitensis*), Hubricht's bluestar (*Amsonia hubrichtii*), Waterfall's sedge (*Carex latebracteata*), threeflower hawthorn (*Crataegus triflora*—a large-leaved little tree), openground draba (*Draba aprica*), Shinner's sunflower (*Helianthus occidentalis* ssp. *plantagineus*), royal catchfly (*Silene regia*, a wonderful plant I know from central Ohio prairies, which has a large range, but small and scattered populations), clasping jewelflower (*Streptanthus maculatus* ssp. *obtusifolius*, with incredible purple flowers), pine-oak jewelflower (*Streptanthus squamiformis*), and Palmer's cornsalad (*Valerianella palmeri*). A peculiar aspect of the woodland portion of the glades is abundant *Usnea* lichens festooning the tree branches and strongly reminiscent of Spanish moss (*Tillandsia usneoides*). Without periodic fire, extreme drought, erosion, or management treatments such as cutting and herbicides, most shale barrens and glades are invaded by woody plants, especially redcedar, though this occurs slowly on the most open, xeric patches. Sadly, most of the shale barrens in Arkansas have been destroyed or compromised by mining for fill.

The shale barrens of Virginia have been studied for a longer time than those in Arkansas. They occur primarily in the Ridge and Valley Province, between the Blue Ridge on the southeast and the Allegheny Plateau to the northwest. As noted by Suzanne Braunschweig and coauthors, these communities were brought to the attention of botanists by E. S. Steele in 1911, who observed that "the variety of plant life is very considerable and together with many plants well known on other substrata, these barrens possess a number peculiar unto themselves." Braunschweig and colleagues list eight species of plants that are endemic to mid-Appalachian shale barrens, plus another ten that are near-endemic, and one, swordleaf phlox (*Phlox buckleyi*), that is "transitional" because it occurs in shaly woods and roadbanks rather than on open barrens. They also note the presence of many disjunct populations, especially of taxa

with western affinities. Examples of disjuncts are chestnut lipfern (*Cheilanthes castanea*), whose primary range is from southwest Texas to southern Arizona, with scattered populations in Oklahoma, Arkansas, eastern West Virginia, and central and western Virginia. Another fern, forked spleenwort (*Asplenium septentrionale*), is disjunct on a shale barren in West Virginia, nearly 1,250 miles from the closest population in western Oklahoma. There are several other disjuncts, most with scattered intervening populations between the West and the mid–Appalachians.

I visited shale barrens in Virginia with Chris Ludwig. The prototypic shale barren occurs in the landscape as portrayed in figure 4.5, on steep, dry slopes, often undercut by streams, where erosion creates an unstable substrate unsuitable for woody plant colonization—except hard-cores like redcedar, plus a few rock chestnut oak (*Quercus montana*), scarlet oak (*Quercus coccinea*), and Virginia pine. Chris and I encountered this situation at Douchat State Park. Walking transversely across the steep, slippery slope on loose shale slivers, lurching from one scattered redcedar to another for handholds, was close to suicidal. Herbaceous plants surviving on this extreme site include whorled milkweed (*Asclepias verticillata*), shale barren pussytoes (*Antennaria virginica*, a regional endemic), prairie violet (*Viola pedatifida*, which according to the usually reliable USDA plants website, is not supposed to occur anywhere in the Southeast except Arkansas), wavy hairgrass (*Deschampsia flexuosa* var. *flexuosa*), flattened oatgrass (*Danthonia compressa*), and slimleaf panicgrass (*Dichanthelium linearifolium*). I admired their fortitude.

The other shale site we visited in Virginia is one of the most sublime
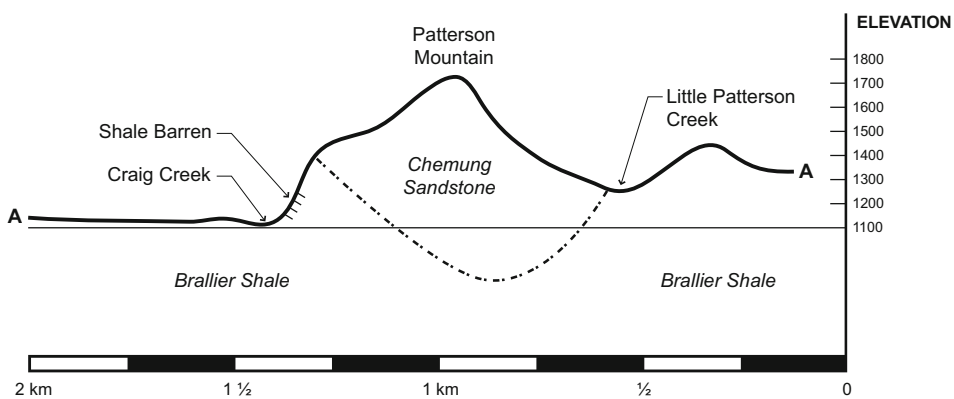
Figure 4.5. Position of a shale barren relative to landform and substrate in Craig Creek Valley, Botetourt Co., Virginia. The shale barrens occur on steep, eroded slopes undercut by the stream. Adapted from Braunschweig et al. (1999).

places I encountered in all my travels for this project: a shale ridge bald in the George Washington National Forest (plates 14 and 15). The geology in this area features limestone in the valleys, overlain by a shale layer, and then topped with sandstone. Hiking up the mountain, Chris and I found abundant mountain laurel (*Kalmia latifolia*) in bloom, which is always worth savoring, as well as eastern turkeybeard (*Xerophyllum asphodeloides*). Turkeybeard is a generic-level western disjunct; its closest relative, common beargrass (*Xerophyllum tenax*), is familiar from my old haunts in the Cascade and Rocky Mountains. Close to the top of the ridge, we entered the shale woodland and bald. What a place. There was no sign that anyone hiked up to this ridge on a regular basis—it is wild and pristine.

Shale ridge balds are oriented south-southwest, averaging around 200°, placing them in direct sunlight about two o'clock in the afternoon. This xeric aspect, combined with the thin, droughty soils, produces a grassland that needs little, if any, fire to maintain itself. The scattered woodland trees are rock chestnut oak, Virginia pine, and black locust (*Robinia pseudoacacia*). Dominant grasses are little bluestem and Indiangrass, accompanied by flattened oatgrass, hairyawn muhly, and arrowfeather threeawn (*Aristida purpurascens*). We found a number of the shale barren endemics and near-endemics, including shale barren pussytoes, shale barren hawkweed (*Hieracium traillii*), Kate's mountain clover (*Trifolium virginicum*), shale barren ragwort (*Packera antennariifolia*), shale barren wild-buckwheat (*Eriogonum allenii*, the only eastern buckwheat outside the Coastal Plain, except Harper's wild-buckwheat [*E. harperi*], a rare plant of limestone glades in Kentucky, Tennessee, and northern Alabama), shale barren goldenrod (*Solidago harrisii*), shale barren pimpernel (*Pseudotaenidia montana*), and white-hair leatherflower (*Clematis albicoma*). Nearby, along a shaly roadside, we saw another of the endemic *Clematis*, Millboro leather flower (*Clematis viticaulis*), as well as swordleaf phlox. That's quite a list of endemics for a small area, which suggests that these shale sites persisted relatively unchanged through glacial cycles, even when higher elevations of the Appalachians were alpine tundra.

The ability to tolerate temperature extremes may be the primary factor that shale barren endemics and near-endemics have in common. One interesting phenomenon that Chris pointed out is the prominence of certain annual "weedy" plants on shale barrens, species that are usually associated with human-disturbed habitats. For example, we found abundant annual ragweed (*Ambrosia artemisiifollia*) and clasping Venus' looking-glass (*Triodanus perfoliata*) on the shale ridge bald. Edaphic grasslands were probably the original habitats of these so-called weeds before humans disturbed the soil over large areas and allowed them to proliferate.

Serpentine Barrens

Serpentine (ultramafic) barrens are a textbook example of an edaphic plant community. They often contain clusters of endemic species and, in regions such as California, serve as a haven for native perennial grasses and other plants in landscapes dominated by exotic annual grasses. A 2011 paper by Christy Briles and coauthors looked at a 15,000-year record of pollen and charcoal in the Klamath Mountains of northern California (another hotspot of endemism). They confirmed that communities remained essentially the same over periods of major climate change on serpentine (ultramafic) substrates, in contrast to substantial change in distributions on nonultramafic substrates. This study provides yet another example of edaphic communities showing long-term stability and serving as climatic refugia.

The term *serpentine* refers to the mottled appearance of exposed ultramafic rock, which somebody apparently thought was similar to the skin of a serpent (I really don't see the resemblance). The term is used by ecologists to refer to a variety of ultramafic rocks and the soils derived from them. Ultramafic rocks include several igneous and metamorphic types with extreme (usually greater than 90 percent) concentrations of mafic minerals, which are characterized by high levels of magnesium and iron. The high magnesium and iron content of ultramafic rock reflects its origin in the earth's mantle, where these minerals are more abundant than in the crust. Tectonic activity leads to the upward movement and exposure of ultramafic rocks. Serpentine soil is also typically high in chromium and nickel, which can be toxic to plants, and low in minerals and nutrients required by plants, such as calcium, potassium, nitrogen, phosphorus, and silica. High magnesium levels also reduce the availability of calcium.

The mineral composition and weathering characteristic of serpentine soils create physiological drought for plants, producing conditions favorable for grassland development. Nevertheless, fire is usually necessary to sustain open prairie or woodland on serpentine sites; as for several other edaphic grasslands, tree invasion just occurs more slowly on serpentine than on other soils. Serpentine occurs over much of the world, in North America most abundantly in California, as described in Arthur Kruckeberg's classic book, *California Serpentines*. Within the study area of this book, serpentine barrens are (or were) distributed in eastern Maryland and adjacent Pennsylvania, and at scattered sites in the Appalachians, with outliers in the Piedmont of Georgia and Alabama and the Ouachitas of Arkansas.

My first visit to a southern serpentine site was at Buck Creek Serpentine Barrens on the Nantahala National Forest in North Carolina, a trip led by

US Forest Service botanist Gary Kauffman, accompanied by Ed Schwartz-man of the North Carolina Natural Heritage Program and Andy Walker of the North Carolina Botanical Garden. The site was discovered by botanist Robert K. Godfrey, who taught at North Carolina State University before moving to Florida State University, where he became curator of the herbarium. God-frey humorously described the location of Buck Creek as "on the backside of Chunky Gal," the latter being the mountain here, which peaks at 4,770 feet. The barrens (actually an open woodland) is higher than I had expected, around 3,600 feet, and it was chilly here in April 2008. It had been a cool spring, and blooming was about two weeks delayed. Still, we found scarlet Indian paint-brush (*Castilleja coccinea*) in flower, plus Appalachian violet (*Viola appalachiensis*), gaywings (*Polygala paucifolia*), dwarf ginseng (*Panax trifolius*), Ruth's littlebrown-jug (*Hexastylis arifolia* var. *ruthii*), and a few others. More than two dozen species of grasses occur in this serpentine woodland, with big bluestem, little bluestem, and prairie dropseed the dominants. The tall culms of big bluestem (last year's growth) were matted down from the winter snows, and new green leaves were just emerging from bunches on the ground. The trees are stunted white oak, patches of Virginia pine (*Pinus virginiana*), and a few other species. Thanks to restoration burning by the Forest Service, the open woodland character of the site is recovering. We observed a vigorous response to a recent fire by buffalo nut (*Pyrularia pubera*).

A species endemic to Buck Creek, Rhiannon's aster (*Symphyotrichum rhian-non*), was described in 2004, and Alan Weakley suggests that at least a couple of other plants here are probably distinct enough to warrant description as new species; this taxonomic work is ongoing. Other rare taxa at Buck Creek include a liverwort, Appalachian threadwort (*Drepanolejeunea appalachiana*), endemic to the southern Appalachians with one disjunct occurrence in the West Indies and typically found in mesic hardwood forest; highlands moss (*Schlotheimia lancifolia*), also endemic to the southern Appalachians and found here on rock rather than on its usual bark substrate; two butterflies endemic to the southern Appalachians, the cullasaja aphrodite fritillary (*Speyeria aphrodite cullasaja*) and the Appalachian crescent (*Phyciodes batesii maconensis*); and two western butter-flies near their eastern range limit here, the dusky azure (*Celastrina nigra*) and the gorgone checkerspot (*Chlosyne gorgone*). Like most rarities, these creatures provide no known ecosystem services and have no economic value—but I am grateful they are here.

The southernmost serpentine site in eastern North America, except per-haps some poorly known areas in Alabama, is Burks Mountain (also known as Burke's Mountain, Burte Mountain, and Burke/Dixie Barrens) on private

land in the Piedmont of Georgia. William Bartram passed through this region in the 1770s. Although he doesn't mention the barrens in this specific area, he may have included them in his description of the hills north of here as "gravelly, dry, barren summits." Bartram also documented elk and bison in this area. Burks Mountain is unusual in several respects. It hosts a mix of longleaf pine (very rare in the eastern Piedmont of Georgia), shortleaf pine, and loblolly pine. Also present are several oaks: the dominant blackjack oak accompanied by post oak, Georgia oak, sand post oak (*Q. margarettae*), and sand laurel oak (*Q. hemisphaerica*). The rarest plant here is Dixie Mountain breadroot (*Pediomelum piedmontanum*), known from here and two counties in South Carolina. The breadroot was not in bloom when I visited Burks Mountain with Malcolm Hodges and Philip Juras in April 2009, nor was another rare plant I'd seen at Broxton Rocks, southern Barbara's-buttons, disjunct here from the Coastal Plain. I was impressed that the barrens are still quite open and grassy, despite no sign of recent fire. The rock (serpentinite) is called soapstone because it has a slippery feel to it. The most exciting find for me that day was a yucca giant-skipper (*Megathymus yuccae*), a widespread but rare skipper whose larvae feed exclusively on yucca (one of those arid-adapted taxa with western affinities).

My final visit to serpentine barrens was to the largest in the East: Soldiers Delight in Maryland. This site, along with other nearby barrens, has been extensively studied in recent years by R. Wayne Tyndall of the Maryland Wildlife and Heritage Service. Little bluestem is the dominant grass on all sites, except one (Pilot) where prairie dropseed is codominant. Soldiers Delight is a famous spot among eastern grassland aficionados. I ran into trouble, however, on two attempts to meet Wayne Tyndall here. I had to cancel a trip in fall 2010 at the last minute due to a tropical storm. I rescheduled for May 2011. After visiting some riverscour prairies on the Potomac River the first day of that trip, I decided to see what I could of Soldiers Delight that afternoon, as the chance of rain for the following day was 90 percent. I lucked out, as the rain started right as I was finishing my walk. I was able to see restoration work in progress and enjoy the abundant flowering of field chickweed (*Cerastium velutinum* var. *villosissimum*), an endemic restricted to a few serpentine sites in Maryland and Pennsylvania. It rained furiously the next day, precluding field work. I have yet to meet Wayne, but he provided me with much valuable information.

Observing the relatively rapid spread of redcedar and Virginia pine on serpentine barrens over recent decades, Tyndall concludes that fire is necessary to maintain open barren and woodland here. The edaphic qualities of the barrens probably permitted grassland vegetation to develop during the Hypsithermal or other past dry periods. Large herbivores may have played a role in maintain-

ing the barrens, as they did in other regions not far to the West, but this has not been documented here. Lightning frequency is relatively low this far north (see chap. 5), so natural ignitions may not be frequent enough to maintain grassland on these isolated sites under the current climate. After the Hypsithermal tapered off around five thousand years ago, Indians maintained the grasslands by deliberate burning. W. B. Marye studied the history of the Maryland and Pennsylvania barrens and concluded that "it was the custom of the Indians in the autumn to set fire to and burn the barrens of York [Pennsylvania] and Baltimore [Maryland] Counties."

Europeans settled the barrens region by 1750. After the Indian population crashed, white settlers grazed livestock on the barrens, which seems to have slowed tree encroachment. Perhaps in emulation of the Indians, the settlers also burned the barrens initially, but Mayre states that this practice was largely abandoned by 1780. Grazing and logging (i.e., cutting of cedars) then became the only processes keeping the barrens open. Edaphic factors slowed but ultimately proved insufficient to prevent tree invasion after grazing and logging tapered off. Today, prescribed burning is necessary for maintenance of these barrens, which would slowly but inexorably disappear under the current climate. Such is the irony of restoring and conserving climatic relicts—it is a bit "unnatural." More ironic, a human-caused shift to a warmer and probably drier climate in this region may ultimately favor, once again, the expansion of serpentine barrens and other grasslands.

Saline Prairies (Barrens)

Saline prairies, more accurately called saline barrens, are critically imperiled globally (G1). These communities are typically a mosaic of short, pasture-like grassland with interspersed bare soil areas known as "slicks." Shrubs and stunted trees occur along the edges or are intermixed to varying degrees. Saline barrens occur in the West Gulf Coastal Plain of central and northwestern Louisiana, eastern Texas, and southern Arkansas; in the Mississippi River Alluvial Plain of eastern Arkansas; and in the Arkansas River Valley in western Arkansas. In Louisiana, where saline prairies have been most intensively studied, saline barrens occur on the Prairie Terrace, the youngest and lowest of the Pleistocene terraces, which may have formed during interglacial periods when high sea level reduced stream gradients, allowing deposition of fine sediments. Saline barrens are among the most rigorous edaphic grasslands in the South, perfectly capable of maintaining themselves in the absence of fire. As stated by Chris Reid and coauthors in a 2010 paper, "Extreme soil properties and droughty conditions are apparently sufficient to maintain prairies in our study sites, which have no

threat of woody encroachment." They speculate, however, that "fire may have been very important in adjacent communities and thus important in a broader landscape context."

The qualities of saline barrens that keep them open and grassy are the "natric" soils, also known as alkali soils. These soils often occur in arid regions, for example in evaporation basins (playas). In the humid South the accumulation of sodium in the soil can be explained by the presence of a dense, impermeable natric horizon not far below the surface of the ground, which prevents downward leaching of salts and other minerals. The natric horizon acts like a clay hardpan by perching water on the surface during wet periods and preventing upward movement of water or exploitation of deeper water by plant roots during dry periods. Thus, like many southern grasslands, these barrens are hydroxeric (or xerohydric) and are alternately hard and powdery dry or waterlogged and sticky. Evaporation during dry periods concentrates salts; unlike saline soils, however, natric soils do not have high concentrations of dissolved salts, but rather high levels of exchangeable sodium and high alkalinity. The source of sodium in some saline barrens appears to be from weathering of sodium-rich feldspars in the loess parent material. Saline barrens share many plant species with sandstone glades and, unsurprisingly, also contain salt-tolerant species from coastal grasslands. An example is the seaside goldenrod (*Solidago sempervirens*), which also shows up on roadsides in northern states that apply salt to deice highways. Many saline barrens are pocked with enigmatic "pimple mounds," which are likely aeolian dunes shaped by winds during Holocene periods of extreme drought. Pimple mounds, having sandier, drier, and less extreme soils, often host trees such as shortleaf or loblolly pine, although some are grassy.

I visited the Winn Weyerhaeuser Saline Natural Area in Louisiana in May 2008 with Chris Reid and Patty Faulkner. The rarest species associated with saline barrens is the federally threatened *Geocarpon minimum*, known as "Tiny Tim." This diminutive plant, not much bigger than the "lead" at the tip of a pencil, had already gone through its life cycle for the year and dried up by the time of our visit. Also here is Nuttall's rayless goldenrod, which I observed in Catahoula sandstone barrens in Texas and on outcrops of the Altamaha Formation in Georgia and Citronelle Formation in Florida. The grasses of saline barrens include the ubiquitous little bluestem, but more prominently, several short, fall-flowering annual grasses: slimspike threeawn, prairie threeawn (*Aristida oligantha*), and poverty dropseed (*Sporobolus vaginiflorus* var. *vaginiflorus*). These are all weedy plants commonly associated with human-disturbed areas such as roadsides, yet they are characteristic of undisturbed saline barrens, where

they thrive under noncompetitive conditions of sparse vegetation and exposed soil. Like other edaphic grasslands, for example shale barrens in Virginia with their annual ragweed and Venus' looking-glass, saline barrens may be among the original habitats for weedy annual plants that later took advantage of soil disturbance by humans. Trampling and rooting by large herbivores also probably provided suitable conditions for establishment.

Among the best saline barrens in Texas are those on sites managed by the Katy Prairie Conservancy. Eight plants endemic to Texas can be found here, which suggests these barrens have been around for a long time. Led by Jason Singhurst, I observed the federally listed Texas prairie-dawn (*Hymenoxys texana*), endemic to three counties in Texas and doing well here despite intensive grazing. This species is usually found near the base of pimple mounds in association with harvester ants (*Pogonomyrmex* spp.). Other endemics I observed include threeflower snakeweed (*Thurovia triflora*, the only species in its genus), Texas saltbush (*Atriplex texana*), Texas willkommia (*Willkommia texana* var. *texana*, whose closest relative is in coastal grasslands in Argentina), and Texas windmillgrass (*Chloris texensis*), which has impressively long spikelets.

In Arkansas, Tom Foti and Theo Whitsell introduced me to the Warren Prairie Natural Area, a three-thousand-acre state-owned site, which contains twenty to thirty saline barren openings (plate 16). This area has abundant pimple mounds, the oldest dated to around six thousand years ago, hence formed within the droughty Hypsithermal Interval. Saline woodlands flank the barrens and grade into typical Arkansas flatwoods. I was amazed to learn that sixty to eighty Henslow's sparrows (*Ammodramus henslowii*) winter here, the northern extreme of their wintering range. My students, colleagues, and I have banded this bird at the southern end of its winter range, in the dry prairies of south-central Florida. It would be interesting to compare habitat use, diet, and survivorship at these two disparate wintering sites.

Piedmont Prairies

Piedmont prairies were little known until recently and were not discussed in the 1993 book chapter on southeastern grasslands by DeSelm and Murdock. Yet grasslands were apparently numerous on the Piedmont, occurring as patches up to twenty-five miles across. In 1997 Larry Barden published the first relatively comprehensive (albeit short) summary of historical observations of prairies and savannas on the Piedmont of North and South Carolina. The evidence for historic grassland on the Piedmont is overwhelming. Grassland animals, particularly bison, were reported regularly. Bison had apparently been extirpated by overhunting, or were very rare, when the de Soto expedition crossed the

Piedmont around 1540, but the Spaniards reported shields of "cow" hide and "horns of cattle" at Indian towns. Since no domestic cattle had been introduced at this time, these body parts must have been from bison. By the 1720s, after Indian populations had declined and bison populations had recovered, pioneer naturalist Mark Catesby reported that "buffaloes ranged in droves," on the Carolina Piedmont, "feeding upon the open savannas morning and night, and in the sultry time of day retiring to the thickets of tall cane along the rivers."

Barden is undoubtedly correct in attributing the large expanses of grassland in the Piedmont at the time of European exploration and settlement to the widespread use of fire by Indians (Larry told me that he thinks prairies on upland sites in the Piedmont have both a nonanthropogenic and anthropogenic origin, whereas prairies on lowland sites would have been forest without Indian burning followed by white haying). During the Revolutionary War, British soldiers would not march through the Blackjacks area (near present-day Rock Hill, South Carolina) because it was so open and exposed. As elsewhere, the Piedmont must have had grassland, at least in the form of open woodlands, before expansion by Indians. For instance, there are grassland-associated endemic plants in the Piedmont. In addition, there is an edaphic explanation; that is, common bedrock types in the Piedmont are mafic. Recall that serpentine barrens occur on ultramafic rock high in iron and magnesium, among other minerals. Mafic rocks are so named because they are also high (but not quite as high as ultramafic) in these minerals. These rocks weather to produce a dense clay soil that favors grassland. As Bob Peet explains, weathering of mafic rocks produces relatively large and flat hills, which provide larger "fire compartments" (patches across which fire spreads) than more highly dissected terrain—albeit considerably smaller compartments than in the Coastal Plain.

If much of the Piedmont was flammable due to a grassy groundcover, and barriers to the spread of fire were relatively few, it would not take many lightning ignitions to maintain grassland vegetation, because fires would spread from points of ignition for many miles. Given a more reliable and frequent source of fire—Indians—grassland became abundant as variably sized patches in a matrix of forest across the Piedmont. By the nineteenth century, however, the extensive Piedmont grasslands had disappeared. Only small remnants persist today, usually in man-made refugia such as powerline rights-of-way, grassy roadsides, and field margins. Xeric hardpan forests (which were probably woodlands before fire exclusion), and glades and barrens on mafic rocks such as amphibolite, hornblende, diabase, and gabbro, also provide refugia for grassland plants in the Piedmont.

My first visit to relict Piedmont prairies was in April 2008, with Laura

Fogo, a biologist with the US Fish and Wildlife Service. Laura loves the prairies and longleaf pine communities of the Piedmont, especially the Uwharrie Mountains. After Laura picked me up at the quaint Carolina Country Inn on the edge of Mt. Pleasant, North Carolina, we drove to the private farm of the Suther family, home to Suther Prairie. There we met John and Louis Suther, who manage the farm that has been in their family since the 1700s, and Larry Barden and Jim Matthews, authorities on Piedmont grasslands. Suther prairie is distinct in several ways—indeed, Bob Peet and Mike Schafale independently told me that they've never seen anything else like it. For one, the five-acre prairie (not including another two acres being restored from fescue pasture) has never been plowed, but rather has been maintained by annual mowing/ haying for two hundred years; recently it has also been prescribed burned. Unlike other remnants, which are mostly on marginal sites, Suther prairie lies in the interior of a large farm. Another unusual aspect of Suther Prairie is that it occupies an alluvial area where the mafic soils remain wet throughout the year. Hence, the flora differs from other remnant Piedmont prairies. The dominant grass is big bluestem, with a larger population here than anywhere in the Piedmont. The next most common species is eastern gamagrass (*Tripsacum dactyloides*). Unusual plants include red Canada lily (*Lilium canadense* var. *editorum*), disjunct here from the Appalachians, and scarlet Indian paintbrush, which is uncommon in the Piedmont. Conversely, many grassland plants associated with drier summer soil conditions and found on other remnants, such as prairie dock, blazing-stars, smooth purple coneflower, wild quinine (*Parthenium integrifolium*), and rattlesnake-master, are absent from Suther Prairie. At the time of my visit Indian paintbrush was in full bloom, accompanied by a profusion of Atamasco lily (*Zephyranthes atamasco*). We are fortunate that Suther Prairie has survived, thanks to the stewardship of the Suther family.

A more typical Piedmont prairie, in that most of it occupies a powerline corridor, is the Picture Creek Diabase Barrens, in Granville County, North Carolina, near the Virginia line. I visited here with Laura Gadd, a botanist now with the North Carolina Natural Heritage Program. In the 1980s this site was proposed for construction of the Superconductor Supercollider, a project that was stopped in large part due to the rare plants here (and later stopped altogether because of the enormous cost). Picture Creek hosts one of the largest remaining populations of the federally endangered smooth purple coneflower. It was too early in the year to see any in bloom. A new species of Barbara's-buttons (*Marshallia* sp. nova) is being described from here. Besides the powerline clearing, most of the site is xeric hardpan forest, with some managed clearings. Laura and I then visited the Eno River Diabase Reserve, a small roadside remnant, where

glade wild indigo had just come into bloom. In addition to the more common wild quinine, this site also has a population of *Parthenium auriculatum*.

At the end of August 2009, I made another trip to the North Carolina Piedmont to view remnant roadside and powerline grasslands, plus some long-leaf pine sites, in the Uwharrie Mountains. With Laura Fogo, Laura Gadd, and a few others, I saw Schweinitz's sunflower (*Helianthus schweinitzii*), another feder-ally listed plant endemic to the Piedmont of the Carolinas. This sunflower has an edible root, and the Catawba Indians, whose territory overlaps strongly with the range of the sunflower, apparently cultivated this plant. At one roadside site, adjacent to a nature preserve managed by the North Carolina Department of Transportation, we observed numerous *H. schweinitzii* in bloom—some 1,600 flowering stems have been counted here. Managers are planning to use fire to expand grassland habitat from the roadside into the adjacent preserve, which is dry oak-hickory forest. Other noteworthy grassland plants we observed on roadsides in this area were slender Indiangrass (*Sorghastrum elliottii*) mixed in with the more widespread yellow Indiangrass (*S. nutans*).

Johnny Stowe, a preserve manager with the South Carolina Department of Natural Resources, showed me around what is often considered South Caroli-na's premier remnant Piedmont grassland: Rock Hill Blackjacks Heritage Pre-serve. Johnny said he was embarrassed to show me this site. He just inherited management responsibility for it, and it was not in ideal shape. The previous manager was "afraid of fire" and had not burned it; instead, he had done some mechanical treatments ("bush-hogging") to control woody plants. This preserve is on gabbro, another mafic rock that produces soils conducive to grassland. The site historically was open prairie mixed with blackjack oak savanna and other communities, and still contains twenty-one rare plant species. A maintained powerline passes through this preserve and has provided a refugium for the native grassland plants. As Johnny pointed out, however, this positive function must be weighed against a negative role of powerline corridors: serving as con-duits for exotic species. Among the exotics here are autumn olive (*Elaeagnus umbellata*), thorny olive (*Elaeagnus pugens*), tree of heaven (*Ailanthus altissima*), Johnson grass (*Sorghum halepense*), Chinese privet (*Ligustrum sinense*), Japanese honeysuckle, chinaberry (*Melia azedarach*), bahiagrass (*Paspalum notatum*), fescue (*Festuca* sp.), bicolor lespedeza, and interstate lespedeza (*Lespedeza* sp.). Inexcus-ably, autumn olive and bicolor lespedeza are still planted by wildlife managers, in the mistaken belief that quail and other game animals are food-limited in these habitats. Johnny will have to use herbicides to knock back these exotics; he obtained permission to do so from the US Fish and Wildlife Service, despite the presence of Schweinitz's sunflower.

I met Chris Ludwig in the parking lot of Difficult Creek Natural Area Preserve, in the Virginia Piedmont, in early June 2009. This site is on mafic Virginia greenstone, which is high in magnesium but relatively low in iron. Chris told me that around 10 to 20 percent of the Virginia Piedmont has mafic soils with strong shrink-swell properties. Little bluestem, Indiangrass, and blackseed speargrass are dominant grasses here, with a lesser amount of big bluestem. The main savanna trees are post oak and pignut hickory (*Carya glabra*). This site has been damaged by planting of loblolly pine and fire exclusion, and is in the process of restoration. Still, it is one of the richest sites for Piedmont endemics and other rarities, including smooth purple coneflower, Schweinitz's sunflower, smooth thistle (*Cirsium carolinianum*), Michaux's sumac (*Rhus michauxii*), spoonshape Barbara's-buttons (*Marshallia obovata*), and *Marshallia* sp. nova, a beautiful plant yet to be described (plate 24). Another site, privately owned Bald Knob, just outside the town of Rocky Mount, contains the largest natural opening on the Virginia Piedmont. The bedrock is highly mafic metabasalt and the grassland is in good shape, with big and little bluestem, rough dropseed (*Sporobolus clandestinus*), blackseed speargrass, Scribner's rosette grass (*Dichanthelium oligosanthes* var. *scribnerianum*), and other grasses. The slope is steep on Bald Knob, showing abundant bare rock with patches of mosses (including the Virginia endemic, Keever's orthotrichum moss [*Orthotrichum keeverae*], on oaks) and prickly pear (*Opuntia humifusa*). Most impressive during my visit, abundant and in bloom, was a newly described species: Piedmont fameflower (*Phemeranthus piedmontanus*). Chris collected the type specimen of this species, for which only five sites are known.

Pine Savannas, Woodlands, and Rocklands

Longleaf pine communities dominated much of the South, occurring on a bewildering variety of substrates and landforms from near sea level to two thousand feet in the Blue Ridge Province of northern Georgia and Alabama. Earlier in this chapter I noted longleaf pine on edaphic sites, from the magnesium-loaded Ketona dolomite of Bibb County, Alabama; the serpentine barren on Burks Mountain, Georgia; and the Catahoula Formation sandstones of Louisiana and Texas to the Altamaha Grit of Georgia and the Citronelle Formation of the Florida Panhandle. Remnant longleaf pine communities also occupy intensely xeric, deep sands (entisols), for example, on ridges along the southeastern rims of Carolina bays. The bays are elliptical depressions scattered across the Coastal Plain and Piedmont from Delaware to northern Florida, but most abundant in the Carolinas.

The origin of Carolina bays has been long debated. Extraterrestrial theories (i.e., that the bays represent impacts from a meteor shower or exploding

comet) have been largely rejected, but their origin is still unclear. To me, the most compelling hypothesis, proposed by James May and Andrew Warne in 1999, is that the bays are "silica–karst" depressions caused by dissolution of limestone beneath deep sands and influenced by long-term changes in sea level (which affect groundwater level). The dry sandy ridges on the bay rims probably were deposited by winds after the bays were formed. They typically feature a xeric longleaf pine–turkey oak community with sparse groundcover. I visited one of the best remaining examples of a Carolina Bay, Woods Bay State Natural Area in South Carolina. The vast patches of blinding bare white sand on the rim reminded me of rosemary (*Ceratiola ericoides*) scrub in Florida. Interesting xeric-adapted plants include combleaf yellow false foxglove (*Aureolaria pectinata*, a hemiparasite on the roots of turkey oak and some other oaks), pine barren stitchwort (*Minuartia caroliniana*), and spiny spikemoss (*Selaginella acanthonota*). There were abundant six-lined racerunners (*Aspidoscelis sexlineatus*), a very speedy lizard I seldom see outside of Florida and one of my favorites since I first captured one at St. Petersburg Beach when I was about eight years old.

In southern Florida, longleaf pine's ecological replacement, south Florida slash pine (*Pinus elliottii* var. *densa*), similarly inhabits some extreme environments, such as pine rocklands on shallow soils overlaying limestone and oolite (a form of limestone composed of ooids, concentric spherical grains) in the southern Everglades, Miami Ridge, and Florida Keys. Longleaf and south Florida slash pine are by no means restricted to extreme sites, however. Rather, as accounted earlier for other grasslands, they are found as remnants on such sites today because they were eliminated by agriculture or silviculture on more fertile soils. Now even xeric, infertile sites, especially in Florida, have been converted to citrus (which doesn't need highly fertile soil) or, increasingly, housing developments. Pine rocklands and longleaf pine sandhills are among the most imperiled communities in Florida.

Unlike true edaphic grasslands, longleaf pine vegetation occurred across a broad range of soil types. In the Coastal Plain, Bob Peet found that two factors—soil moisture (from super-xeric to hydric) and silt content in the A horizon—explain most of the variation in species composition and richness (fig. 4.6). Longleaf pine and other natural vegetation have been eliminated by agriculture from dry, high-silt sites (dry ultisols). Across the rest of this mosaic, species richness and composition correspond closely to soil gradients. At all spatial scales, sandy xeric sites (entisols) are least species rich. As reviewed in chapter 3, the highest richness on a very fine scale (up to 10 square meters) is found in savannas with wet, silty soils, whereas at the scale of 1,000 square meters, the highest richness is on either well-drained or wet silty soils (e.g., Mississippi loess plains and seeps
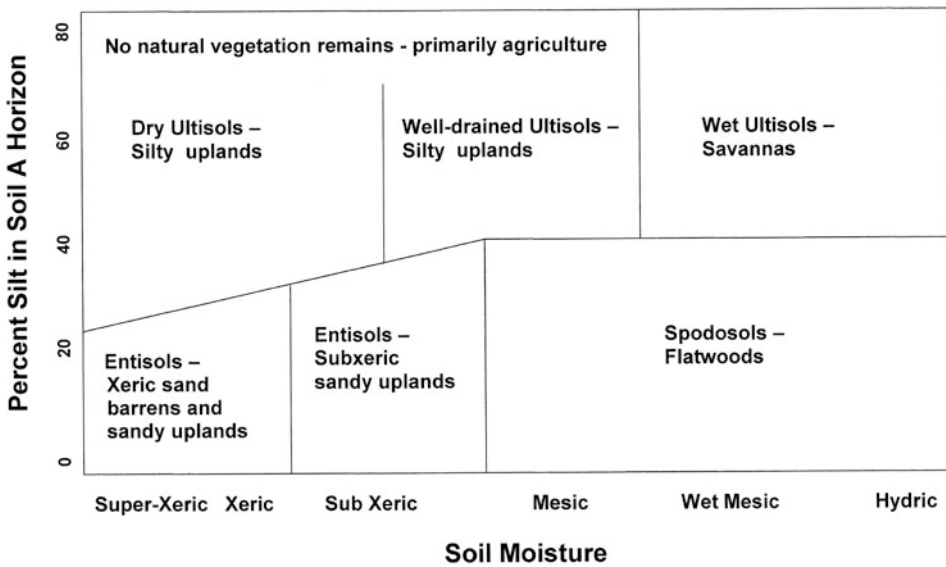
Figure 4.6. A model landscape of longleaf pine vegetation on the Coastal Plain in relation to soil silt content and soil moisture. Longleaf pine communities once dominated most of the landscape, across all soil classes shown here. Adapted from Peet (2006).

in the Tallahassee Red Hills). Because species composition varies markedly across soil conditions, conservation of the longleaf pine ecosystem, with all associated species, requires representation of communities across soil types and other physical conditions. Ideally, protection would be achieved in large, diverse sites where environmental gradients are unfragmented, ecotones are intact, and populations of all associated plants and animals are large enough to persist for a long time.

I observed variation in species composition in response to soil and land-form in longleaf pine communities of the Sandhills region of North Carolina, in the good company of Bruce Sorrie of the North Carolina Natural Heritage Program, Alan Weakley, and Laura Gadd. Bruce had just published his field guide, *Wildflowers of the Sandhills Region*, which helped me prepare, just a little, for the relentless onslaught of plant species names I would hear in the field. The Sandhills is the innermost zone of the Coastal Plain, from North Carolina to Georgia, just below the Fall Line where the Piedmont begins. The sands, most deposited during the Miocene, are underlain by mid-Cretaceous clayey sands and gravels that slow the percolation of rainwater and send it sideways to form seepages and streamheads on slopes. We toured several sites within the impressive 65,000-acre Sandhills Game Land. Nine known species of plants are strictly endemic to the Sandhills. We observed two of them, Sandhills blazing-star (*Liatris cokeri*) and a new species named in 2011 in Bruce's honor, Sandhills

heartleaf (*Hexastylis sorriei*), plus many other rare and fascinating plants, including Michaux's sumac, dwarf bristly locust (*Robinia nana*), Sandhills thistle (*Cirsium repandum*), white meadowbeauty (*Rhexia mariana* var. *exalbida*), and honey-cup (*Zenobia pulverulenta*, the only species in its genus). During the day we saw six fox squirrels (*Sciurus niger*), either pure black or black with partially white faces, more than I'd ever seen before in one day. In the Coastal Plain this large and attractive squirrel is closely associated with longleaf pine communities.

The Sandhills is a marvelous exhibition of the influence of landform, soils, hydrology, and fire on vegetation. In some areas we saw abundant blackjack oak, probably indicative of clay near the surface. We observed seepage areas and streamside pocosins; where they are well burned, they convert to canebrakes. The stream heads contain the Coastal Plain tulip-tree (*Liriodendron tulipifera* var. 1, apparently from a different Pleistocene refugium than the other main genotype) with pond pine and black gum (*Nyssa sylvatica*). Perhaps most intriguing of the edaphic features we viewed was a "bean dip," colloquially named for the abundance of legumes, but composites and grasses are also diverse here. Bob Peet describes bean dips in his longleaf book chapter as "shallow depressions where fine-textured soils have either washed or blown in from the neighboring landscape and become trapped." Over time nutrients build up in the depressions, which become extremely species rich. The bean dip we visited contains 104 plant species within a 1,000-square-meter plot, 17 of which are grasses. While we stood in the bean dip, discussing its ecology and admiring the plants, a spectacular five-foot-long pine snake (*Pituophis melanoleucus*) crawled casually through our circle. This snake is declining across most of its range as suitable upland habitat becomes scarce.

WATER

I must give water short shrift in this book. In defining the scope of this project, with my word limit in mind, I decided to keep my feet mostly dry. I avoid discussion of salt, brackish, and tidal marshes, freshwater marshes, most wet prairies, sawgrass sloughs, and similar graminoid-dominated wetlands, even though many of these fall within my definition of grassland. For these communities, long periods of inundation (hydroperiod) or tidal cycles restrict woody vegetation and allow grasses, sedges, rushes, or other graminoids to dominate. The wettest systems I address are the marl prairies and dwarf cypress savannas of the Everglades–Big Cypress region, seepage slopes (e.g., pitcherplant bogs) of the Coastal Plain, and wet prairie communities of the Florida dry prairie mosaic.

Most of these communities have hydroperiods of up to a few months, but less than half of a typical year. Seepage slopes, on the other hand, do not have a true hydroperiod—they are continually saturated and boggy (except during extreme drought, when the water table drops sharply) but are very rarely inundated.

Riverscour Prairies

A dramatic example of how water can maintain open grassland is riverscour prairies. Grassy areas along streamsides are common. When those grassy patches are substantial and composed of prairie grasses and forbs, they are justifiably called prairies. I observed several riverscour prairies during the course of this project, the largest in the vicinity of the Great Falls of the Potomac in Virginia and Maryland, just below the falls, and downstream by Chain Bridge Road within the District of Columbia. Significant floods occur on the Potomac at intervals of 2.5 to 7 years. At Great Falls Park, which is part of the George Washington National Parkway, a sign (fig. 4.7) indicates impressive past flood-

Figure 4.7. Water levels from past floods, just below the Great Falls of the Potomac, Great Falls Park, Virginia.

stage water levels well above the gorge of the Potomac. According to the Virginia Natural Heritage Program, which classifies the grassland here as Central Appalachian Riverside Outcrop Prairie, this vegetation occupies a zone 2–17 meters (7–56 feet) above mean water level. Some 15 to 90 percent of the community is exposed metamorphic bedrock with mafic and ultramafic intrusions.

The plants in the Potomac riverscour prairies, especially the grasses, are typical of tallgrass prairie far to the west. The most abundant is big bluestem, accompanied by Indiangrass, little bluestem, and switchgrass, plus several more species of grasses and characteristic xerophytic forbs such as narrow-leaved mountain-mint, sticky goldenrod (*Solidago simplex* var. *racemosa*), late purple aster (*Symphyotrichum patens* var. *patens*), and nodding onion (*Allium cernuum*). Flood-damaged trees and shrubs are scattered throughout. Total plant species richness is very high, averaging 88 taxa (range 51–138) in 400-square-meter plots. Prairie vegetation persists on these sites due to a combination of shallow, xeric soils and regular scouring by floods. Fire is rare and not necessary to maintain the community.

South Florida

The characteristics of an ecosystem's hydrologic regime, including the magnitude, frequency, timing, duration, seasonality, and rates of change of water levels, play key roles in regulating ecological processes. Especially in Florida, hydroperiod is right up there with fire as a process that determines the structure and composition of natural communities. *Wetland* and *upland* are not very useful concepts in Florida; indeed, they can be highly misleading. A community can be wetland for part of the year (summer and fall in central and south Florida) and dry upland during the rest. In south Florida, pine rocklands are usually dry, with most sites wet for only short periods following heavy rains or storm surge, but with some sites shallowly inundated by slow-flowing surface water for up to two months during the rainy season. Marl prairies have hydroperiods of around two to four months (more in some years). Glades marshes have hydroperiods greater than six months, cypress domes (dome swamps) six to nine months, and strand swamps three to ten months. Sloughs are almost always flooded except during strong drought. Human alteration of hydroperiod through construction of drainage ditches and impoundments, withdrawal of groundwater, and other actions have enormous impacts on these communities, equivalent in magnitude to excluding fire from fire-dependent communities.

The Everglades–Big Cypress region, lying in a basin south of Lake Okeechobee between lands of higher elevation along both coasts, is a mosaic of communities with different hydroperiods. I focus here on two community

types that fall within my definition of grasslands: marl prairies (including pond/ dwarf cypress savannas) and pine rocklands. Marl prairies are restricted to the south Florida mainland. In Everglades National Park, marl prairies lie between the Miami Rock Ridge and the lower slough and glades marshes and in narrow glades on Long Pine Key. The Miami Rock Ridge, the southern extension of the Atlantic Coastal Ridge, is composed of a soft, often exposed, oolitic limestone formed during Pleistocene interglacial periods when most of the tip of the Florida Peninsula was under the sea (as it will be again before long). Pine rocklands occur on the Miami Rock Ridge (which has a high point of twenty-three feet) from the city of Miami southwest to Long Pine Key; in the Lower Florida Keys, especially Big Pine Key and vicinity; and in a small portion of the Big Cypress National Preserve.

I first visited marl prairies (plate 20) for this project with my son Clay in early May 2009, led by Jimi Sadle, an adept botanist for the National Park Service. Jimi is stationed in Everglades National Park, but he also showed us around Big Cypress National Preserve. May is when the dry season peaks and ends, and this had been a drier winter/spring than usual. As botanists down here say, the plants were "crispy." Marl prairie is a unique endemic community; there is nothing else like it. The soils are highly alkaline marls or sandy marls, 2 to 24 inches deep, underlain by limestone. Marl in this region is a white calcareous mud formed from calcite precipitated by an assemblage of green algae, blue-green algae, and diatoms, known as periphyton. Marl is highly impermeable, causing water to pond during the wet season, with an average depth of about eight inches. Particularly in the southeastern Everglades, limestone pinnacles and solution holes are exposed through the marl, forming a complex and enchanting microtopography.

When we visited marl prairies in May, they were dry as a bone. No water, no mud, just grasses and other plants growing in the thin marl soil amidst exposed, pinnacled limestone. Returning in early July with my wife, Myra, and younger son, Max, I'm wading through shin-deep water in a marl prairie off of Turner River Road in Big Cypress National Preserve. Fish (apparently mostly mosquitofish, *Gambusia holbrooki*) are swimming through the prairie around my ankles. Fish in a prairie somehow seem deviant. I expected muddy marl to cling to my sandals, but there was none. The marl prairies in Big Cypress usually have more sand and less marl than in the Everglades; the substrate here is mostly a thin layer of spongy periphyton and sand over limestone. This experience is difficult to reconcile with my visit here in early May. The extreme seasonal contrast makes life challenging for trees. Some marl prairies are sparse savannas, sometimes considered a distinct community; the "trees" are stunted pond

cypress (*Taxodium ascendens*). Also called dwarf, scrub, or hat-rack cypress, these ancient bonsai-like trees are usually less than twelve feet tall with a diameter at breast height of less than four inches. They may be hundreds of years old, some more than a thousand, and often have gnarled crowns and buttresses that are huge for their size. Epiphytes abound on the dwarf cypress. In May Jimi led us through a dwarf cypress savanna with many bromeliads in bloom, including the gorgeous red and purple reflexed wild pine (*Tillandsia balbisiana*).

During the wet season one could mistake a marl prairie for a marsh, not knowing that the prairie will soon become dry for eight to ten months. An important biological distinction is that the longer-hydroperiod marshes are species poor, usually with fewer than twenty plant species, whereas marl prairies often contain more than a hundred plant species. Still, around 90 percent of the cover in a typical marl prairie is contributed by only two or three dominant species, which, depending on the site, include hairawn muhly (*Muhlenbergia sericea*), spreading beaksedge (*Rhynchospora divergens*), Florida little bluestem (*Schizachyrium rhizomatum*, a state endemic), black bogrush (*Schoenus nigricans*—this is the species that occurs "out of place" in the upland glades of the Florida Panhandle), Elliott's lovegrass (*Eragrostis elliottii*), sand cordgrass (*Spartina bakeri*), and a short form of sawgrass (*Cladium jamaicense*). Other characteristic species that we observed during the May or July visits were rosy camphorweed (*Pluchea rosea*), southern fogfruit (*Phyla stoechadifolia*), starrush whitetop (*Rhynchospora colorata*), swamp lily (*Crinum americanum*—it's not supposed to be out in the open like this), alligatorlily (*Hymenocallis palmeri*), arrowfeather threeawn, and narrowleaf yellowtops (*Flaveria linearis*). We observed three rose-gentians: annual sea-pink (*Sabatia stellaris*), Bartram's rose-gentian (*S. bartramii*), and bitter-bloom (*S. angularis*); the last was blooming in profusion along Wagon Wheel Road in the Big Cypress, in an area that burned two years earlier.

Driving down the lonely road from the Everglades National Park headquarters just outside Florida City to the little "town" of Flamingo at the end of the road is exhilarating. Open vistas stretch in every direction, mile after mile of marl prairies and sawgrass sloughs interrupted by occasional tropical hardwood hammocks, pine rocklands, and Florida royal palm (*Roystonea elata*) hammocks. Except during peak periods of the tourist season, the road is astonishingly empty. During most of the year, if you get out of your car and walk even a few feet, you are besieged by mosquitoes. This must partially explain the absence of people. And, of course, there are snakes. Clay and I spotted a fine eastern diamondback by the edge of the road, which we photographed as he coiled, only half menacingly, and then glided off into the palmetto.

An arresting sign along the road to Flamingo alerts the driver or cyclist to

Rock Reef Pass (fig. 4.8). This is not a pass like you might think of out West, a low area between mountains, but rather is a divide between watersheds. It is a high point, yet it is only three feet above sea level. Given the rate of sea-level rise (ten inches since the 1930s and projected to rise another three to six feet or so by the year 2100), this area will soon be inundated. Not far off the road, in a marl prairie/pine rockland ecotone near Long Pine Key, Jimi shows us the only plant endemic to the southern Everglades: two-spike crabgrass (*Digitaria pauciflora*), a bluish and highly pubescent perennial bunchgrass. Only two occurrences are known: here and a small, recently discovered population in Big Cypress National Preserve. Its entire range—and virtually all of south Florida—was under the sea during the last interglacial, which peaked around 125,000 to 120,000 years ago, when sea level was about 6 meters (19.7 feet) higher than today. Has this species evolved here since then, or did it move in from another area where it no longer occurs? What about the marl prairie community—did it develop only recently? We know that communities similar to the modern-day marl prairies have come and gone over time. Debra Willard and Christopher Bernhardt write in an issue of *Climatic Change* devoted to sea-level rise in Florida: "The long-term influence of sea level fluctuations on

Figure 4.8. Rock Reef Pass, along the road in Everglades National Park. A pass in this part of the world is a high point in the landscape. This pass, along with some 60% to 80% of the Everglades, will likely be inundated by the rising sea by the year 2100.

the region is represented by the stratigraphic record of alternating fresh-water marls and marine sediments deposited since the Pliocene. This record indicates that the modern Everglades is the most recent in a series of freshwater wetlands that have occupied the Everglades basin during the last few million years."

Not far down the road from the *Digitaria* occurrence, about nine miles from the coast, is the "white zone," distinguished by the whitish, bare saline marl easily seen from the air. This is the southwestern extent of pines in the Everglades, and they are stunted and surrounded by invading red mangroves (*Rhizophora mangle*). The inland migration of the white zone and the encroachment of mangroves into what was pine rockland has been documented from aerial photos and field work since the late 1930s and is a clear signal of sea-level rise. Ecologist Frank Egler was a wise man, the fellow who wrote that "ecosystems are not only more complex than we think, but more complex than we *can* think." Egler was the first to publish an article about the white-zone phenomenon in 1952. He described the vegetation of the southern Everglades as responding slowly to rising sea level, reduction of the freshwater aquifer, modification of drainage patterns, reduction in fire frequency, and other environmental changes. These changes have accelerated since Egler conducted his studies. There is no evidence that marl prairies can migrate inland and northward in response to sea-level rise, and we have no ability yet to create marl prairies in areas such as abandoned sugar cane fields to the north.

Marl prairies will likely disappear within two or three human generations. With them will go the two-spike crabgrass, populations of many other rare species, and the entire range of a much-researched and federally endangered bird, the Cape Sable seaside sparrow (*Ammodramus maritimus mirabilis*). This highly specialized sparrow occurs only in marl prairies in the southeastern portion of Big Cypress National Preserve and in the vicinity of Taylor Slough in Everglades National Park. Research shows that it is very sensitive to water levels, with nests unsuccessful when levels are too high. It is one of many species that, in the face of sea-level rise, we must either take into captivity indefinitely or watch go extinct in the wild.

Ridges or islands of higher ground in extreme south Florida are often occupied by pine rocklands. These communities are characterized by an open canopy of south Florida slash pine and a diverse, open shrub/subcanopy layer with more than one hundred species of palms and hardwoods, most derived from the West Indies. The herbaceous layer is also rich, with many plants endemic to south Florida. The oolitic limestone is at or very near the surface, with very little soil development. Organic acids dissolve the surface limestone in places, creating solution holes. Because pine rocklands sit on some of

the highest ground in south Florida, they have been disproportionately lost to development. Some 99.5 percent of the pine rocklands on the Miami Rock Ridge have been destroyed, which is especially tragic because these were the biologically richest rocklands—some of the remaining tiny fragments hold 200 to 300 plant species. Keith Bradley (one of the premier field botanists in south Florida) told me that, ironically, urban rockland fragments are often in the best condition due to the frequent fires ignited by crackheads, homeless people, and neighborhood kids.

Many conservationists today play down the value of small urban natural areas, arguing that only conservation of large landscapes will maintain complete food webs and provide ecological services. I once argued similarly, but have realized the error of my ways. In the case of the Miami Rock Ridge, little fragments are packed with local endemics. The rocklands in Everglades National Park, which total about 20,000 acres, were naturally isolated from those on Miami Rock Ridge and the Keys, and are less diverse, with fewer endemics and Antillean taxa. Besides their biodiversity, the pine rockland fragments in the vicinity of Miami have enormous scientific and educational value. They offer a glimpse of what the natural landscape of the Miami Rock Ridge once looked like, and they are places where urban residents can learn and practice natural history, or simply get off the pavement.

WIND, STORMS, AND SEA-LEVEL RISE

The southeastern United States is a windy place, with one of the highest frequencies of tropical storms, hurricanes, and tornados in the world. In 1528, as Cabeza de Vaca and his party traveled northward up the length of the Florida Peninsula from where they landed in the vicinity of Sarasota Bay, Cabeza de Vaca noted in his journal "so many fallen trees on the ground that they barred our way." He wrote that many of the trees "were split from top to bottom from the lightning that strikes in that part of the world, where there are constantly great storms and tempests." The mapped tropical storm and hurricane tracks from 1851 through 2004 turn the entire state of Florida, and the coastal portions of other southeastern states, completely black (plate 5). In September 1989, Hurricane Hugo made landfall near Charleston, South Carolina, with winds of 135 miles per hour, and proceeded across the Francis Marion National Forest, one of the main strongholds of the longleaf pine ecosystem and red-cockaded woodpecker in the Carolinas. Winds disproportionately affected larger, older trees, with some 50 to 60 percent of sawtimber-size trees killed. Cavity trees of

the woodpeckers are especially prone to snapping off at the cavity. Only 229 of 1,765 pre-Hugo cavity trees survived, and the woodpecker population plunged by 63 percent.

But all this is natural, right? High winds, coastal storm surges, and lightning help maintain sunny, open-canopy conditions and thus are crucial factors for maintaining grassland in coastal regions. Anthropogenic climate change, however, alters natural disturbance regimes, such that processes that once maintained grasslands and other ecosystems now threaten them. Increased hurricane intensity, for example a greater proportion of Category 4 and 5 storms, has been documented over recent decades and is forecast to continue over the next century or longer. Combined with sea-level rise from thermal expansion of ocean water and melting of mountain glaciers and polar ice sheets, the storm surges from intense hurricanes now threaten coastal ecosystems such as coastal grassland and pine rocklands. As Mike Ross of Florida International University and colleagues document, the "press" disturbance of increasing sea level is now combined with the "pulse" disturbance of increasing hurricane intensity and storm surge. The impact on coastal freshwater-dependent communities, such as pine rocklands, is severe.

Nowhere in the United States is so much biological diversity at high risk of loss from sea-level rise and increased storm surge than south Florida, with the Florida Keys being "ground zero." In the Lower Keys, the unique geology, with surficial oolite underlain by a coralline limestone, allows a relatively thin freshwater lens to float on top of underground saltwater. As the sea rises, the salt groundwater level also rises, pushing the freshwater lens upward, as well as inundating more of each island with each major storm. Eventually the freshwater lens will disappear; not long thereafter, most of the land will, too.

The Florida Keys have become progressively smaller and more isolated as a consequence of sea-level rise since the Last Glacial Maximum. Pine communities similar to today's pine rockland were widespread across the larger land area of the Keys—for example, pine cones and wood fragments dated to between 8,350 and 8,600 years ago have been discovered in sediments under forty feet of water, forty miles west of Key West. Just since 1935 pine rocklands on some Lower Keys have declined by more than 50 percent (fig. 4.9). The future is grim for freshwater-dependent communities in the Florida Keys. A study by Keqi Zhang and colleagues used high-resolution LiDAR (Light Detection and Ranging) imagery to develop a detailed digital elevation model for the Keys and then modeled inundation from sea-level rise to the year 2100. A modest 0.6-meter (2-foot) rise in sea level would inundate about 70 percent of the total land surface of the Keys. A 1.5-meter (5-foot) rise in sea level, which may
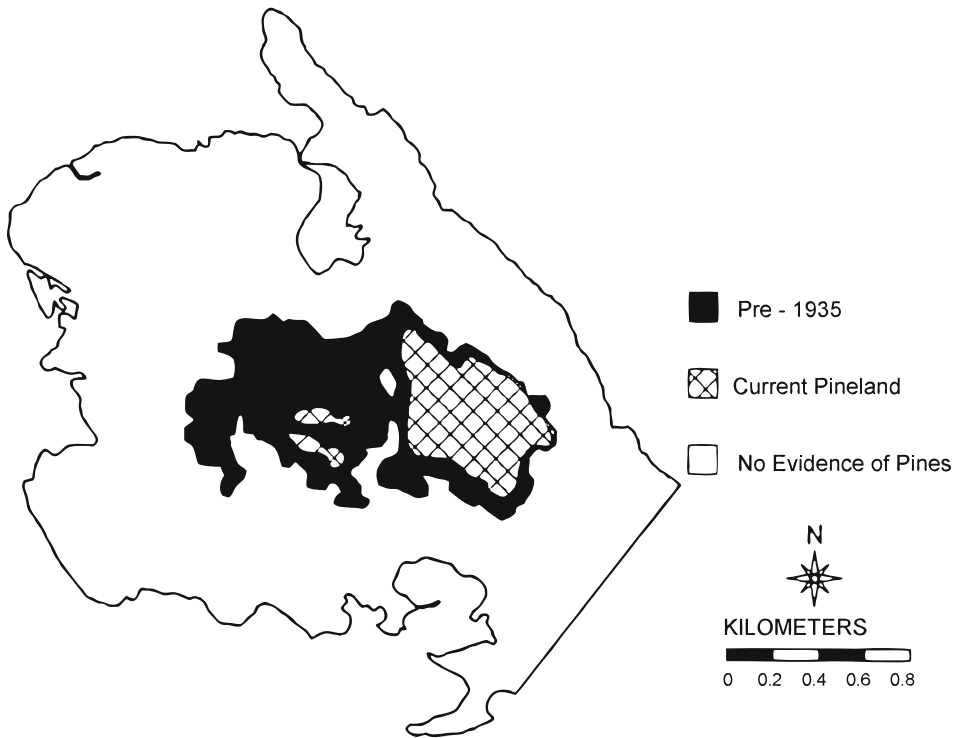
Figure 4.9. Historical and current extent of pine rockland on Sugarloaf Key, Florida. A combination of sea-level rise and increasing intensity of hurricanes and storm surge is responsible for this decline. Reproduced from Ross et al. (2009) with permission of the Ecological Society of America.

be more likely by 2100, would inundate 91 percent of the land surface, with the Lower Florida Keys (most of which are less than 2 meters in elevation) disproportionately affected. Pine rocklands, the most endemic-rich community in the Keys, reach a maximum elevation of only 3 meters (9.8 feet).

As summarized in chapter 3, the Lower Keys contain a number of endemic taxa—most at the subspecies or variety level—that presumably evolved since the Keys became isolated from the mainland and one another only around 6,000 years ago. Several of these species stand to lose all of their current habitat with sea-level rise by 2100. The Key tree-cactus (*Pilosocereus robinii*), a federal endangered species, has developed root rot and is dying out, in large part due to soil saturation related to rising sea level. Other narrow endemics, which I observed in the field with Keith Bradley and on other trips, likely to go extinct in the wild include Big Pine partridge pea (*Chamaecrista lineata* var. *keyensis*; plate 21) and rockland (deltoid) spurge (*Chamaesyce deltoidea* ssp. *serpyllum*).

Virtually all available habitat for the Florida Key deer (*Odocoileus virginianus clavium*), Lower Keys marsh rabbit (*Sylvilagus palustris hefneri*), and some other animals will be eliminated. It is difficult to imagine a world without Key deer, which are of similar size and behavior of a skinny Labrador retriever. As Joyce Maschinski and coauthors discuss in *Climatic Change*, conservationists will be forced to make painful decisions about whether to bring these imperiled species entirely into zoos and botanical gardens, freeze their tissues in gene banks, translocate them outside their current range (e.g., onto Caribbean islands with more topographic relief), or document their extinction in the wild.

All coastal ecosystems are threatened by sea-level rise and increased storm surge. In Texas, Jason Singhurst introduced me to a coastal prairie at Candy Cain Abshier Wildlife Management Area in April 2009. Coastal prairies in Texas and Louisiana, which many ecologists consider an outlier of tallgrass prairie, have been severely reduced in area. In Texas, perhaps more than 5 percent of sandy coastal prairie remains, but well under 1 percent of the more fertile clay coastal prairie, now mostly converted to rice. The Abshier site experienced serious flooding from Hurricane Ike the previous year. The site's managers have been regularly mowing, but not burning, and a dense grass thatch has built up on the ground. Jason and I agreed that burning is needed here. We observed little bluestem, slender little bluestem (*Schizachyrium tenerum*), hairyawn muhly, slenderfruit nutrush (*Scleria georgiana*), pineland yellow-eyed grass (*Xyris stricta*), coastal plain yellow-eyed grass (*X. ambigua*), Indiangrass, big bluestem, chalky bluestem (*Andropogon capillipes*), and many other plants. Lance-leaved violets (*Viola lanceolata*) were in bloom, and we saw leaves of the annual dwarf sundew (*Drosera brevifolia*). However, we could not find several species known from this site, such as small butterwort (*Pinguicula pumila*)—could it have been wiped out by storm surge? The site was generally in poor condition. It is not unlikely that saltwater inundation, followed by a drought (i.e., no rain to wash the salt away), combined with the dense thatch, resulted in a synergistic perturbation that some plants could not tolerate.

Only at Attwater Prairie National Wildlife Refuge, a sandy coastal prairie on the high inland end of the coastal prairie gradient, were effects of the storm unnoticeable. Here I had hoped to see the Attwater's prairie-chicken (*Tympanuchus cupido attwateri*), an endangered subspecies of the Greater prairie-chicken native to coastal Texas and Louisiana, and the only prairie-chicken extant in the South. Instead, I got to hear the beeping of the radio transmitter attached to a hen on a nest, thanks to Mike Morrow and Rebecca Chester, US Fish and Wildlife Service biologists who are studying prairie-chickens. The nest was protected by predator-deterrent fencing. I also got a "lifer"—a white-tailed

hawk (*Buteo albicaudatus*) soaring majestically above us for a long time. Its US distribution is only in coastal Texas.

Tornados and other storms are also frequent in the South. A 2012 analysis of National Weather Service data by The Weather Channel found that tornado frequency is higher in Florida than in any other state—12.3 tornados annually per 10,000 square miles between 1950 and 2010—though extremely large tornados are uncommon here. Like hurricanes, tornados open forest canopies. I observed a large tornado swath through montane longleaf pine in the Talladega National Forest in northern Alabama with Bill Garland and Johnny Stowe. The vast majority of trees were snapped off. Unfortunately (but typically), the US Forest Service is salvage-logging the site (i.e., cutting and removing dead and damaged trees), which precludes research on ecosystem recovery after a disturbance event and removes structures, such as snapped off and downed trees that provide important habitat for many organisms. In chapter 5, we will explore interactions among disturbances and top-down effects of herbivory and predation. The effects of many interacting processes are often not predictable from looking at single processes in isolation. Only the Big Picture tells the real story.

REFERENCES

Grasslands and communities (general): Gleason 1926, Whittaker 1962, Quarterman et al. 1993, Anderson et al. 1999

Blackland prairies (including Black Belt and Jackson prairies): Gosse 1859, Mohr 1901, Rostlund 1957, Rankin and Davis 1971, Foti et al. 2003, Peacock and Schauwecker 2003, Schauwecker and MacDonald 2003, Zollner et al. 2003, Barone 2005, Barone and Hill 2007, Hill and Seltzer 2007, Echols and Zomlefer 2010, Jim Allison's website: http://jimbotany.com/castaneasupplement_pt1.htm

Other calcareous grasslands and limestone glades: Lockett 1869 (1969), Gattinger 1901, Braun 1928a and 1928b, Braun 1950, Anderson 1982, Baskin and Baskin 1986, Bridges and Orzell 1986, Boettcher and Kalisz 1991, Quarterman et al. 1993, Baskin and Baskin 1999, Baskin et al. 1999, Ludwig 1999, Baskin and Baskin 2003, MacRoberts et al. 2003, Baskin and Baskin 2004, Lawless et al. 2006, Baskin et al. 2007

Sandstone, igneous, and metamorphic glades and barrens: Harper 1906a and 1906b, McVaugh 1943, Quarterman et al. 1993, Griffin et al. 1995, Griffin and Snow 1998, Reid and Spooner 1998, Shure 1999, Pringle and Witsell 2005

Shale barrens: Steele 1911, Platt 1951, Braunschweig et al. 1999, Pringle and Whitsell 2005, Witsell 2007

Serpentine barrens: Marye 1955, Kruckeberg 1984, Mansberg and Wentworth 1984, Tyndall 1992, Tyndall and Hull 1999, Kauffman et al. 2004, Harrison and Viers 2007, Briles et al. 2011, Juras 2011

Saline prairies or barrens: MacRoberts et al. 2009, Reid et al. 2010

Piedmont prairies: Schafale and Weakley 1990, Barden 1997, Juras 1997, Davis et al. 2002, Tompkins et al. 2010, Blevins and Schafale 2011

Pine savannas, sandhills, montane longleaf: May and Warne 1999, Platt 1999, Stowe et al. 2002, Varner et al. 2003, Peet 2006, Sorrie 2011

Marl prairies, pine rocklands, sea-level rise, hurricanes, tornados: Cabeza de Vaca (1542) 1993, Egler 1952, Ross et al. 2000, Earley 2004, Ross et al. 2009, Maschinski et al. 2011, Noss 2011, Saha et al. 2011, Willard and Bernhardt 2011, Zhang et al. 2011, Strauss et al. 2012, http://www.weather.com/outlook/weather-news/news/articles/top-tornado-states_2012-03-06

Beetles: White 1983

NatureServe Explorer: http://www.natureserve.org/explorer/

❧

Fire, Big Animals, and Interactions

The prevailing vegetation is open forests of long-leaf pine, so open that wagons can be driven through them almost anywhere.

> Roland M. Harper (1914, writing about the Florida
> Panhandle and neighboring Georgia and Alabama)

The preceding chapter concentrated on physical factors, especially geology, soils, landform, and hydrology, which create or maintain grassland within the South. In this chapter I consider a range of abiotic and biotic processes and their interactions. These processes include two major positive feedbacks—fire and large herbivores—identified in the general model as reinforcing and accelerating grassland development following a shift to a drier or more seasonal climate. Large grazing and browsing herbivores abounded within North American grasslands, including southern grasslands, for millions of years. That southern grasslands contain a mix of grazing-adapted rhizomatous (sod-forming) grasses and bunchgrasses suggests that megaherbivores influenced the development of these communities. At times the influence of herbivores may have surpassed the role of fire. Megaherbivores had natural predators, which probably exerted top-down control over their populations and affected their evolution of anti-predator morphologies and behaviors over long spans of time.

Fire has been influential in grasslands even longer, judging not only from geological and paleoecological evidence, but also from the many traits of plants and animals in these ecosystems that are most parsimoniously explained as

adaptations to fire. Many or most southern grasslands developed over tens of thousands to millions of years in close relationship with fire. Even many edaphic grasslands require fire to stem continual invasion by woody plants. Finally, I consider other interactions that may be important in grassland maintenance, including interactions between fire and herbivory, and among fire, topography, hydroperiod, and other factors.

BOTTOM-UP, TOP-DOWN, AND SIDEWAYS

Many interactions among abiotic and biotic factors influence grassland communities. To place these factors into perspective, let's reconsider the general model of grassland origin and maintenance (fig. 5.1). This model includes a suite of factors that potentially regulate grassland development and persistence. For particular types of grassland, or even sites within types, the proportional role of factors varies. Fire outweighs the influence of all other factors on the maintenance of grassland types such as pine savannas, whereas in some edaphic or flood-controlled grasslands (e.g., saline barrens or riverscour prairies) fire is of minor or no importance. Some peculiarities of species composition, for instance, local endemic taxa and disjunct populations, cannot be explained by this model because they represent historical contingencies.
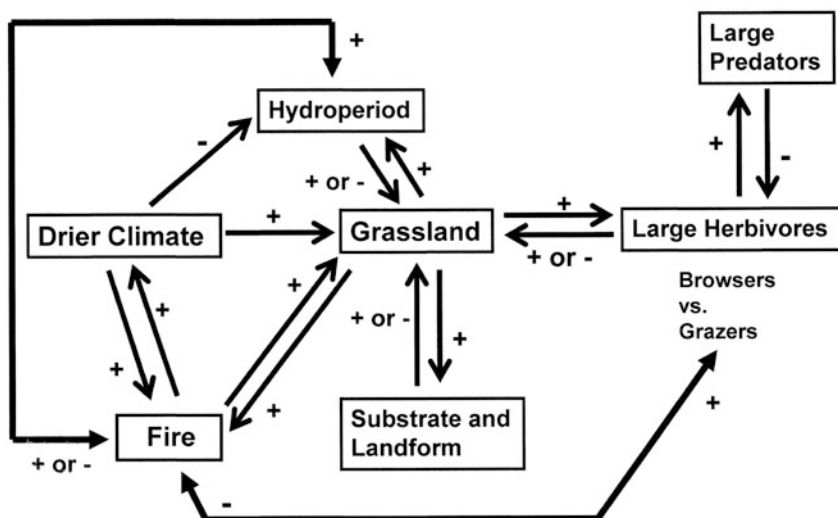
Figure 5.1. A general conceptual model for the origin and maintenance of southern grasslands. See chapter 2 for explanation.

The general controlling factors on grassland composition, structure, and function can be placed into three categories: bottom–up, top–down, and what I call "sideways" controls (i.e., fire and other disturbances). Their relative importance varies among communities, but also within a community over time. For instance, a fire or hurricane can disrupt top–down trophic control and accentuate bottom–up processes, in that the flush of vegetation regrowth after a major disturbance may overwhelm both herbivores and their predators for a period of time. As shown by McLaren and Peterson for the balsam fir (*Abies balsamea*)–moose (*Alces alces*)–gray wolf (*Canis lupus*) system on Isle Royale, Michigan, if a stand-replacing disturbance occurs when moose density is low, vegetation regrowth is not constrained by consumers. When moose, and then wolf, populations recover, top–down control returns. The scientific literature, produced by people who like to make strong points (as do I), gives insufficient consideration to spatial and temporal variation in the strength of controlling factors. In real ecosystems, bottom–up, top–down, and sideways controls operate simultaneously, but their relative importance fluctuates over time.

Bottom-Up Control

Bedrock, soils, topography, available energy, water, and other physical factors serve as bottom–up controls on the composition and diversity of biological communities. They are *bottom-up* in the sense that they influence plant species composition, richness, and productivity, which in turn affect composition and abundance of animals up the food chain from herbivores to top carnivores. Chapter 3 considered the influence of climate (e.g., energy availability), water, nutrients, and other factors on species richness within and among plant and animal communities, whereas the broader influence of physical factors on southern grassland structure was reviewed in chapter 4.

Although top-down control has recently received the most attention in the ecological literature, few ecologists question the importance of bottom–up factors. In 2011 Bradley Cardinale and colleagues reviewed 368 independent experiments on the influence of plant species richness on ecological processes. They found that loss of plant species reduces the standing biomass of the producer community and the efficiency by which primary producers assimilate inorganic resources. There was high support for the hypothesis that the effects of plant species richness are due to some form of complementarity (i.e., different species playing mutually supportive roles). Most important, there was strong evidence that ecosystem processes show accelerating declines with plant species loss, which argues for a conservation strategy that seeks to maintain or restore the plant species richness characteristic of a community. This review

does not rule out the potentially significant role of consumers (from herbivores to predators and parasites) in maintaining plant species richness, but it shows that plant species richness influences processes throughout the food web.

Top-Down Control and Ecologically Pivotal Species

The ascendance of the hypothesis that ecosystems are regulated from the top down, a concept now known as trophic cascades, can be traced to a four-page essay in *The American Naturalist* by Nelson Hairston, Frederick Smith, and Lawrence Slobodkin in 1960. They argued that the world is green because populations of voracious herbivores are held in check by their natural enemies: predators, parasitoids, parasites, and pathogens. This hypothesis stimulated heated debate, which has moderated with increasing acceptance of trophic cascades in ecosystems. Proponents of top-down control continue to state their case boldly. For example, Jim Estes and multiple coauthors argued in *Science* in 2011 that "the loss of apex consumers is arguably humankind's most pervasive influence on the natural world." This argument has merit, though I find it overstated in that it plays down the importance of bottom-up and sideways regulation of ecosystem dynamics, as well as the overarching impacts of human population growth, direct habitat destruction, and other threats. Grassland ecologists may be dismayed by the scant attention to fire in most top-down models.

I prefer the concept of strongly interactive or *ecologically pivotal* species to a narrow emphasis on top predators (apex consumers)—despite my career-long devotion to carnivore conservation. Top predators are just one type of strongly interactive species. Michael Soulé and colleagues, in 2003 and 2005, made a crucial point: Species that interact strongly, either directly or indirectly, with many other species should be given special attention in conservation, because population declines in such species will have ramifications throughout the ecosystem. Such species should be maintained, not just in minimally viable populations, but in ecologically effective populations that perpetuate their diversity-enhancing roles. Think for a moment about a natural community with which you are familiar. It is not difficult to imagine how a drastic decline of an ecologically pivotal species in that community, even if it is not yet truly rare, could have repercussions on community structure that surpass the extinction of species that play lesser roles. Beaver (*Castor canadensis*) creating a succession of communities in stream valleys is a familiar example. The overarching role of ecologically pivotal species provides no excuse for allowing extinction of less interactive species, but it provides a powerful rationale for maintaining ecologically effective populations of the most pivotal species.

Keystone Predators

Ecologically pivotal or strongly interactive species are of several types. One type is the apex consumers that receive so much attention in the modern literature. Bob Paine of the University of Washington conducted the classic experiments in the 1960s, demonstrating how a top predator (in his experiments, a starfish in the intertidal zone) could enhance species richness of lower trophic levels by preferentially preying on a superior competitor herbivore (a mussel) and thereby allowing many inferior competitors to coexist. This *keystone species* hypothesis has similarities to the intermediate disturbance hypothesis discussed in chapter 3, in that both predators and disturbance can prevent competitively dominant species from monopolizing resources. Nutrient limitation can do the same thing.

Over the last few decades, many examples of keystone predator effects have been documented, for example, reintroduced wolves (*Canis lupus*) controlling moose (*Alces alces*) and elk (*Cervus elaphus*) in the Greater Yellowstone Ecosystem. Top predators once played an important role in southern grasslands and still do within limited areas. Recall the tremendous diversity of grassland-associated megaherbivores here from the Miocene through the Pleistocene. Like most big herbivores, they were surely capable of overgrazing, overbrowsing, or otherwise damaging vegetation—potentially leading to ecosystem collapse—if superabundant. Highly competitive species of herbivores could have excluded inferior competitors. In a 2010 paper, Bill Ripple and Blaire van Valkenburgh make the case that Pleistocene megaherbivores were predator limited, contradicting the common view that the largest herbivores were (and are) invulnerable to predation as a consequence of their large body sizes and their reproductive strategy of producing a small number of well-protected young. On the basis of multiple lines of evidence, including predator dental wear patterns and stable isotope ratios, Ripple and van Valkenburgh suggest that proboscideans (the taxonomic order containing elephants) and probably other megaherbivores were kept at densities below carrying capacity by natural predators. Lions and sabertooth cats, for example, had broad diets that included horse, camel, bison, ground sloth, and mastodon. Unfortunately, limitation by predators probably made these herbivores more susceptible to extinction when humans joined the predator guild. As the megaherbivores went extinct, so did most of their predators.

The top nonmarine predators in the South at the time of European settlement were puma (*Puma concolor*, including the Florida panther), red wolf (*Canis lupus rufus*), black bear (*Ursus americanus*, an omnivore, which occasionally takes

large animal prey), American alligator, and American crocodile (*Crocodylus acutus*, in south Florida only). All of these predators are reduced in distribution and abundance in the South, so we are no longer able to observe their natural top-down influences. Even the alligator, which has recovered across most of its range, is intensively managed by fish and wildlife agencies, so that all individuals above a certain size (ca. five or six feet in length) are killed by licensed hunters—even within so-called conservation areas. Big alligators, which once grew to nearly twenty feet, eat much larger prey than little alligators and thus have vastly different effects on the food web. As my mentor Larry Harris of the University of Florida frequently pointed out, the alligator today is not playing anything close to the substantial keystone role that it most certainly played in the past. We may not think of alligators as grassland animals, but I have encountered them in pine savannas, dry prairie, and other grasslands as they travel among water bodies, especially during drought (just ask my dog, who was surprised by one in a dry prairie and leapt howling several feet into the air). In addition, terrestrial animals must regularly cross streams and sloughs when moving through the landscape and would be vulnerable to alligator attacks.

Another predator, the coyote (*Canis latrans*), currently inhabits most of the South. Most state wildlife agencies classify the coyote as an exotic nuisance species and allow (indeed, encourage) people to shoot them. Such a policy is wrongheaded. It is factually incorrect to label the coyote a nonnative species. The likely ancestor of the modern coyote, *Canis lepophagus*, occurs in late Pliocene fossil sites in Florida. Remains of the modern coyote occur in Late Pleistocene (Rancholabrean) deposits in Florida and elsewhere in the South (Alabama, Mississippi, West Virginia). Small wolves (perhaps the modern red wolf, whose taxonomic status remains questionable) reappeared in Florida and elsewhere in the Southeast at the end of the Pleistocene, after an absence of nearly one million years. When the small (red) wolf reappeared, the coyote disappeared, suggesting competitive displacement. Just a few decades ago, perhaps partly in response to the decline and extinction of the red wolf in the wild, coyotes began dispersing into the South from the west and north, with most of the South colonized by the 1960s through 1980s. Although small numbers of captive coyotes were released and hunted with hounds in parts of the South during the mid-1900s, the vast majority dispersed here unaided, thereby fully meeting the criterion for a native species through natural range expansion.

Although the impacts of coyotes and other large predators on terrestrial food webs in the South are not yet well understood, abundant research from the West indicates coyotes function as apex predators and enhance species richness at lower trophic levels. In a 1997 paper, Dave Maehr (who tragi-

cally died in 2008 while radio-tracking bears in Florida by aircraft) expressed concern about the range expansion of the coyote into south Florida because coyotes ostensibly compete with bobcats (*Lynx rufus*), black bears, and puma in other parts of North America. Concern about competition among these species, however, is probably unwarranted. Coyotes overlap spatially with other large carnivores throughout much of North America when viewed at coarse resolution, but the usual pattern is for the larger species (especially wolves) to exclude coyotes from wilder areas and force them into marginal habitats, such as near roads and human settlements. This has been documented following the reintroduction of the gray wolf to Yellowstone. Coyotes, bobcat, and puma co-occur across much of the West. In Idaho, overlap in habitat and diet among these three species is minimal in summer but increases in winter due to heavy snow restricting prey and predators to lower elevations; at this time puma kill coyotes and bobcats in defending or usurping food caches. In the South we can predict that the highly opportunistic coyote will shift to smaller prey or to areas of higher human population density in the presence of puma. There is a recent documented case of a panther (puma) killing and eating a coyote in southwest Florida. Where other native large carnivores are absent, the coyote would per-form a valuable function by keeping mesopredators such as armadillos (*Dasypus novemcinctus*), opossums (*Didelphis virginiana*), raccoons (*Procyon lotor*), and feral cats (*Felis catus*)—as well as deer (*Odocoileus virginianus*) and hogs (*Sus scrofa*)—in check and enhancing populations of ground- and shrub-nesting birds, reptiles, and other native species. This role is well documented in the West, and there is every reason to suspect that coyotes play a similar role in the South.

A 2004 paper by Daniel Thornton and colleagues shows that coyotes and bobcats in south-central Florida are ecologically segregated and therefore not competing. Coyotes in this region (which currently has no resident panthers) prey primarily on large ungulates and include a substantial amount of fruit in their diet, whereas bobcats prey primarily on rodents and rabbits; the two species also segregate spatially at the scale of home range core areas. Research in South Carolina shows a similar diet for coyotes—primarily deer and fruit—although in a Tennessee study, rodents were the largest component. Some conservationists worry about coyote predation on gopher tortoises; however, coyotes probably do so less regularly than domestic dogs, and such predation pales before the impacts of roads and development on tortoise populations. Possibly, in the absence of red wolves, natural selection might drive coyotes to become more like their larger canid relative, thus filling an ecological niche that has been vacant for a long time. Red wolves and panthers apparently had no problem coexisting.

Concerns about coyotes attacking people are ridiculously overblown. My old buddy Marty Main of the University of Florida, who studies coyotes, panthers, and other carnivores, points to a University of California study, which identified eighty-nine reports of coyote attacks nationwide from 1988 through 2003, with most of those in California. This compares to 368,000 dog bites reported by emergency rooms in a single year; in 2007, thirty-three people died from dog attacks. The public should demand that their wildlife agencies tell the truth about coyotes and allow recovery of this native predator. Regardless of wildlife agency policies, control of coyotes is probably futile. This is a highly adaptable animal. Experience in the West shows that as control efforts cause coyote population densities to decline, coyotes compensate by producing larger litters. We cannot defeat the coyote.

The need for top-down control of some kind to reduce overabundant feral hogs, and often deer, in grasslands and other ecosystems is obvious. Hogs were introduced to the South in 1539 by Hernando de Soto, who had a large swarm of them accompany his exploration party to provide meat. The adaptable hogs went feral and proliferated across the South. Any hiker in Florida can see large patches of pine savanna, dry prairie, and the herbaceous layer of forests devastated by hog activity. Botanists Edwin Bridges and Steve Orzell observe in central Florida that "hog rooting has severely impacted the population sizes of native endemic orchids in less than a decade, and over time has the potential to alter community composition from perennial grasses with fine fuels that carry landscape-level fires to a patchy mix of annual and short-lived perennial herbs that alter fire behavior dramatically." Hog damage seems to increase year after year, as cash-strapped land-managing agencies either abandon efforts to control hogs by trapping, fencing, or shooting, or trap halfheartedly, failing to keep up with the prodigious reproductive capacity of these animals, which may produce two litters per year.

To be honest, I have no idea whether a fully restored native predator guild is capable of making a significant dent in the hog population in Florida or elsewhere in the South. Nevertheless, this is an experiment worth trying. Healthy populations of panthers, coyotes, bobcats, large alligators, native snakes, and raptors (i.e., large snakes, hawks, owls, and caracara take baby pigs) might together exert control. In landscapes where the native predator guild cannot be fully restored, we should increase trapping and shooting. We will probably never eradicate this opportunistic and fecund animal, but native predators, augmented by human-caused mortality, might maintain hog populations below levels where significant impacts on the ground cover, soils, and ground-dwelling animals occur.

The highest priority for carnivore conservation across the eastern United States is recovery of the puma (also known as cougar, mountain lion, and panther). This animal once occupied most of the continent, except extreme deserts and northern boreal and tundra regions. Today eastern puma (Florida panther) persist only in south Florida, where federal and state wildlife agencies refuse to follow the recovery plan, which calls for reintroduction into identified areas of suitable wildland habitat across the South (see chap. 6, fig. 6.2). Recovery depends on reintroductions, as the available habitat in south Florida is saturated (i.e., the panther population is at or near carrying capacity) and mortality rates (especially from intraspecific strife and roads) are high. Projected sea-level rise over the next century is predicted to reduce current panther habitat by approximately one-third. A further urgent threat is the proliferation of Burmese pythons (*Python molurus bivittatus*). Research in Everglades National Park by Michael Dorcas and colleagues determined that mammal populations are plummeting due to predation by pythons. From 2003 to 2011, for example, observations of raccoons decreased by 99.3 percent, opossums by 98.9 percent, and bobcats by 87.5 percent—a remarkable example of top-down regulation by an exotic apex predator. Not only do pythons likely compete with panthers for prey, but pythons may eat panthers; within their native range they are known to take leopards (*Panthera pardus*).

The panther is not a grassland species, but rather a habitat generalist. Early radio-telemetry research, especially by Dave Maehr, suggested that the panther used mostly forest, avoiding open areas. This was a reasonable conclusion, given available survey technology, because panthers are reclusive and seek dense cover by day. Before the advent of geographic positioning system (GPS) collars, radio-telemetry was conducted only during daylight hours. Now, with GPS telemetry and other research, we know that panthers make extensive use of nonforest habitat, especially at night. Panthers have been observed by biologists within the expansive dry prairie of south-central Florida, as well as in pine flatwoods—for example, I found tracks within flatwoods of the Joshua Creek tract (see chap. 1) near my home. This area has overabundant hogs, deer, and cows, and would benefit from panthers.

All panthers observed over the last several decades north of south Florida have been males, mostly young adults, wandering northward in a futile search for mates. One male traveled almost to Atlanta. No known females have yet dispersed out of south Florida because of human-created barriers (such as the channelized Caloosahatchee River, as well as major highways) that females are loath to cross. The panther near my home came to a sad end—its decapitated carcass was found along a road a few miles from where it had been residing in

the state forest for a few weeks. The murderer has not been identified. This is the real impediment to recovery of the puma: too many people, a substantial proportion of them ignorant and prejudiced against predators. Such attitudes must be overruled by the majority, who appreciate the panther—named by school children the state animal of Florida. Meanwhile, maintaining and restoring large wild areas and restricting vehicle access are proven methods for reducing human persecution of predators.

Other Keystone and Foundation Species

The keystone concept has been expanded to include any species whose impact on an ecosystem is large, disproportionately so, for its abundance. As I discuss later in this chapter, large herbivores can play a keystone role. Keystone species also include so-called ecosystem engineers—species such as beaver and gopher tortoises, which construct habitats used by many other species.

The gopher tortoise is one of the most ecologically pivotal organisms within its range, primarily in pine savannas and associated upland ecosystems from the southern tip of South Carolina to extreme eastern Louisiana and south through the Florida Peninsula. More than three hundred invertebrates and vertebrates are reportedly associated with gopher tortoise burrows. Mark Deyrup of Archbold Biological Station, however, provides a more nuanced interpretation. Deyrup notes that commonly cited numbers of gopher tortoise commensals (i.e., other species inhabiting gopher tortoise burrows) are inflated, since most of those species are not true commensals—some probably just fell into burrows accidentally and were found there by researchers. He suggests that, across the range of the tortoise, ten known species of arthropods are obligate commensals and another ten or so are regularly, but not exclusively, associated with burrows. And then there is the gopher tortoise shell moth (*Ceratophaga vicinella*), which lays its eggs on the shells of dead tortoises, where the larvae feed exclusively on the keratin plates. Disturbance of dead tortoise shells by humans, combined with the continuing decline of the tortoise, jeopardizes this highly specialized species. Many vertebrates, even if not obligate commensals of gopher tortoise burrows, may depend on them to support viable populations. The gopher frog (*Lithobates capito*) and eastern indigo snake, for example, do not exclusively use gopher tortoise burrows for shelter, but are seldom, if ever, abundant in the absence of tortoises and their burrows.

Other ecologically pivotal species in the South include the fox squirrel and the red-cockaded woodpecker, both closely associated with longleaf pine. The fox squirrel regularly eats fungi, including the fruiting bodies of the hypogeous (underground) mycorrhizal fungi that inhabit the roots of pines. In their

mutualistic relationship, the fungi help the pines gather nutrients from the soil and increase their growth rate; in return, the pines provide carbohydrates and a growth substrate for the fungi. On nutrient-poor sands, the pines may depend on their fungal partners. Peter Weigl and colleagues suggest that the wide-ranging fox squirrel, by dispersing fungal spores, is a key player in this interaction; without the squirrel, individual pines would not be inoculated with the fungus.

The red-cockaded woodpecker, which prefers longleaf pines when present, can be considered a keystone species because the birds create nesting cavities in an ecosystem that, due to frequent fire, has few snags (standing dead trees) that survive for long. Snags are where most woodpecker species excavate cavities, but the red-cockaded woodpecker is unique in building its cavities in old, living trees infected with redheart fungus (*Phellinis* [*Fomes*] *pini*), which softens the heartwood of the tree enough for the woodpeckers to do their job. These cavities, after being abandoned by the woodpeckers or usurped by other cavity nesters, provide homes to dozens of vertebrates and invertebrates. Continuing the longleaf pine example, flammable grasses (such as wiregrass) and longleaf pine (which drops highly flammable needles and converts lightning strikes to ground fires) are quintessential foundation species (i.e., abundant species that determine the physiognomy, character, and dominant ecological processes of the ecosystem), although I and others have incorrectly labeled them keystone species in the past.

Sideways Control

Bottom-up and top-down factors are discussed in the ecological literature within the theoretical context of food webs. A community is regulated by bottom-up factors if the productivity or diversity of plants (in turn determined by climate, soils, and other physical factors) is the primary control of diversity at higher trophic levels, whereas it is regulated by top-down factors if apex predators (or perhaps, large herbivores) keep lower-level consumers in check and thereby allow more species of plants and animals to coexist.

In grasslands and some other ecosystems, effects of disturbances such as fire, wind, flood, ice storms, and landslides may have a stronger effect on the community than bottom-up or top-down factors, as we usually think of them. Because disturbances are primarily physical (with important biotic exceptions such as large herbivores), some biologists consider disturbance a bottom-up process. In other ways, however, disturbance acts like a top-down control, for example by preventing competitive exclusion among species and promoting high species richness. William Bond and Jon Keeley suggest that the effects of fire are analogous to herbivory and that fire is different from other disturbances

in that it "feeds on complex organic molecules (as do herbivores) and converts them to organic and mineral products." They argue that "evidence for trophic cascades in terrestrial ecosystems is disputed," but that evidence for fire creating "cascading changes in species composition" is incontrovertible.

Fire has extraordinary properties; nevertheless, other disturbances have effects similar to fire in terms of opening up physical space for recruitment and thinning tree canopies. I argue that fire and other disturbances are different enough from either bottom-up or top-down controls to warrant a category of their own: *sideways control*. From the perspective of grassland taxa, sideways factors may be better thought of as ecological drivers than as disturbances, because the species that dominate or characterize the community (foundation species), among others, depend on these factors. In the remainder of this chapter, I concentrate on fire, large herbivores, and the interactions among various bottom-up, top-down, and sideways factors.

FIRE

Although nearly universally appreciated by ecologists today as a key ecological force, fire remains controversial within other professions and in broader society. Smokey Bear is alive and well. Consider the three quotations below, which illustrate the antiquity of fire, the acceptance of its importance by a leading ecologist in the early twentieth century, and yet continued propaganda campaigns against fire:

> Fossil charcoal indicates that wildfires began soon after the appearance of terrestrial plants in the Silurian [420 million years ago (Ma)]. Combustion occurs when atmospheric O_2 concentrations are above 13% and variation in O_2 levels correlates with fire activity throughout Earth history. (Bowman et al. 2009)

> In Florida, it is evident that fire is a part of Nature's program. (Harper 1914)

> Don't let wildfires burn Florida. (Smokey Bear, standing in a fire-ravaged forest; billboard on I-95, upon entering Florida from Georgia)

The article that brought home to me the importance of fire in the Coastal Plain is a 1911 paper in the *Bulletin of the Torrey Botanical Club* by the perspicacious Roland M. Harper. Entitled "The Relation of Climax Vegetation to Islands and Peninsulas," Harper begins with an account of his explorations of

the Lake Tsala Apopka area in Citrus County, Florida. He was struck by the difference in vegetation between the landscape surrounding the lake, which was "high pine land" consisting of open longleaf pine savannas, and the vegetation found on islands and peninsulas of this convoluted lake, which was dense hardwood forest (hammock), considered the climax vegetation of the region. Harper observed that the only difference in the soils between the high pine community and the hammock was due to the vegetation itself, that is, a thin layer of humus over the sandy soil of the hammocks. Harper observed similar contrasts in vegetation around other lakes and on islands and river peninsulas in Florida and elsewhere in the Coastal Plain. After considering and rejecting a number of alternative hypotheses to explain this phenomenon, Harper concluded: "For the Florida hammock peninsulas, if not for all the other cases referred to, the key to the situation can be expressed in a single word: FIRE." Harper explained how lightning fires spread across the landscape for many square miles and maintain high pine vegetation. Where the spread of fire is interrupted by water bodies, however, as on islands and peninsulas, fire-sensitive hammock vegetation is able to develop.

Harper noted that most fires by the time of his writing were set by humans, but that "the increase in number of fires due to this cause has been partly counterbalanced by the numerous highways, clearings, etc., which serve as barriers to fire." This is the earliest recognition I've found of passive fire exclusion, which is a major cause of the loss of fire-dependent vegetation. In 2004 Brean Duncan and Paul Schmalzer of the Kennedy Space Center determined from historical and current aerial photos, supplemented by modeling, that only 10 percent anthropogenic landcover (especially in the form of linear barriers such as roads) causes a 50 percent reduction in fire extent in east-central Florida. And those linear barriers keep increasing!

Harper's writings are full of respectful references to the role of lightning-set fires in the ecology of the Coastal Plain. In some articles he points out the inadequacy of the ecological concepts of "climax" and "succession" (putting both words in quotes) for this fire-prone region. It is interesting to compare Harper's attitude toward fire with that of his contemporary, the esteemed botanist John Kunkel Small. I do not mean to detract from Small's enormous contributions—for example, his dissertation, published as *Flora of the Southeastern United States* in 1903 and revised in 1913 and 1933, remains an extraordinary reference, and he contributed substantially to conservation—but he showed little appreciation of fire. In many of his writings he refers to the devastation caused by fire, putting fire into the same category as drainage and land clearing for agriculture. He concludes a 1927 paper like this:

Furthermore, we had witnessed the wanton destruction of the gigantic humus-deposit of the Okeechobee basin—perhaps the largest in North America—and its unique hammock formation primarily by FIRE! The destruction of these works of ages in less than a decade is one of the several major crimes of the Commonwealth.… DRAINAGE and FIRE are fast turning the Florida peninsula back to the desert it was when last elevated above the sea!

To be fair, Small was writing about primarily human-set fires (at least that was his assumption), combined with other human actions such as drainage of large wetland complexes. But Harper, in contrast, saw human-caused fires as generally beneficial, because they help offset the passive fire exclusion caused by roads, clearings, and other anthropogenic firebreaks. Nowhere in Small's writings do we find an understanding of the ecological role of fire, which is so evident in Harper's papers. Long-held biases against fire, as still seen in messages from Smokey Bear and other forest industry and agency propaganda, are hard to erase.

Perhaps the most significant point regarding the effects of fire in a relatively wet region such as the southeastern United States is that it can determine whether or not an area is covered by forest or grassland. Over large areas of the earth, forest and grassland are alternative stable states. Two papers in 2011 by Carla Staver and colleagues demonstrate this phenomenon. In one paper (in *Ecology*), which focuses on Africa, the authors develop an empirical model and conclude that "given relatively conservative and empirically supported assumptions about the establishment of trees in savannas, alternative stable states for the same set of environmental conditions…are possible via a fire feedback mechanism." Their shorter paper in *Science* considers fire-tree cover feedbacks in Africa, Australia, and South America. In regions of intermediate rainfall (100–250 cm, or 39–98 inches) and mild seasonality (dry season shorter than seven months), tree cover is bimodal, with fire alone determining whether a given area is forest or savanna. The authors note that savannas occurring today in areas wet enough to support forest were probably formed during periods of drier or highly seasonal climate (e.g., Late Miocene) and that the fire-savanna relationship is a positive feedback loop (i.e., fig. 5.1). This paper provides an excellent demonstration of the role of a sideways factor—fire—in maintaining grassland in regions that "should be" forest according to climate. I remain puzzled as to why many ecologists fail to recognize that the Coastal Plain (and neotropical pine savannas from Belize to Nicaragua) meet the climatic criteria of intermediate rainfall and mild seasonality, and also were maintained in a savanna state by fire. When fire is excluded, most pine savannas quickly convert to forest.

Many reasons exist for appreciating fire in ecosystems. For instance, as noted in chapter 3, some plant species rarely germinate or flower except after fire, in some cases only after fire within the characteristic lightning fire season (albeit a few species apparently escape competition by blooming earlier). Some plants are stimulated to germinate by smoke. Animals associated with fire-dependent communities often do not breed or survive in the absence of fire. As a direct result of active or passive fire exclusion, many southern grasslands and their characteristic species have declined since EuroAmerican settlement and landscapes have become more homogeneous. Prescribed burning, intelligently conducted, can help restore many of these ecosystems.

I address several questions regarding fire in southern grasslands:

1. What are the ecological effects of fire?

2. What are some plausible adaptations of plants and animals to fire?

3. What are the relative roles of lightning ignitions and human ignitions in the maintenance of southern grasslands?

4. What are some lessons for improved management of fire and fire-dependent ecosystems in the South?

Ecological Effects of Fire

Scientific understanding of the role of fire has matured considerably over the past century, moving away from the view of fire as a negative disturbance to one where fire is a fundamental architect of species-rich ecosystems. Common working hypotheses among fire ecologists today are that fire (1) reduces competition for key resources; (2) promotes regeneration of many plants; (3) maintains populations of fire-tolerant species and the communities they compose; (4) inhibits invasion of species intolerant of fire; (5) recycles nutrients and affects water and sediment delivery throughout watersheds; and (6) creates and maintains, at one spatial scale or another, a shifting mosaic of habitat structure and postfire recovery stages. The fundamental working hypothesis is that certain plant communities and even entire landscapes are fire-dependent in the sense that they depend on fire to maintain their characteristic species composition, vegetation structure, spatial pattern, and ecological processes. As Bond and coauthors observed in 2005, "Biomes of large parts of the world are far from their climate potential supporting flammable formations such as grasslands and savannas. We label these fire-dependent ecosystems." A corollary is that, if fire

is excluded or its behavior substantially changed in these ecosystems, distinct elements of biodiversity will decline or disappear.

As explained in chapter 4, some southern grasslands rarely, if ever, burn, and their existence can be explained by rocks, soils, erosion, flooding, or other factors. Others are controlled mainly by edaphic, hydrologic, or other physical factors, but require help from fire or herbivores to inhibit tree invasion. Nevertheless, both in the South and worldwide, a close relationship exists between extensive grasslands and fire. The positive feedback loop between grassland and fire (fig. 5.1) is strong.

We can look in more detail at the effects of fire and fire exclusion in particular ecosystems. Fire ecologist Ron Myers developed a state-and-transition model (fig. 5.2) of vegetation change in relation to fire on xeric upland sites in central Florida. A state is an alternative, persistent vegetation type, whereas transitions are trajectories between states. Transitions may be transient or persistent, and are often triggered by disturbances—or lack thereof. In uplands of central Florida, depending on fire frequency and seed sources, several differ-
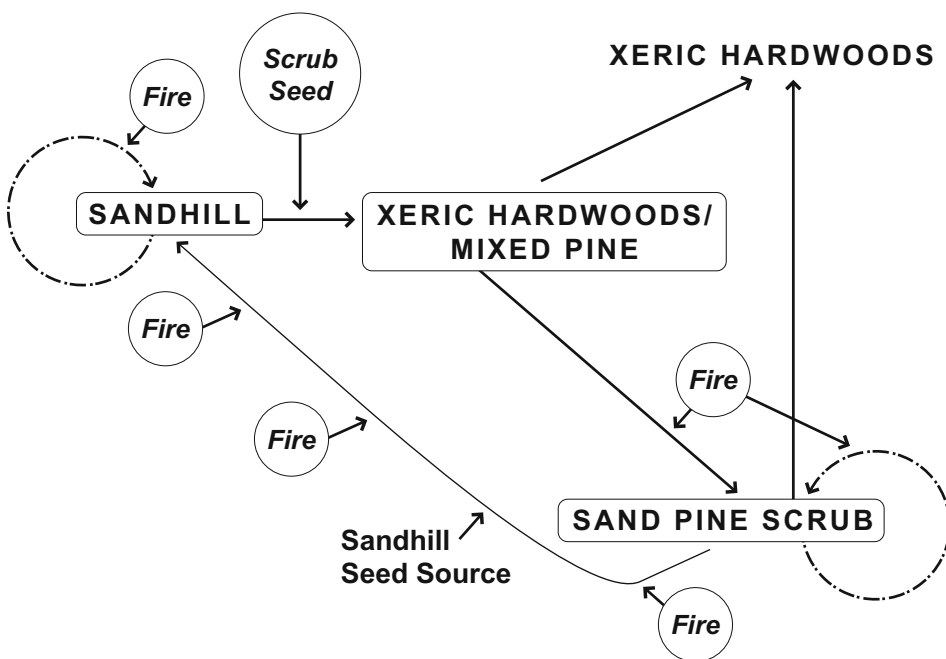
Figure 5.2. Model of vegetation development, maintenance, and change on xeric upland sites in central Florida. Depending on fire frequency and seed sources, sandhill (high pine), xeric hardwoods/mixed pine, and sand pine scrub are alternative stable states on the same soils. In the long absence of fire, a xeric hardwoods community develops, which is also a self-perpetuating stable state. Adapted from Stout and Marion (1993) after Myers (1985).

ent quasi-stable plant communities may develop on the same soils. Longleaf pine sandhill is the dominant vegetation on frequently burned sites and is self-maintaining under these conditions. With reduced fire frequency and increased input of seeds from scrub plants, a xeric hardwoods/mixed pine community may develop—or alternately (not shown in fig. 5.2) species composition may not change much, but ground cover declines with increasing canopy cover. In the long absence of fire, this community may transform to a xeric hardwoods community, called xeric hammock and commonly dominated by sand live oak (*Quercus geminata*), which seldom burns and is self-perpetuating due to non-flammable fallen leaves and little fine fuel. With fire, a xeric hardwoods/mixed pine community may change to sand pine scrub, which if burned regularly, may persist as rosemary scrub or oak scrub with little sand pine (not shown). With increasing frequency of fire, and input of seeds from sandhill plants, scrub may convert back to sandhill, although this probably happens rarely.

Transition probabilities between alternative stable states vary widely, and nonlinear dynamics and abrupt thresholds between states are common. An important concept in this respect is *resilience*, which in the modern literature usually refers to the ability of a system to absorb disturbance and to change gradually while retaining the same basic composition, structure, and function (including feedbacks). For example, in figure 5.2, sandhill is a highly resilient community, so long as fire occurs frequently. Xeric hardwoods/mixed pine is an alternative stable state, under conditions of reduced fire, which may transition to one of two alternative stable states: xeric hammock (without fire) or scrub (with fire). Transitioning from scrub back to sandhill is more energetically demanding. The probability of a xeric hammock shifting back to xeric hardwoods/mixed pine, and from there to sandhill, is presumably very low (see fig. 5.2). Such asymmetries in transition probabilities illustrate another concept, *hysteresis*, where a shift in stable state occurs faster and easier in one direction than in the other. Management may change transition probabilities. Experimental gap creation (canopy openings), grass seeding, and prescribed fire in a xeric hammock, for instance, might eventually push the system past a threshold, beyond which recovery of a xeric hardwoods/mixed pine community occurs rapidly. From there, continued frequent fire might return the system to sandhill.

State-and-transition models for vegetation change with and without fire, seed sources, and other ecological drivers should be developed for other grassland communities. Especially when made quantitative, for example with empirically determined transition probabilities, these models can be extremely helpful for informing management decisions.

Adaptations to Fire

The question of whether particular plant or animal traits evolved as adaptations to fire has been controversial. Consider these quotations:

Plants, animals, and possibly life itself, have evolved through a long process of natural selection in an environment where lightning and fires so initiated have been an important factor, more important than many ecologists may realize. (Komarek 1964)

Fire-dependent plant communities burn more readily than non-fire-dependent communities because natural selection has favored development of characteristics that make them more flammable. (Mutch 1970)

There are few studies of the evolution of fire-adaptive traits, and many plant traits have been uncritically labeled as 'fire adaptations' without any rigorous analysis either as to the functional importance of the trait, or its phylogenetic origin. (Bond and Keeley 2005)

Concerning Bond and Keeley's point, postfire sprouting in plants has been described as a fire adaptation, but this trait could have evolved in response to browsing by large herbivores. The hypothesis that plant species have been naturally selected for flammability also has proven difficult to test. A controversy began with the paper by Robert Mutch in 1970, which proposed that certain plants evolved traits to promote as well as to tolerate fire, thus gaining a competitive advantage over fire-sensitive plants in areas with high ignition rates. Because Mutch presented his hypothesis at the species and community level—a trait spread because populations and communities benefited from it—he was widely criticized for advocating group selection and for ignoring the possibility that differences in flammability could have arisen in response to other selective pressures. As alternatives to fire, herbivory, drought tolerance, and nutrient retention have been suggested as selective pressures that produced plant tissues that turned out to be flammable.

Healthy debate regarding the evolution of adaptations should be encouraged. Nevertheless, it seems likely that an ecological force as ancient and as powerful as fire would provide strong selection for adaptations that enable a plant or animal to alternately avoid, tolerate, or exploit fire. Moreover, several authors have proposed individual-level selection arguments based on niche construction (i.e., creating a favorable environment for yourself and

your offspring) for the evolution of flammability. In frequent-fire ecosystems, there is no need to invoke sacrifice of individuals to benefit the population by promoting fire through flammability, because there is no genetic sacrifice involved. As Bill Platt and coauthors pointed out in their seminal article on longleaf pine demography in 1988, pine trees convert lightning strikes to ground fires, during which very few adult trees are killed. The adults are resistant to low-severity fire because they have relatively thick bark. Given a natural regime of frequent fire, not enough pine straw, grass thatch, small dead branches, or other fine fuels accumulate to produce fires that are hot enough to kill adult trees. Trees in the extended seedling ("grass") stage also survive, as do subadults that have bolted past the vulnerable stage of about three to four feet in height or survive within small unburned patches that are characteristic of heterogeneous natural fires.

In pine savannas, both the fallen pine needles and the dominant grasses are highly flammable, facilitating the ignition and spread of fire. Paul Gagnon and coauthors suggested in 2010 that pyrogenicity (i.e., a step beyond flammability, in that frequent fire is promoted) can be favored by natural selection if individual plants burn rapidly and keep fire off the ground, hence protecting belowground organs and nearby propagules (i.e., their offspring). Self-immolators need not be altruistic—they are protecting themselves and their kin.

Pines have been particularly well studied in relation to fire. Two general categories of pines, with respect to life-history evolution in fire-prone ecosystems, are frequent-fire species and infrequent-fire species (table 5.1). Pines associated with grasslands (i.e., woodlands and savannas) are frequent-fire taxa and have adaptations that allow them to survive in such an environment. Nevertheless, longleaf pine, the species showing the ultimate adaptations to high-frequency, low-severity fire in North America and usually associated with open-canopy savannas, is found in denser stands with greater hardwood cover under certain conditions. As described by J. Morgan Varner and coauthors, the montane longleaf pine communities of northeastern Alabama and adjacent Georgia feature longleaf pine, blackjack oak, and sand hickory (*Carya pallida*) as codominants in the canopy layer—yet these "forests" still have one- to five-year fire–return intervals. In Florida, where longleaf pine typically is found in savannas with relatively few tree-sized hardwoods, it also occurs in denser "upland mixed woodland," sharing dominance with several species of oaks and hickories. As reviewed by Bill Platt and Mark Schwartz, fire intervals in these communities may be ten to twenty years.

Perhaps the most remarkable adaptation of some pines to fire—and difficult to interpret in any other way—is delayed seedling development, that

Table 5.1. Traits of pine species commonly interpreted as adaptations to fire.

Frequent–Fire Species	Infrequent–Fire Species
Mostly long-needled (e.g., longleaf pine, slash pine) and needles are highly flammable	Mostly short-needled (e.g., sand pine, Virginia pine); needles may be flammable
Thick bark (protects cambium from fire) Most adults survive fire	Thin bark High adult mortality with fire
No serotiny, little dead branch retention	Serotiny is common (cones open when exposed to high heat)—correlated with dead branch retention, which enhances flammability
Germination in bare mineral soil exposed by fire	Germination often in bare mineral soil
Extended seedling stage ("grass stage") and delayed height growth, 5–20 years in some taxa, with protected apical meristems	No extended seedling stage or delayed height growth
Seedlings and adults have low vulnerability to fire, with rapid growth through fire-vulnerable sapling stage	All stages are fire vulnerable
No basal resprouting	Basal resprouting after fire in some species
Reproduction after stand-maintenance fire varies annually, not stimulated by fire (i.e., "mast years" are years of high seed production) and is patchy, resulting in uneven-aged stands	Mass reproduction after stand replacement fire, creating generally even-aged stands
Relatively long lived (> 300 years)	Relatively short lived (< 200 years)
Generally open-canopied stands with dense herbaceous vegetation ("grasslands")	Dense stands with little herbaceous vegetation or other understory except after fire
Often self-pruning of lower dead branches (removes fuel ladders to inhibit canopy fire spread) as well as "thermal pruning" (removal of lower branches by fire)	Self-pruning uncommon (i.e., dead branches are retained)
Relatively low dispersal capacity?	Relatively high dispersal capacity?

Note: Two life-history strategies, illustrated by species associated with frequent fire vs. species associated with infrequent fire, are ends of a continuum. Some pine species show mixtures of traits and can occur under both open-canopy and closed-canopy conditions.

is, the grass stage. The stemless grass stage looks like a bright green clump of bunchgrass on the ground. It is highly resistant to fire and has been reported for several species of pines worldwide. It occurs in three subsections of the subgenus *Pinus*, suggesting that this adaptation evolved independently more than once. In the South the grass stage occurs in longleaf pine and south Florida slash pine. Longleaf pine is the best-studied pine with respect to the grass stage. Individuals of most tree species begin height growth quickly from the seedling stage, given sufficient light. In contrast, longleaf pine seedlings remain in the fire-resistant grass stage for two to fifteen years, sometimes longer, during which time they develop taproots up to 5 meters (16.4 feet)

deep, with root growth as rapid as 50 centimeters (20 inches) within fifteen days after germination. When the root collar diameter reaches about 1 inch, longleaf pine juveniles undergo rapid height growth (the "bolting stage"), reaching 1–3 feet in height within a single season under favorable conditions and becoming safe from the effects of low- to moderate-intensity fire when they are above the flame zone of about 1 meter (3.3 feet). Although mortality is high below this height, especially in the vicinity of adult trees with abundant fallen needles, enough seedlings survive under a frequent fire regime to perpetuate individual genetic lineages. The large gaps and relatively low recruitment of longleaf pine in frequently burned savannas likely reflect intense competition among roots for nutrients more than any direct negative effect of fire.

People not familiar with fire-prone southern grasslands are impressed to see how quickly these ecosystems recover biomass after a fire during the growing season—or during the late spring "transition season" between dry and wet, which is when most lightning-ignited fires occur in the Coastal Plain. Depending on site conditions and weather, regrowth begins almost immediately, and within two to three weeks the site is flush with new green grasses and forbs. Rapid recovery after fire is not limited to plants. My colleagues have seen Florida grasshopper sparrows, arguably the most fire-dependent vertebrate in North America, fly right over the head of an advancing fire to forage in the newly burned ground. Some of these fire-loving birds shift their territories, even within a breeding season, into freshly burned areas. Growing-season fire undoubtedly kills some young on nests, but the birds are adapted to this disturbance; after a fire, they renest quickly. On a landscape scale, a mosaic of patches burned from less than one to two or three years before nesting may be critical to persistence.

The red-cockaded woodpecker also depends on frequent fire. Research by Fran James of Florida State University demonstrates that the more frequent the fire, the higher the quality of the groundcover and the more positive the population response of the woodpeckers. The reason for this strong fire dependency is becoming clear, and it is a fascinating natural history story. It turns out the woodpecker preys mostly on arboreal ants living in mature pine trees. The primary prey species is the acrobat ant (*Crematogaster ashmeadi*), whose life history has been described by James' colleague at Florida State, Walter Tschinkel. Colonies of these ants live in chambers in the outer bark of living trees that were developed and abandoned by bark-mining moth larvae. How is fire important to this multispecies relationship? Fran's tentative explanation is "the calcium hypothesis." Calcium limitation can be a problem for birds. A large clutch of

eggs contains more calcium than the entire mother bird's body. Without fire, much of the calcium in pine flatwoods becomes locked up in shrubs such as gallberry (*Ilex glabra*), which become denser with time since fire. Burning releases calcium, and exchangeable calcium increases in the soil after fire in high-wiregrass sites, from where it moves through the food web. Calcium released by fire shows up in arboreal ants within eighteen months; this was shown through studies tracking radioactive strontium, which moves through an ecosystem similarly to calcium. The woodpeckers then get the calcium they need from the ants.

The relationship of insects in grasslands to fire is paradoxical. Fires kill insects, many of which are not mobile enough to escape the flames and heat. Yet, many insects are specialists on fire-maintained grassland communities. Moths are among the diverse insect groups in these systems. I know lepidopterists who adamantly oppose the use of fire for grassland management because butterflies and moths are killed; they argue that grasslands should be mowed or grazed instead. But that is not how most of these ecosystems developed. As reported in Lawrence Earley's *Looking for Longleaf*, Steve Hall of the North Carolina Natural Heritage Program has not only documented moth and grasshopper species endemic to longleaf pine communities, he has discovered "fire followers," which actively colonize recently burned areas—just like the Florida grasshopper sparrow (which, by the way, feeds mostly on grasshoppers, which are also diverse in grasslands). Insects associated with fire-prone habitats cope with fire in a variety of ways: escaping (if they can), finding refugia in wet ecotonal areas that do not burn as hot, or burrowing into the ground. Still, many individuals and populations perish from burned sites and must recolonize these sites from unburned areas.

A way to maintain diversity of insects and other fire-sensitive organisms in fire-dependent grasslands is to promote heterogeneity on a relatively fine scale, where patches of unburned groundcover and shrubs can serve as fire refugia. Heterogeneity in fine fuel loads (a consequence of patchy fires) in longleaf pine savannas produces heterogeneity in the severity of subsequent fires. This patchiness promotes coexistence, shared dominance, and high species richness of plants. Natural fires tend to create heterogeneous mosaics of vegetation, whereas managed fires are usually (but do not have to be) more homogeneous. As noted in a 2009 US Forest Service report by Jon Keeley and coauthors, "Prescription burns may not mimic lightning-ignited patterns in that they are often designed to produce homogeneous burning patterns that may not reflect the historical range of ignition patterns and heterogeneity of unburned and high-severity patches."

Lightning versus Humans in the Maintenance of Fire-Dependent Ecosystems

Were the extensive grasslands described by the early European visitors to the South a product of frequent lightning fires that predate and are largely independent of human activity, or were they an artifact of deliberate burning and other activities of the Native Americans? I addressed this question briefly in chapter 2, but make some additional points here. The lightning versus human question is controversial and disciplinary, with most anthropologists, geographers, and historians lining up on the human agency side of the fence and most ecologists, other biologists, and naturalists on the natural processes side. Again, some quotations from the literature illustrate the divergence of views on this question:

> By 1492 Indian activity throughout the Americas had modified forest extent and composition, created and expanded grasslands.… Agricultural clearing and burning had converted much of the forest into successional (fallow) growth and into semi-permanent grassy openings (meadows, barrens, plains, glades, savannas, prairies), often of considerable size. Much of the mature forest was characterized by an open, herbaceous understory, reflecting frequent ground fires. (Denevan 1992)

> Although anthropogenic fires have undoubtedly extended areas of flammable vegetation, there is now abundant evidence that natural fires occurred long before humans … and that flammable ecosystems predate anthropogenic burning by millions of years. (Bond et al. 2005)

> The very high frequencies of growing season fires recorded in annual rings of these [longleaf and slash pine] trees indicate that fire regimes were primarily driven by synoptic climatic conditions rather than by cultural burning practices. (Huffman 2006)

> As important as lightning fire was to the coastal plain … anthropogenic fire did even more to maintain the longleaf pine-grassland forest. (Way 2008)

The relative importance of human versus lightning ignitions can be expected to vary over time and space depending on the prevailing climate (especially the lightning regime), human population size, and human cultural patterns and behaviors. Some grasslands, such as the Big Barrens of Kentucky, are of relatively

recent origin; they were apparently expanded and maintained by fires set by Indians. Many other southern grasslands are far older than human colonization of the New World, though like all ecosystems they have changed over time. Some of the ancient grasslands are primarily edaphic, whereas others (especially in the Coastal Plain) are dependent on lightning fires, and many were shaped and maintained by both factors, as well as by large herbivores in the past.

True wildfire is set by a natural ignition source, which in the South is almost always a lightning bolt. Wildfire is a venerable 420-million-year tradition, an earth process that will continue long after humans are gone. Yet, some people deny this tradition and ardently believe that humans are responsible for the creation of virtually all fire-dependent ecosystems. For example, anthropologist Kat Anderson, writing in the book *California Grasslands*, claims that "most if not all of the great grasslands of the world, from the Serengeti Plains to the prairie bioregion of the contiguous United States, were maintained with fires set by native peoples." As noted earlier, Charles Mann, in *1491*, portrays the Florida Peninsula, much of the Gulf Coast, east Texas, and most of the Mississippi River watershed as a "humanized landscape…dominated by anthropogenic fire." No evidence is provided by Anderson, Mann, or Albert Way in the quotation above to support such statements. This is in stark contrast to the abundant evidence offered, for example, by Jean Huffman (cited earlier) in her detailed dendrochronological (tree history) study of fire scars on longleaf pine stumps and dead slash pines in the Coastal Plain.

Those who have convinced themselves that humans created virtually all grasslands would do well to reconsider their position in light of climatological and paleoecological evidence. Plates 3 and 4 illustrate average thunderstorm days and lightning flash frequency, respectively, for the contiguous 48 states. Notice the lower Coastal Plain, in particular—this is more than enough lightning activity to explain dominance of the region by fire-dependent ecosystems. Paleoecological research shows that grasslands in North America, including the South, have been present for millions of years, and as discussed earlier, many grassland taxa have evolved adaptations to tolerate or exploit fire. Traveling away from the Coastal Plain, inland and northward, the time between fires increases steadily (fig. 5.3), reflecting the reduction in lightning activity along this gradient (albeit the wet Mississippi Alluvial Valley has long fire-return intervals even close to the coast). Generally speaking, in regions with less lightning activity, Indians played a larger role in maintaining grasslands through their use of fire.

David Bowman and coauthors, in 2009, published a review of "fire in the earth system." An excerpt from their article summarizes the history of humans and fire globally:
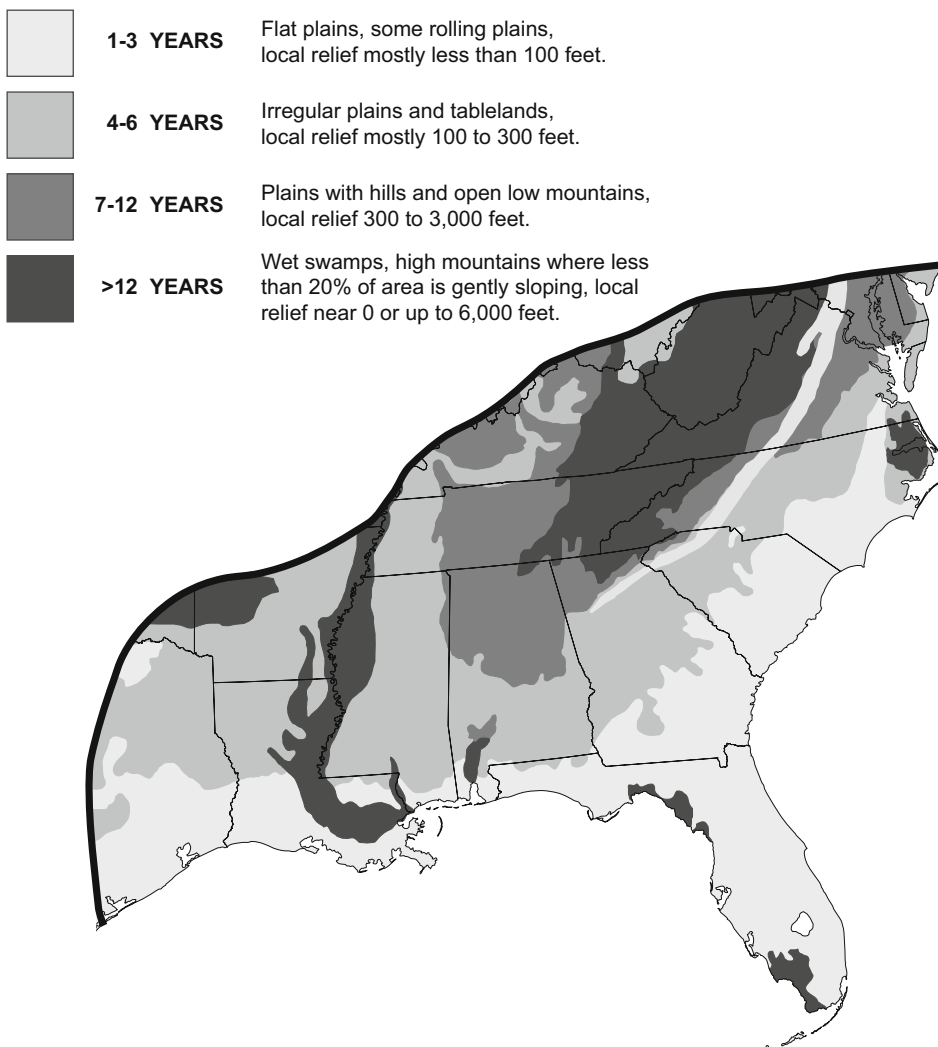
Figure 5.3. Presettlement fire frequencies for the most fire-exposed portions of the landscapes of the southeastern United States. Adapted from Frost (1995, 1998) and Frost (pers. comm.).

The [climatically determined] spread of highly flammable savannas, where humans originated, likely contributed to their eventual mastery of fire. The hominid fossil record suggests that cooked food may have appeared as early as 1.9 Ma [millions of years ago], although reliable evidence for controlled fire use does not appear in the archaeological record until after 400,000 years ago.... The routine domestic use of fire began around 50,000 to 100,000 years ago ... and hunter–gatherers used fire to reduce fuels and manage wildlife and plants beginning tens of thousands of years ago.

Hence, global history shows that savannas and other fire-dependent eco-systems arose long before humans began using fire for various purposes, but the human-fire relationship is nevertheless quite old. In the New World, where humans have been present for up to 15,000 years (albeit the arrival date is still uncertain and much debated), use of fire is much more recent.

In cases where Native Americans or later white settlers did regularly use fire to manage vegetation, it is worth considering how the anthropogenic fire regime differs from the fire regime in the absence of humans. Ed Komarek of Tall Timbers Research Station was one of the first to document such differences, pointing out in 1964 that "man-caused fires occur largely in the winter months whereas the lightning-ignited fires are nearly all summer fires." Komarek's data (fig. 5.4) show that lightning fires peak in May and June, which in most of Florida constitutes the transition period from the dry dormant season to the wet growing season, whereas thunderstorms are most frequent in July and August. This discrepancy reflects the readiness of the vegetation to burn. Lightning during the transition season strikes relatively dry vegetation (in fact, some thunderstorms are rain free), igniting fire more easily than later in the summer. In northern portions of my study area, especially a belt extending from Arkansas to the Ohio Valley, lightning fires are most common in August,
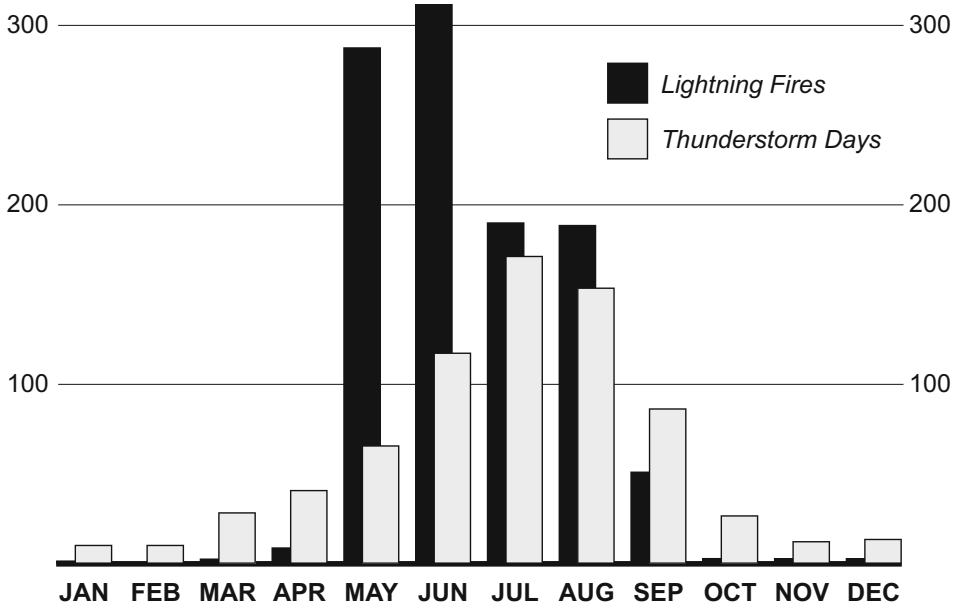
Figure 5.4. The natural fire season based on thunderstorms and lightning in Florida. Note that fire incidence peaks before thunderstorm activity, because the drier conditions in May and June increase the probability of ignitions. Adapted from Komarek (1964).

when occasional thunderstorms interrupt the summer drought. In contrast, fires set by Indians and white settlers occurred primarily in the late fall and winter across the South. As noted earlier, many plants respond to season of burn, with quite a few species flowering only or most profusely after growing- or transition-season fire. Such fires also are more effective in controlling woody plant encroachment and shrub densities and heights.

Fire Management

There is a bumper sticker that rubs me the wrong way: "PRESCRIBED FIRE, NOT WILDFIRE." A slightly more palatable version is "More Prescribed Fire Means Less Wildfire." I have seen these and similar bumper stickers in several states; they have been produced and promulgated mostly by forestry agencies and organizations. Such messages are misleading because they suggest that fires set deliberately by managers are good, whereas fires set by lightning or other uncontrolled sources are bad. The philosophical implication of such messages is that people can manage the land better than nature can. This message, though well meaning from a narrow human-safety point of view, is dangerous. It inspires misunderstanding and fear of a natural ecological process. Instead, let's teach people about the ecological benefits of fire and the problems that arise when wildfires are excluded or suppressed. Instead of damning wildfires, let's explain why lightning-ignited fires should be left to burn wherever possible and why the best prescribed fires—in terms of their ecological effects—are those carefully designed and managed to mimic wildfire in terms of seasonality, frequency, intensity, heterogeneity, and other attributes.

Many foresters and land managers use the term *wildfire* indiscriminately to refer both to fires started by lightning and those ignited by humans (other than land managers), including both arson and accidental ignitions. The latter can occur from unattended campfires, discarded cigarettes, or hot catalytic converters igniting vegetation on grassy roads. To improve clarity in discussions about fire, I suggest we reserve the term *wildfire* for truly wild, lightning-ignited fires. Arson and accidental fires are in an entirely different category, as they often occur outside the natural fire season and in places that might not otherwise burn; they are also more likely to pose safety risks to people and property than true wildfires. That said, in the South I see few wildfires by any definition that do more harm than good. I have visited many sites that the press described as "devastated" by fire, only to find them nicely thinned out, with abundant regeneration of grasses, forbs, palmettos, pines, oaks, and other vegetation all around. Not long after I drove by the Smokey Bear billboard quoted earlier, I viewed from the highway an area where wildfire, according to the newspapers

and television, had "destroyed" the forest just two months previously. It looked great! The vegetation was in much better shape than the adjacent, dense fire-excluded pine flatwoods and tree farms.

Please don't get me wrong. I am an adamant proponent of *prescribed fire* (which, however, is jargon virtually meaningless to the public). Prescribed burning is legitimately applied as a substitute for wildfire in cases where (1) habitat patches are too small and isolated to experience lightning strikes often enough by chance, or to intercept fire spreading across the landscape; (2) habitat patches are surrounded by urban development or highways, where uncontrolled fire poses a significant risk to public safety; or (3) where, due to past fire exclusion by humans, a period of cool, restorative burns and sometimes hand raking of fine fuels and mechanical treatments are needed to reduce fuel loads to the point where wildfires can occur without causing uncharacteristically high rates of tree mortality or other problems. Paul Gagnon and coauthors, in a 2010 paper, offer good advice: "We propose that where restoration and conservation of fire-prone ecosystems is a goal, land managers should strive not only to burn, but to do so in ways that are consistent with historical, climate-driven fire regimes."

Fire management, including improperly conducted prescribed burning, can have negative impacts on natural communities. One practice with impacts that are rarely acknowledged by managers is the construction of fire lines (also known as firebreaks). Fire lines are taken for granted as a necessary way to compartmentalize fires and prevent fire spread into areas not intended for burning. The ecological impacts of fire lines have been poorly studied—a literature search turns up nothing substantial—but naturalists and managers who pay attention have amassed abundant anecdotal observations of their effects. I have observed a rapid increase in the width and density of fire lines in managed areas across the South, especially in Florida, which suggests an urgent need to study their impacts and, in the meantime, reduce their use until impacts are fully understood.

A nonscientific but nontrivial objection to fire lines is that they are incredibly ugly. They are often plowed directly on trails (fig. 5.5), where they make walking a miserable experience and alienate visitors from nature—this is not a good approach to public education. Among the observed and hypothesized ecological impacts of fire lines are (1) they fragment habitat and populations by creating movement barriers to small animals that avoid openings (e.g., the road ecology literature shows that some small vertebrates and invertebrates refuse to cross even unpaved dirt roads); (2) they disrupt hydrology, for example, by interrupting or diverting sheet flow of water; (3) they facilitate the spread of

Figure 5.5. A typical fire line (plowed firebreak) constructed on a hiking trail at Savage/Christmas Creek Preserve, Orange County, Florida. Fire lines are proliferating out of control in the South and pose a number of ecological threats.

exotic species, including nonnative plants (e.g., the strongly invasive cogon grass*, Imperata cylindrica*) and the red imported fire ant, which thrive on disturbed soil; and (4) they are often placed in ecotones, such as along seepage slopes and pocosin edges, where they do the most damage. Natural ecotones are local hotspots of species richness and provide habitat for many imperiled taxa. For example, in the Green Swamp of North Carolina, the federally endangered pocosin loosestrife (*Lysimachia asperulifolia*) is most abundant in ecotones between pocosin and savanna. It is threatened in part by fire lines plowed along these ecotones. Drastically reducing the use of fire lines is one of the foremost things we can do to improve fire management. Most managed areas should only require fire lines around their outer perimeters, to protect neighbors who may not appreciate the natural flow of fire across the landscape.

Burning during inappropriate seasons also can have deleterious impacts on fire-dependent ecosystems. After a couple of decades of positive direction within agencies, when many managers shifted from dormant-season to growing-season burning, the trend now in Florida (with a few commendable exceptions) is back toward prescribed burning between late summer and early spring, a time

period when few fires occur naturally. Edwin Bridges and Steve Orzell, two premier field botanists and ecologists of the South, recently wrote (personal communication), "In our experience there has been a dramatic decline in the extent of intact ('less altered') pine savannas in just the last decade or so, and we would predict that the total area of natural vegetation in northern and central peninsular Florida that has relatively intact ecosystem processes is less than 50% of what it was in 1990." This decline in savanna quality can be traced directly to mismanagement of fire, often incorrect seasonality. Pointing out that late wet-season burns are as inadvisable as winter burns, Bridges and Orzell go on to say:

> Fires at inappropriate times, when they are often detrimental to native plant biodiversity, are now the common practice.… There has been an inexplicable movement towards burning late in the wet season or early in the dry season in central Florida (mostly between July and November), at a time when large landscape-level fires did not naturally occur. Late wet season burns fail to adequately consume shrubs due to low fire intensity and the re-growth of native grasses and forbs can be retarded by post-fire flooding.… Fires in this period can also result in nearly complete consumption by fire of the reproductive output of the dominant summer to fall flowering grasses and forbs. Additionally, these species are forced to begin post-fire re-generation as the dry season begins, and wait perhaps six months before reliable rainfall returns in late May or early June. The increase in woody species and reduction in diversity of native (often endemic) grasses and forbs in these sites with these inappropriately timed fires is already apparent at sites known to us, and within another decade the continuing damage may become irreparable.

Given the negative consequences, why do land managers continue to plow excessive fire lines and burn during inappropriate seasons? The reason for abundant fire lines is straightforward: small fire compartments make prescribed burning easier to control, regardless of whether such intensive control is practically necessary or ecologically beneficial. Regarding seasonality, burning in winter, when winds are usually more predictable and air temperatures lower, makes the job easier and more comfortable for the fire crew. Most egregious, in the Coastal Plain forestry and land-managing agencies typically enforce "burn bans" that preclude burning during the dry spring transition season, the time when natural fires occur with the greatest frequency and most positive effects, but when the risk of fires getting out of control is ostensibly higher (but this is debatable). The transition season is when we should be burning most regularly in the lower Coastal Plain. Along with reduction of fire lines, elimination of burn bans is

essential for prescribed fire to simulate ecologically beneficial wildfire.

We should have some sympathy for the individual land manager. These people are grossly underpaid and often poorly educated about the ecological role of fire (albeit some are among the top experts). They must do what their bosses tell them—burn *x* acres in a given year, but not during a burn ban. What must change is agency culture. The gold standard for a successful burn should not be what is easiest, most comfortable, or even safest, but rather what best mimics the characteristic fire regime for the natural community type in question, while not posing unacceptable safety risks.

Buildup of fuels and difficulties applying fire due to burn bans, smoke concerns, and other issues have led many managers to resort to mechanical or chemical means of vegetation management: mowing, roller chopping, disking, chain-sawing (e.g., tree thinning), and herbicide treatments. Such treatments may be needed when grasslands have gone a long time without fire or where fire has been applied only during the dormant season (especially late winter), which tends to enhance shrubby growth, unless done very frequently.

A combination of mechanical treatments and fire is often applied to reduce saw palmetto (*Serenoa repens*) cover in the southeastern portion of the Coastal Plain. Saw palmetto is a desirable native plant in many ways; for instance, it is one of the major foods of the Florida black bear (*Ursus americanus floridanus*). As noted in chapter 3, saw palmetto is a monotypic genus and paleoendemic of the lower Coastal Plain—a living fossil. Nevertheless, increases in density and height of saw palmetto in pine flatwoods and dry prairies, due to reduced fire frequency or burning during the winter, have reduced grass cover and floristic richness and made habitats unsuitable for animals that require grassy conditions, such as fox squirrels and grassland birds. Emma Willcox and Bill Giuliano showed that roller chopping during the growing season may be necessary for substantial reductions in palmetto density, cover, and height. Other studies suggest that after a certain point of structural restoration—saw palmetto knocked back to lower stature and density—fire during the transition or growing season is all that is needed to maintain optimal density.

An exhaustive review of saw palmetto biology and management by Linda Duever shows that the effects of fire are complex. Frequent fall burning may lead to declines in palmetto cover (but, as noted, also may have undesirable impacts on other plants). Winter fires have been documented to increase palmetto cover, but early versus late winter burns have different effects, because carbohydrate reserves are low at the beginning of the winter and high at the end. Hence, early winter burns may depress cover, while the more common late winter burns stimulate vegetative growth. In general, growing-season burns

stimulate flowering more than vegetative growth and seem to provide the best long-term management approach. Roller chopping may depress flowering and fruit production for years, with negative consequences for bears and other wild-life. Herpetologists often oppose roller chopping because of its direct impacts on reptiles and amphibians (i.e., they get chopped).

A 2010 review by Eric Menges and Doria Gordon of surrogates for fire in Florida found that mechanical and chemical treatments accelerate vegeta-tion's structural recovery, but do so best when combined with fire. My PhD student Joyce Klaus found that mechanical treatment (mulching) combined with fire was the most effective approach for restoring conditions conducive to survival of larval amphibians in fire-suppressed wetlands within a longleaf pine savanna in South Carolina. Besides those mentioned here, undesirable effects of mechanical treatments noted in the literature include soil disturbance, increases in invasive species, and rapid resprouting of hardwoods. Fire is an ancient evo-lutionary force, whereas mechanical and chemical surrogates are evolutionarily novel to organisms. Managers should be extremely cautious in applying surro-gates. More generally, they should avoid being overzealous and overmanipula-tive in their management. Ecological surprises are usually not pretty.

The good news about fire management is that, in landscapes where fire was a frequent and dominant natural process, virtually every species benefits—or at least recovers—from properly timed fires. Jodi Slapcinsky and coauthors, in a 2010 paper, reviewed up to fourteen years of monitoring data for eighteen rare plant species across several natural community types in Florida to assess demographic responses to fire. Half of the species showed a positive response and half showed a neutral response, in terms of density, frequency, flowering, and recruitment. There were no negative responses to fire, and many of the neutral responses appeared to be due to prescribed burns conducted during an inappro-priate season (fall or winter). Hence, there is no sense in delaying burning until species-specific responses are better understood—just get out there during the appropriate season and burn! Better yet, wherever possible, let lightning do the job for you. An ideal goal is to protect and restore landscapes large and undevel-oped enough that unmanaged wildfire can play its proper ecological role.

HERBIVORES

Predation is the top-down factor most commonly proposed to regulate com-munity structure. Large herbivores, however, also can exert substantial top-down control. Norman Owen-Smith advanced the "keystone herbivore" hypothesis

to explain how large herbivores create a "mosaic diversity of habitats," including patchworks of short and tall grasses, which in turn promote coexistence of a wide variety of species. It might seem improbable that grazing animals could favor the spread of grasslands. Bond and Keeley commented, in 2005, that "the spread of grasses has often been attributed to coevolution with mammal grazers. However, it is hard to see how, by consuming grass, grazers could promote the spread of grasslands at the expense of forest." As much as I admire their work, I think Bond and Keeley miss the point here. It is not by eating grass that megaherbivores promote grassland. Rather, as studies of modern elephants in African savannas and strong inferences about the role of extinct herbivores in American grasslands show, the physical effects of large herbivores—trampling, rooting, wallowing, and otherwise destroying woody vegetation—is more consequential than the direct effects of their herbivory. As Daniel Axelrod pointed out regarding the origin of the grassland biome in North America:

> The question arises as to whether trees were eliminated solely by fires. An additional factor…is the effect that the large browsing fauna of the late Pleistocene and early Holocene may have had on the tree-shrub cover. Today in central Africa…the destructive action of large mammals is evident. Elephants uproot trees, break branches, debark tree, and in general open up forests and woodlands, expand the savanna, and have locally converted it into an open acacia scrub-grass, or a local grassland…. Other mammals that heavily browse, debark, uproot, trample and break trees and shrubs include, though on a lesser scale, gazelle, wildebeest, Cape buffalo, eland, camel, hippopotamus, giraffe, rhinoceros, kudu, and some pigs…. These and other mammals had counterparts in the late Pleistocene and early Holocene of the Great Plains, notably species of ground sloth, deer, elk, moose, saiga, extinct llama, mastodon, peccary, wapiti, camel, ass-like horse, horse, bear, giant beaver, mammoth, shrub-oxen and others.

The megaherbivores mentioned by Axelrod are abundantly documented as Late Tertiary and Quaternary fossils in the South. Bruce Means of the Coastal Plains Institute suggests that large herbivores were an important selective force in longleaf pine savannas. Because they probably favored longleaf pine seedlings for their rich carbohydrate stores (just as hogs do today), the savanna landscape prior to the extinction of megaherbivores likely had much lower tree density than that observed by early Europeans. As noted in chapter 2, megaherbivores appear to have kept levels of fine fuels and corresponding fire frequency low in portions of North America during the Late Pleistocene. As megaherbivores

declined near the close of the Pleistocene, in what is now the northeastern and midwestern United States, fire activity increased, as indicated by pulses in charcoal deposition. The same sequence may have occurred in the South.

This evidence seemingly contradicts the suggestion by Ripple and van Valkenburgh that megaherbivores were predator limited. If this were so, how did the herbivores remain abundant enough to suppress fire and yet also maintain low tree density? More research on this web of relationships is needed, but we should bear in mind that multiple levels of control occur in ecosystems. Predators may have kept megaherbivores from becoming so abundant that they damaged their habitat to the point of grassland decline or desertification. Nevertheless, megaherbivores probably were numerous enough to keep fine fuels, fire frequency, and tree density at relatively low levels for some period of time.

Grassy Balds

The grassy balds of the southern Appalachians are some of the most distinctive grasslands of the South. They are without question among the most glorious. My personal favorite is Roan Mountain, straddling the North Carolina–Tennessee line, around sixty miles northeast of Great Smoky Mountains National Park (plate 31). Harvard botanist Asa Gray, who explored and collected plants here in 1841, wrote that he could ride his horse for several miles along the Roan crest without encountering a tree to obstruct his view. Gray called Roan Mountain the most beautiful mountain east of the Rockies. I think he was correct. I visited Roan Mountain and a few other choice places in the southern Appalachians in June 2008 with my wife, Myra, to celebrate our wedding anniversary and to conduct research for this book (and thus claim a tax deduction for travel expenses—one of the great things about having your hobby identical to your profession). We rented a cabin in Roan Mountain State Park on the Tennessee side of the peak for a few days. I recommend it.

One fine morning we met several biologists in the parking lot where the Appalachian Trail crosses Highway 261/143 at Carvers Gap on the state line. A resort, Cloudland, was once right up the hill to the south; John Muir stayed here around 1898 to recover his health. We were here for a field trip focusing on management of grassy balds, which lie mostly to the north of the highway. It was a spectacular day. The brilliant narrow-endemic Gray's lily (*Lilium grayii*) was in full bloom, as was one of the dominant grasses of the bald, tufted hairgrass (*Deschampsia cespitosa*), a grass I know from the prairies of the Willamette Valley of Oregon; it is on the southeastern edge of its range here on Roan Mountain. Other dominant graminoids on grassy balds are flattened oatgrass (*Danthonia compressa*) and Pennsylvania sedge (*Carex pensylvanica*). Among the other plants

we observed in bloom were Catawba rhododendron (*Rhododendron catawbiense*); flame azalea (*Rhododendron calendulaceum*), which is uncommon here; and the distinctive Carolina bugbane or tassle-rue (*Trautvetteria caroliniensis*).

While we admired the view from the top of Grassy Ridge at 6,190 feet, a thunderstorm rolled in. Although no lightning struck close by, the wind was almost enough to knock you down. Dark shadows of clouds streamed rapidly across violently waving grasses, creating perfect conditions for photography. The rain began in earnest as we headed back down the mountain, and we were drenched and cold by the time we reached the cars in the pass. The memory of those billowing grasses and clouds is the kind of thing you want to hold in your semiconscious mind in the middle of the night. And then there is the prospect of snow buntings (*Plectrophenax nivalis*), the tundra bird that people in northern states see in flocks on winter roads. Snow buntings also winter here on the grassy balds of the Roan Mountain highlands. I'll be back to see them.

Two general types of balds are recognized in the southern Appalachians: heath balds and grassy balds. Heath balds are species-poor ericaceous shrub-lands, called "laurel slicks" locally because, from a distance, their uniform canopy makes them appear smooth and slippery. Grassy balds are species-rich communities that typically contain more than two hundred plant species per site, often including several rare and endemic species, especially on rock outcrops (e.g., Appalachian avens [*Geum radiatum*], Venus's pride [*Houstonia pupurea* var. *montana*]). Grassy balds superficially resemble the alpine tundra zone of high mountains, but alpine tundra occurs today only in the most northern stretch of the Appalachians. At their southern latitudes, the Appalachians supported tundra only during glacial intervals. Rather, the balds of the southern Appalachians occur within an elevation zone that usually supports spruce-fir forest. Indeed, the balds are embedded within a matrix of red spruce (*Picea rubens*) and Fraser fir (*Abies fraseri*), and they do not differ from the forest in topography, soils, or other physical properties.

What does all this have to do with herbivores? Experts agree that herbivores, in the form of nonnative sheep, goats, cows, and horses, grazed many of the balds from the early 1800s until the 1930s to 1950s. After livestock were removed, invasion by woody plants increased rapidly, such that most balds that are not actively managed today are converting to forest. That much is agreed on. Where authorities differ is on the origin of the balds and the factors that maintained them over long periods of time. In a 1999 book chapter on high-elevation outcrops and barrens (including balds) of the southern Appalachians, Susan Wiser and Peter White acknowledge that the first European settlers reported some open balds, but conclude that the majority of balds were created

by those settlers, presumably by manually cutting trees and stocking the balds with their livestock during the summers.

Other authorities hypothesize that the balds are much older and of non-human origin. Bob Peet and Alan Weakley pointed out to me an interesting twist on this controversy: those researchers who claim a recent anthropogenic origin of grassy balds have worked primarily in the more southern sites, mostly within Great Smoky Mountains National Park, which are more disturbed and weedy, and where the history of human use is well documented. In contrast, the researchers who emphasize nonhuman factors in the origin and early main-tenance of the balds have worked mostly in more northern examples, such as Roan Mountain, which are more pristine, have deeper soils, and contain few exotics. All sorts of natural explanations for the origin of balds have been offered, from past periods of heat and drought (e.g., Hypsithermal) to present climate extremes (strong wind, heavy snow, etc.). Fire has been suggested, but these cold, damp places rarely burn. Indians are invoked, too, but there is no sign of former settlements or intensive use. As Wiser and White note, most of the hypotheses of bald origin have little evidence to support them.

The explanation for the origin and maintenance of grassy balds that I find most compelling is the "chain of herbivores" hypothesis proposed by Peter Weigl and Travis Knowles. This hypothesis suggests that a combination of cli-mate and the activities of a progressively changing guild of large herbivores created and maintained the grassy balds of the southern Appalachians. The hypothesis may apply to similar communities in Europe (e.g., the "poloni-nas" in the Eastern Carpathians of Romania and Serbia) and some portions of western North America (e.g., the grass balds of several peaks in the Oregon Coast Range, such as Marys Peak and Grass Mountain, where I spent many pleasurable days during the 1990s). According to this hypothesis (fig. 5.6) the high mountains of the southern Appalachians were covered by tundra during glacial periods of the Pleistocene. Although probably snow-covered in winter, the grassy tundra was exploited in summer by megafauna, including mam-moths, mastodons, giant ground sloths, and other beasts, moving up from lower elevations. A diverse assemblage of large mammals inhabited this region, going back to the Miocene/Pliocene fauna of the Gray Fossil Site, which is almost literally right down the hill from Roan Mountain.

Continuing with the hypothesis, extensive grass and sedge-dominated communities were maintained after the Last Glacial Maximum by the forag-ing and tree-destroying activities of the megaherbivores. After these herbivores went extinct near the close of the Pleistocene, their role was partially filled by the surviving large herbivores: white-tailed deer (*Odocoileus virginianus*), elk, and

"Chain of Herbivores" Hypothesis
(Weigl and Knowles 1995)
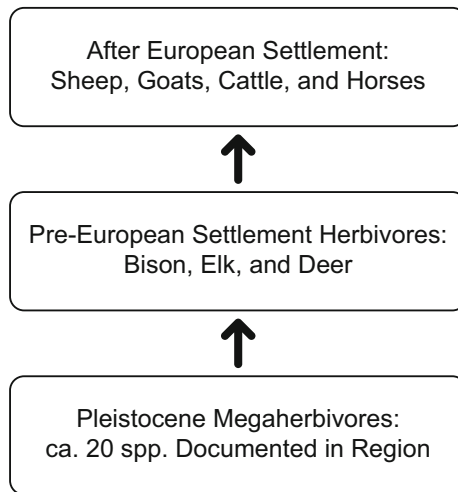
Figure 5.6. The chain of herbivores hypothesis for the maintenance of grassy balds in the southern Appalachians following their formation from alpine tundra during the Last Glacial Maximum. Adapted from hypothesis of Weigl and Knowles (1995).

then later, bison (*Bison bison*). These herbivores were reported as abundant in this region, and some populations made seasonal migrations up and down the mountains. Nevertheless, these species probably were not as effective in maintaining grassy balds as their Pleistocene counterparts, so the complex of high-elevation grasslands gradually shrank, but did not disappear. As the remaining native herbivores were depleted through hunting by Indians and early white settlers, the grassy balds continued to diminish. Nonnative livestock introduced by white settlers in the early nineteenth century, however, may have kept the balds from disappearing altogether. When livestock were removed from the balds in the middle of the twentieth century, ironically in large part to conserve these mountain ecosystems, tree invasion increased, resulting in the patchy distribution of relatively small balds we find today.

What Weigl and Knowles suggest accords well with knowledge of the climatic and faunal history of these mountains since the Pleistocene. The grassy balds that remain today are probably mere remnants of formerly much more expansive open areas. If indeed these balds (or treeless mountaintops) were created by cold climate, maintained by megaherbivores, and have been closing in since livestock were removed, should livestock be reintroduced to the balds? This is already being done on an experimental basis, for example cattle (*Bos taurus*)

on The Nature Conservancy's Big Yellow Mountain Preserve and recently goats on part of Roan Mountain. Some biologists worry about the potential impacts of livestock. Mike Schafale, for example, argues that thick grass cover probably inhibits woody plant invasion at present, so grazing could potentially enhance invasion (especially by blackberry) by thinning the grasses and creating areas of bare soil. Cattle are generally not tree destroyers and may not substitute for megaherbivores in keeping balds or other grasslands sparse in woody plants.

I would guess that animals with more of a penchant for eating or knocking down trees and shrubs are needed up here. Short of reintroducing modern relatives of Pleistocene megafauna in a rewilding experiment (which is probably not a good idea, although it would be amusing to see herds of elephants on these balds), perhaps our best bet is to reintroduce elk and bison on an experimental basis. Elk and bison have been reintroduced elsewhere in the South (for example, elk on reclaimed strip mines in Kentucky, elk and bison at Land Between the Lakes in Kentucky and Tennessee; plate 28), and I expect most visitors would rather see them than goats, sheep, or cows. Whenever feasible, we should use native herbivores for management of natural areas, as they are likely to integrate better into the community. In the meantime, a number of treatments—mowing, manual cutting of woody vegetation, and grazing—should be employed experimentally as we figure out how to best manage these unique ecosystems.

Salt Licks and Buffalo Traces

The chain of herbivores hypothesis can be extended well beyond the grassy balds of the southern Appalachians. Across much of the South, north of the Coastal Plain (where grassland was more continuous), a succession of Pleistocene megaherbivores, modern native ungulates, and to some extent livestock concentrated in particular areas and, through their foraging, trampling, and general rowdiness, maintained wide strips and patches of grassland within a matrix of forest. These grasslands are ancient enough that at least two endemic plants are closely associated with them. Especially in Kentucky and portions of adjacent states, but extending as far south as northern Georgia, are ancient trails of megafauna, commonly known as "buffalo traces" (plate 29), which run to and from salt licks where animals congregate. Speaking of the salt licks of the Ohio Valley, one visitor, John Filson, remarked in 1784: "Many fine salt springs constantly emit water.… The amazing herds of buffalo which resort thither, by their size and number, fill the traveler with amazement and terrors, especially when he beholds the prodigious roads they have made from all quarters as if leading to some populous city."

Buffalo traces almost certainly extend back in time much further than the herds of modern bison observed using them by white settlers. They were created by much bigger beasts, far longer ago. Consider Big Bone Lick. Yes, this is a comical name (I bought a great hat there), but for a very significant place. Big Bone Lick, in Boone County, Kentucky, about twenty miles southwest of Cincinnati, is acknowledged as the birthplace of American vertebrate paleontology. During the Pleistocene and until recently, Big Bone Lick was a swampy area surrounding salt and sulfur springs. Animals came to lick salt from the springs, and a good number of them got mired and left their bones to fossilize in the mineral-rich muck. Recorded megafauna include mammoth (*Mammuthus columbi*), mastodon (*Mammut americanum*), unidentified Proboscidea, Harlan's ground sloth (*Paramylodon harlani*), Jefferson's ground sloth (*Megalonyx jeffersonii*), ancient bison (*Bison antiquus*), ancient horse (*Equus* cf. *complicatus*), tapir (*Tapirus* sp.), stag moose (*Cervalces scotti*), Harlan's musk-ox (*Bootherium bombifrons*), and a variety of carnivores. Big Bone Lick continued entrapping animals until quite recently, with modern bison, elk, white-tailed deer, modern horses (*Equus caballus*), hogs, and cattle among the victims. Thus, here at Big Bone Lick we have a record of the complete chain of herbivores hypothesized by Weigl and Knowles to have maintained grassy balds of the neighboring Appalachians.

The first European to visit Big Bone Lick may have been Baron Charles de Lougueuil, a French military commander, who collected mastodon fossils here (or nearby) in 1739. Rumors of the locality spread rapidly, and within the next several decades perhaps thousands of specimens were collected from the site. Although some significant specimens found their way into museums, most of the fossils collected by amateurs appear to have been lost. We owe the major scientific discoveries at Big Bone Lick to Thomas Jefferson. As Mark Barrow describes in his book, *Nature's Ghosts*, which reviews the history of naturalists confronting extinction, Jefferson became obsessed with megafauna after cataloguing some mysterious bones, which he called "the Mammoth, or big buffalo" and more generally known as "the incognitum." Jefferson fervently wanted to believe that this huge beast still survived somewhere in North America—its existence would be a source of American pride and would counter the claim of haughty Europeans that America's fauna was inferior.

In 1771 Jefferson asked his old friend, General George Rogers Clark, to mount an expedition to Big Bone Lick, but threat of Indian attack precluded the trip. The scientific collecting expedition had to wait until 1807, when at the behest of Jefferson, George's younger brother, William Clark (the man who had just crossed the continent and back with Meriwether Lewis, in part to search for megafauna) traveled to Big Bone Lick and collected some three hundred

specimens. Many of those fossils originally went into Jefferson's personal collection; most are housed today at the National Museum of Natural History in Paris and the Academy of Natural Sciences in Philadelphia. Most subsequent study of the Big Bone Lick fauna has been based on the Clark-Jefferson specimens, with no new major discoveries of Pleistocene fossils there until the 1960s.

Big Bone Lick was one of several salt licks that Pleistocene and later megafauna used in northern Kentucky, and these licks were connected by buffalo traces. Early white settlers described these trails as up to three wagons in width. It is fun to visualize herds of mammoths, mastodons, and giant ground sloths ambling down these trails from salt lick to salt lick. One of the prominent salt licks is Blue Licks, today the site of Blue Licks Battlefield State Park near Mount Olivet, Kentucky. The park was established to commemorate the Battle of Blue Licks in 1782, often regarded as the final battle of the Revolutionary War. Early descriptions of Blue Licks describe it as a place, like Big Bone Lick, where animals gather to lick salt deposits around the springs. Legendary frontiersman Simon Kenton visited Blue Licks in the 1770s and described "flats upon each side of the river … crowded with immense herds of buffalo, that had come down from the interior for the sake of the salt." A couple of decades later the Reverend James Smith provides this account in his diary: "As you approach the Licks, at the distance of 4 or 5 miles from it, you begin to perceive the change. The earth seems to be worn away; the roots of the trees lie naked and bare; the rocks forsaken of the earth, that once covered them, lie naked on the neighboring hills, and roads of an amazing size, in all directions, unite at the Licks, as their common center. Here immense herds of buffalo used formerly to meet and, with their fighting, scraping etc., have worn away the ground to what it is at present." Such is the power of large herbivores to alter a landscape!

I visited Blue Licks with Marc Evans and Joyce Bender in September 2008. There is much of interest at this site, but the truly amazing story is of a little plant, Short's goldenrod (*Solidago shortii*), a narrow endemic that may owe its existence to megaherbivores (plate 30). *Solidago shortii* was first collected in 1840 by a physician, C. W. Short, on a limestone outcrop at Rock Island, in the Falls of the Ohio. This shallow area of rapids was a major crossing point of the Ohio River for animals using a buffalo trace that ran northward into what is now Indiana. The Falls and the only known population of the goldenrod were destroyed by engineers who built the McAlpine Locks and Dam (completed in 1927) to make this stretch of the river more navigable. A full century after Short's discovery, in 1939, Lucy Braun rediscovered Short's goldenrod at Blue Licks and described it as abundant in overgrazed cow pastures; it also occurs in other disturbed habitats and in small glade-like openings.

Until very recently, Blue Licks was the only known site for Short's goldenrod, but it was not treated kindly; significant areas of habitat were destroyed in the 1970s for construction of a campground at the state park. The plant survived in a few pastures, but those were then converted largely to fescue, again almost driving the goldenrod extinct. The remaining population is now protected within a designated nature preserve, most of it an overgrazed pasture where I observed the plants blooming during my visit. Incredibly, in 2001, a new population of Short's goldenrod was discovered by botanists in Harrison-Crawford State Forest in Indiana, on limestone bluffs along the Blue River, just a half-mile upstream from the Ohio River. This habitat is similar to the limestone outcrops along the Falls of the Ohio, where the species was first discovered.

One scenario for the evolution of Short's goldenrod is adaptation of a population of an ancestral species to the xeric, thin-soiled limestone outcrops along the Falls of the Ohio and the Blue River. From there, the species could have spread to the similarly xeric, heavily grazed and trampled habitat of the buffalo traces. Alternately, the goldenrod could have coevolved with megaherbivores, in the sense of adapting to the unique habitat of their trails over a long period of time, and then subsequently spread to limestone outcrops along the trails. Blue Licks and the Falls of the Ohio were connected prior to 1800 by a buffalo trace, and megaherbivores could have transported seed from one locality to the other. The same buffalo trace extended into Indiana and crossed the Blue River in the vicinity of the recently discovered Indiana population. By any scenario, the goldenrod is intimately tied in its evolution and its ecology to megaherbivores.

Another plant associated with megaherbivores is running buffalo clover (*Trifolium stoloniferum*). This species was distributed much more broadly than Short's goldenrod, extending from West Virginia to Kansas. It is currently extant in small areas of Indiana, Kentucky, Ohio, Missouri, and West Virginia, especially on limestone substrates. Like Short's goldenrod, habitat for running buffalo clover is thought to have been maintained by bison migrating and grazing along established trails. It likely evolved earlier, when Pleistocene megaherbivores created these trails.

Alan Knapp and coauthors proposed in 1999 that bison play a keystone role in tallgrass prairie through their grazing, nutrient redistribution and cycling, wallowing, and other activities. We can assume a similar role for bison and other megaherbivores in the South. Nevertheless, the status of bison in the South prior to European settlement is surprisingly muddled. At least two species of bison, *Bison latifrons* and *B. antiquus*, inhabited the South during the Pleistocene. The giant bison, *B. latifrons*, was twice the size of the modern bison, with a horn-spread of six feet or broader; it went extinct by 15,000 years ago. The ancient

bison, *B. antiquus*, probably derived from *B. latifrons*, was smaller and had horns of about three feet from tip to tip. It disappeared in the early Holocene, around 10,000 years ago, at the latest. The modern bison, *B. bison*, probably descended from *B. latifrons*, but its period of occupancy in the South is debated; there are no Holocene fossils. With a few enticing exceptions, the earliest (Spanish) explorers did not report seeing bison, but rather only breast plates, skins, horns, and other artifacts on Indians, which could have been obtained through trade with western tribes. The oral traditions of some tribes contain stories of bison—but those of other tribes do not. The most comprehensive review of bison east of the Mississippi is *The Long Hunt*, written by Kentucky historian Ted Franklin Belue. Unfortunately, this book repeats the assertion that longleaf pine savannas and other grasslands east of the Mississippi River were all created by Native Americans through their use of fire; as discussed earlier, this supposition is incorrect.

Cabeza de Vaca saw bison in the South in the 1530s, which he said "come from the north, across the country further on to the coast of Florida, and are found all over the land for four hundred leagues." This would appear to be ample proof that bison were distributed across the Southeast, except that "Florida," at this time extended as far west as Galveston Bay, Texas (which, however, is within my study region). In the 1540s de Soto ate "fresh beef" near the Savannah River, but the Indians did not tell him from where they obtained it. De Soto and his men did not actually see bison until crossing the Mississippi River into what is now Arkansas in 1541. Reports of bison by early explorers remained scarce until 1675 when, according to Belue, "Bishop Gabriel Díaz Vara Calderón recorded the first credible seventeenth-century buffalo sighting in peninsular Florida." Belue then writes, however, that an earlier castaway, Hernando d'Escalante Fontaneda, reported "wooly cattle" near present-day Tallahassee from the 1550s to the 1560s, but that historians debate the veracity of this account. Later reports of bison in the Southeast were near the Little Tennessee River in 1673 and in the Carolinas by 1700. Reports became more numerous through most of the eighteenth century, but then began ebbing toward the end of the century, with William Bartram reporting that bison, once abundant on the Georgia Piedmont, had been eliminated by hunting there by 1773. The last bison east of the Mississippi River were extirpated by 1808 in Ohio and Illinois, by 1823 in Tennessee, in 1830 in Indiana, and in 1832 in Wisconsin.

Belue stops short of stating the most plausible explanation for the puzzling population trend of bison east of the Mississippi River over the last five hundred–plus years. My interpretation is that bison were scarce east of the Mississippi River when the first Europeans arrived due to overhunting by Native Americans. Others have suggested that Paleo-Indians (e.g., the Clovis culture)

were probably responsible for the extinction of the Pleistocene bison. The use of fire by Indians would have otherwise favored bison and, in fact, may have initially aided the dispersion of modern bison eastward into areas, such as Kentucky, where grasslands were expanded by Indian-set fires. After the Indian population was decimated by European diseases and persecution by the 1600s, the bison rebounded, only to be overhunted again and eventually extirpated nearly continent-wide by EuroAmericans.

We still do not know when modern bison first appeared east of the Mississippi River. It was probably sometime before Europeans arrived (as suggested by the Spanish accounts cited here), but perhaps not before modern tribes arrived. Erhard Rostlund, in a 1960 paper, points out that, although Indian languages of the Southeast include words for buffalo, no Indian place name referring to buffalo is known in the region. Rostlund concludes that "the absence of buffalo terms from Indian place names in this region can only be explained, I think, by the assumption that the buffalo itself was absent when these tribes arrived." The mystery of the modern bison's appearance in the Southeast notwithstanding, ancestral bison inhabited the region since the Late Pliocene, ca. 3 million years ago, followed by a second dispersal from Asia 1.5 million years later, in the Middle Pleistocene. After going extinct in the Late Pleistocene or early Holocene, bison returned to the region several thousand years later in the form of *Bison bison*. They came here on their own hooves—and therefore are fully native—and play an ecologically pivotal role in grasslands. Bison have been reintroduced into parts of the South, for example a tiny herd in Paynes Prairie outside Gainesville, Florida, and a larger population (along with elk) at Land Between the Lakes in Kentucky and Tennessee. These are fenced, intensively managed populations; as such, bison no longer play the keystone role that they previously performed in southern grasslands.

Livestock

It would be wonderful to see free-roaming bison once again traveling the buffalo traces of the South and beyond. This seems unlikely within the near future, however, in part because buffalo traces were paths of least resistance through the landscape; as such, they have been largely converted to roads. Bison could undoubtedly be more widely reintroduced to the South than they have been so far, but cultural resistance to recovery of large native animals will make this a slow process.

What about using livestock—such as cows, which are close relatives of bison—as surrogates for native ungulates? Livestock (but not necessarily cows) were able to keep some southern grasslands, such as grassy balds, relatively open after the

demise of their native counterparts. Nevertheless, livestock grazing—and more broadly, the livestock industry—can have a variety of harmful impacts on grasslands and other natural communities, depending on how the animals are managed and how ranchers treat native species, including native plants and predators. No comprehensive review exists of the ecology of livestock in southern grasslands. Given their long history of development with large herbivores, most southern grasslands appear resilient to grazing, compared to arid western ecosystems such as desert grasslands and the sagebrush steppe of the intermountain West. Cattle and bison overlap extensively in their diets, and both species select recently burned areas, when available. They differ, however, in several ways. The most significant difference is that cattle prefer areas close to water, hence their notorious impacts to streams, riparian zones, and wetlands. In general, native megaherbivores were likely much more mobile than cattle, albeit they also concentrated in certain areas, most notably around salt licks and trails (i.e., buffalo traces).

Florida is the original cowboy state, with the first cattle brought here by the Spanish nearly five hundred years ago and with organized ranching initiated with the founding of St. Augustine in 1565. Later Florida cowboys were known as "crackers" from the cracking of their cow whips. Cattle grazing here probably had minimal or localized impacts in the days of the open range, before cattle were fenced and confined to relatively small areas for long periods of time, before supplemental feeding and veterinary interventions increased their populations dramatically, and before native grasslands were converted to nonnative monocultures. Impacts of cattle production today can be substantial. Some areas of Florida, including public lands, are grazed so heavily that fire does not carry well, due to the depletion of fine fuels, and many streamsides and marshes are trampled muck. Florida's biologically rich upland/wetland slope-moisture gradient, which encompasses wet pine savannas, seepage slopes, cutthroat seeps, wet prairies, floodplain marshes, and depression marshes, can be heavily degraded by high cattle densities. Field ecologists have observed that areas with long histories of grazing have lower densities of the more palatable native grasses, such as bluestems (*Andropogon* and *Schizachyrium* spp.) and increased dominance of wiregrass and other less palatable species. Research shows that fire ant densities are higher within grazed than ungrazed areas, with often severe impacts on ground-nesting birds, whose young are devoured by the ants. Studies in several southern states document significant impacts of fire ants on northern bobwhite, and fire ants may be partially responsible for the recent precipitous decline of the endangered Florida grasshopper sparrow.

Feral hogs, introduced to the South by de Soto in 1539, were noted earlier as a threat that might be reduced through restoration of native predator popu-

lations and increasing trapping. In longleaf pine savannas, feral hogs are more damaging than cattle, because they feed heavily on the pine seedlings in the grass stage (which are resistant to fire but not to herbivory). A single hog can consume up to four hundred pine seedlings in one day. The English established a major salt pork industry based on free-range hogs. In his 2006 account of the history of longleaf pine, Cecil Frost documents "saturation" of landscapes by hogs as early as 1700 in Virginia and parts of the Carolinas and offers evidence that hogs were a major factor in the demise of longleaf pine in the Coastal Plain. Feral hogs continue to have severe impacts on natural ecosystems of the South, but they are nevertheless promoted by wildlife agencies as game animals.

Cattle are a major industry in the South, especially in Florida, where approximately eleven million acres of grazing lands (nearly one-third of the state's land area) contribute hundreds of millions of dollars annually to the state's economy. Perhaps the most detrimental practice of the cattle industry in Florida has been conversion of native grasslands to so-called improved pasture. A native grassland is improved, from the standpoint of ranchers, by clearing, tilling, and reseeding it with a monoculture of nonnative pasture grass, most commonly bahiagrass (*Paspalum notatum*). "Semi-improved pastures," also known as mixed pastures, contain nonnative forage grasses interspersed with native grasses and forbs. Management such as weed control and fertilizer applications is less intensive in semi-improved pastures than in improved pastures.

A 2010 study by Emma Willcox and colleagues at the University of Florida found that monoculture pastures in central Florida lost more spatial heterogeneity when grazed than did mixed pastures. Reduced heterogeneity led to reduced species richness and abundance of birds. Most negatively affected by increasing grazing intensity were the short-distance migrant, neotropical migrant, and permanent resident guilds. The authors recommend that "if a range of avian species are to be supported on monoculture and mixed pastures, spatial heterogeneity of plant structure and composition must be maintained." In contrast to studies in tallgrass prairie and elsewhere in the Great Plains, where intermediate grazing pressure often maximizes heterogeneity, this Florida study shows that heterogeneity is highest under very low grazing intensity. These results echo the conclusions of the review of southeastern grasslands by DeSelm and Murdock, who observed that "high-intensity grazing and other forms of intensive management generally result in decreased species numbers and structural complexity."

Improved monoculture pasture is no substitute for native grasslands—not by a long shot. A broad gradient exists, however, from native grassland to improved pasture. Most large ranches are mosaics of native grasslands and other natural communities, plus semi-improved and improved pasture. In Florida, rangelands

constitute some of the most significant de jure and de facto conservation land in the state. Moreover, some vertebrates of high conservation concern, especially the crested caracara (*Caracara cheriway*) and burrowing owl (*Athene cunicularia*), prefer improved or semi-improved pasture and rather heavily grazed areas to ungrazed native grasslands. Joan Morrison and Steve Humphrey, in 2001, reported that 82 percent of seventy-three active caracara nest sites that they located in central Florida were on privately owned cattle ranches. Breeding pairs of caracara were rare on public lands managed as natural areas. Caracara home ranges had a higher proportion of improved pasture than random sites or the overall study area. Pastures have low-stature grasses, which these birds prefer because they often forage by walking through grassland. We can only speculate what factors made native grasslands suitable for caracara in Florida before improved pastures appeared in the relatively recent past, but more frequent fire and native megaherbivore activity are likely candidates.

The burrowing owl in Florida similarly prefers short grass, with most recent breeding pairs in pastures, residential areas, and other mowed sites. These adaptations suggest evolution with megaherbivores, presumably during the Pleistocene or earlier, with the caracara and burrowing owl specializing on the more intensively grazed patches or trails. Recall that these two birds are among the many disjuncts from the semiarid West, reflecting the former biogeographic connection across the Gulf Coastal Corridor. Many pastures contain large oaks and pines, which make them usable by fox squirrels, and most support fair densities of gopher tortoises and some other grassland fauna.

The Florida grasshopper sparrow—probably the most endangered bird in mainland North America—does not nest successfully in pasture. Its territories spill over into pastures during years of high density (which appear to be a thing of the past), and nests have been found on pasture edges, but the dense sod of pasture grasses fails to provide the bunchgrass clumps that the sparrow uses for nesting, or the bare ground and "runways" that it requires to forage and escape predators. Conversion of native dry prairie to improved pasture is the primary factor in the historic decline of the Florida grasshopper sparrow.

The negative aspects of cattle ranching must be weighed against the positive value of keeping large areas undeveloped. Probably the optimal approach, which has worked reasonably well in Florida, is for government agencies to purchase conservation easements on ranches and make them profitable enough that the landowner will comply with a management plan that reduces cattle stocking density below a level where negative impacts occur. Conversion of native grassland to monoculture pasture should be strongly discouraged. However, because some imperiled native species prefer grazed areas, and use improved pastures,

a heterogeneous mosaic of heavily grazed, moderately grazed, lightly grazed, and ungrazed (but burned!) grassland might be ideal from the standpoint of maintaining native biodiversity.

Fire-Herbivore Interactions: Pyric Herbivory

Herbivory and fire often are applied independently in grassland management, though these two processes were historically interdependent. A growing number of rangeland ecologists recommend that fire and grazing be applied jointly to simulate the diversity-enhancing effects of bison herds and fire on grasslands. The term *pyric herbivory* was coined by Samuel Fuhlendorf and colleagues to describe how herbivory, shaped by fire, creates a shifting mosaic of disturbance patches across a grassland landscape, which in turn promotes biodiversity. In this model grazing animals interact with fire and increase landscape heterogeneity by selecting burned versus unburned patches and by removing fine fuels, thereby reducing fire occurrence in selected patches, while leaving ungrazed patches full of fuels ready to burn. The interactive effect of fire and grazing on diversity is stronger than the effect of either factor alone. Their model is well supported by experiments in tallgrass prairie and by several studies in African savannas. Carla Staver and coauthors, in 2009, showed that a combination of herbivory by medium and large mammals and fire is necessary to suppress tree density in African savannas and that "browsing, like fire, suppresses tree density by imposing a demographic bottleneck on the maturation of saplings to adults." Studies from several regions show that some grassland birds, insects, and small mammals depend on recently disturbed habitats, whereas other species fare better when several years elapse between disturbance events.

A pyric herbivory approach to grassland management will work best in large wildland landscapes, where herbivores (ideally native species) and fire are able to interact unconstrained as they did over evolutionary time. Fuhlendorf and colleagues recognize that applying fire and grazing at smaller spatial extents is still in an experimental phase and that "a critical determining factor to the effects of pyric herbivory is the relationship of grazing pressure to the number of fires and the amount of area burned each year." Finn Pillsbury and coauthors, in a study of fire and cattle grazing interactions and their effects on birds in tallgrass prairie patches, showed that the utility of pyric herbivory as a management strategy is less clear in highly fragmented grasslands. They conclude that "the future success of this management scheme for fragmented grasslands hinges on if, after an optimal stocking rate is identified, adequate habitat can be maintained for a diverse bird community, or whether fragmentation will perpetually limit the efficacy of this method in these landscapes." As I see it, the

lesson for southern grasslands, for which the pyric herbivory model has not yet been tested, is to (1) maintain and restore large, wild grasslands in regions where these were part of the presettlement landscape; (2) experiment with combined herbivore-fire management treatments in these large grasslands; and (3) experiment with great caution or not at all in smaller grassland patches.

INTERACTION OF FIRE AND HYDROLOGY

Terrestrial ecologists in the Coastal Plain will tell you that fire and hydrology are the two major factors controlling the distribution of vegetation. Landform and soils matter, too, but fire and water take precedence because small changes in their activity produce profound changes in plant communities. For example, a slight change in elevation, even on the order of a few inches, produces a different hydroperiod, in turn affecting colonization, persistence, and reproduction of various species of plants. Fire and water regularly interact along these gradients. In the Florida Panhandle westward to Mississippi, seepage slope communities develop in relatively hilly areas with 30- to 50-foot relief. Groundwater seepage along the slopes keeps the ground continuously saturated, while fires burning downslope from upland pine communities maintain an open condition by pruning back wetland shrubs that would otherwise encroach from further downslope (fig. 5.7). When fire frequency is reduced, these biologically rich and distinctive ecotonal communities are quickly lost.
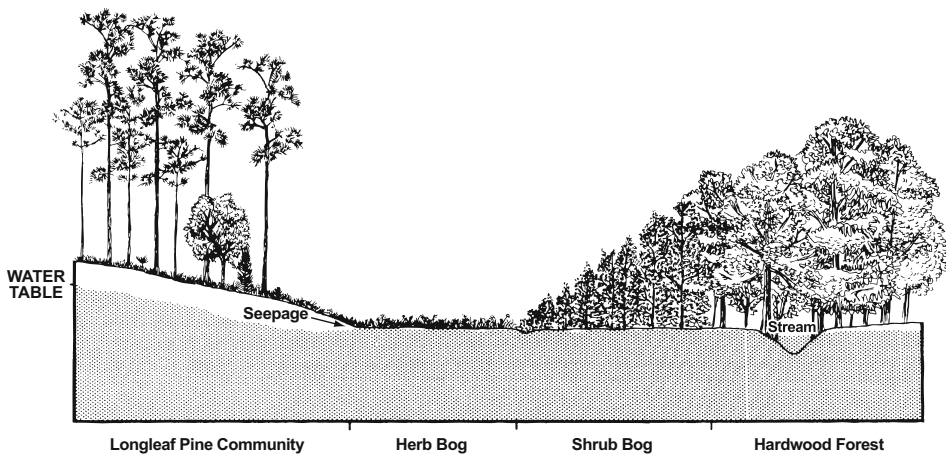
Figure 5.7. Fire interacts with the slope-moisture gradient in parts of the Coastal Plain to maintain open, saturated seepage slope communities and prevent wetland shrubs from encroaching upslope. These species-rich ecotonal communities are among the first to disappear after fire exclusion. Courtesy of Bruce Means.

Florida Dry Prairie

Florida dry prairie provides a splendid example of the interaction of elevation, hydrology, fire, vegetation, and fauna in a region with subdued topography. This ecosystem, perhaps the most remarkable large and virtually treeless grassland of the South, was described by Roland Harper in 1927 as having "views strongly suggestive of the Great Plains." The dry prairie, which once covered more than 1,900 square miles of south-central Florida (fig. 5.8), is not necessarily dry, but rather is a complex mosaic of plant communities determined by slight differences in soils, elevation, and hydroperiod, with the lowest, wettest sites inundated for a few weeks during a typical year. As noted in chapter 3,

Figure 5.8. The pre-agricultural Florida dry prairie (hatched area), which covered approximately 5,000 km² (more than 1.2 million acres). From Noss (2006), provided by S. Orzell and E. Bridges.

this is one of the most species-rich grasslands in the South and globally. Six types of dry prairie were defined by Steve Orzell and Edwin Bridges on the basis of quantitative vegetation and soil sampling: dry-mesic, mesic, wet-mesic spodic (spodosols: acidic sandy soils), wet-mesic alfic (alfisols: higher-fertility soils with more clay accumulation), acidic wet, and calcareous wet prairies. Susan Carr reviewed community descriptions and analyzed species response curves using plants collected at Kissimmee Prairie Preserve, the largest remaining expanse of dry prairie. Susan and my postdoctoral associate, Robin Bjork, used this information to generate a list of indicator species, which nonspecialists could use to identify communities. Four communities (plus subtypes) could be distinguished consistently in the field using the indicator species method: wet prairie, wet-mesic prairie, mesic prairie, and subxeric prairie (fig. 5.9). Preliminary work by our research team showed that these communities could be recognized on aerial photographs (Digital Orthophoto Quarter Quads or DOQQs) and mapped using a combination of field data, photo interpretation, and automated imagery analysis ("unsupervised classification") of the DOQQs.

The critical lesson for conservation is that landscape-scale heterogeneity in the dry prairie allows high numbers of species to coexist by sorting out along environmental gradients. To function properly, these landscape mosaics must remain largely unfragmented by roads, drainage ditches, and fire lines. Where these artificial linear features exist, they should be removed to the greatest extent feasible. The Florida grasshopper sparrow appears to be acutely sensitive to landscape-scale processes in the dry prairie. This species nests in patches of prairie that have burned within the previous one to two years and have suitable hydrologic conditions. The birds breed in low densities across the landscape; they may require hundreds of thousands of acres of relatively contiguous or connected dry prairie to maintain a viable population in the long term.

A nagging question is why this tiny sparrow, which averages just 17 grams (0.6 ounce) in weight, with an average territory size of only five acres, needs so much land to support a population. The answer appears to be that habitat suitability for this species is constantly shifting over space and time in response to variation in fire history and hydrology. In any given year, a relatively small proportion of the landscape is suitable habitat—and next year (or next month) it may be distributed differently. Due to variability in rainfall, for example, some nests placed in apparently high-quality habitat are suddenly flooded after a heavy rain, with all the nestlings drowned. Although some territories remain relatively stable in position over the years, many others continually shift in response to these dynamic conditions, even within a

high abundance
low abundance

SCIENTIFIC NAME	Wet Prairie	Wet Mesic Wetter.........................Drier		Dry Mesic Wetter...............................Drier		Subxeric
Coreopsis floridana						
Andropogon perangustatus						
Fuirena scirpoidea						
Dichanthelium erectifolium						
Bigelowia nudata						
Eriocaulon decangulare						
Chaptalia tomentosa						
Xyris ambigua						
Pluchea rosea						
Oxypolis filiformis						
Dichanthelium leucothrix						
Quercus minima						
Carphephorus carnosus						
Dichanthelium strigosum var. glabrescens						
Ctenium aromaticum						
Xyris elliottii						
Lachnocaulon anceps						
Aristida spiciformis						
Erigeron vernus						
Andropogon brachystachyus						
Sorghastrum secundum						
Schizachyrium stoloniferum						
Dichanthelium portoricense						
Dichanthelium chamaelonche						
Rhynchospora plumosa						
Pityopsis graminifolia						
Pterocaulon virgatum						
Andropogon ternarius var. cabanisii						
Vaccinium myrsinites						
Xyris caroliniana						
Carphephorus corymbosus						
Lyonia fruticosa						
Hypercium reductum						
Gaylussacia dumosa						
Liatris tenuifolia						
Lechea torreyi						
Gymnopogon chapmanianus						
Rhynchospora intermedia						
Vaccinium stamineum						
Quercus myrtifolia						
Balduina angustifolia						

Figure 5.9. Four community types in the Florida dry prairie at Kissimmee Prairie Preserve State Park, arranged from wet (left) to dry (right), can be recognized in the field based on the presence of indicator species. Each community type has overlapping but characteristic sets of indicator species. Indicator species were defined based on species response curves developed by Susan Carr. Figure produced by Robin Bjork; from Noss et al. (2008).

single breeding season. The end result is a sparse and precarious population, which is now declining rapidly for reasons that researchers who have studied this sparrow do not understand.

Another question that has long puzzled ecologists is what keeps the Florida dry prairie so free of trees. In most respects, including soils, fire ecology, and species composition in the groundcover, dry prairie appears virtually identical to pine flatwoods. Roland Harper commented on the dry prairie:

> The vegetation differs from that of the flatwoods…in hardly any way except the absence of trees, and the reason for that is obscure. The soil seems to be the

same fine gray sand as in the flatwoods, and no more subject to inundation, but it may be that there is hardpan or something of the sort near enough to the surface to interfere with the roots of trees. The fact that the prairie soil is hardly one percent cultivated would seem to indicate that it is inferior to that of the flatwoods in some way.

The dry prairie is located in the region of peak thunderstorm activity in North America (plate 3); hence, frequent fire is an obvious explanation for sparse tree cover. But flatwoods occur within the same region, and they burn frequently, too. Edwin Bridges suggests that dry prairie may burn even more frequently than flatwoods because the extremely flat landscape, with few interruptions from topographic features, produces immense fire compartments—hence, before humans fragmented the landscape, a single lightning strike could produce a fire covering tens or even hundreds of thousands of acres. Flatwoods, in contrast, occur in more dissected landscapes with natural firebreaks, so fire compartments are typically smaller.

Bill Platt and coauthors hypothesize that a fire-hydrology interaction is responsible for the restriction of trees from dry prairie. In their model, no difference in fire regime is necessary to explain the existence of dry prairie. In a typical landscape in central Florida, the characteristic lightning fire regime favors a balance between fire-adapted trees and warm-season grasses; hence, pine savanna is the dominant matrix vegetation (fig. 5.10). Dry prairie occurs at slightly lower elevations than pine flatwoods, however, and therefore is more subject to inundation (contrary to Harper's observation). When seasonal flooding is added to the environmental regime, the system shifts toward a prairie state because flooding stresses trees (fig. 5.11). Timing is important, too. Because fire activity peaks naturally during the transition from the dry to the wet season, trees in low-lying areas are subject to a "double whammy" of fire followed by flood, which makes survival of seedlings difficult. I am persuaded that some combination of the Bridges model and the Platt model explains the existence of dry prairies. With recent alteration of fire and hydrologic regimes in central Florida, trees have become more abundant in dry prairies than they were historically. Thus, managers must spend considerable time manually removing trees. Restoring natural hydroperiod, for example by filling old drainage ditches, may be necessary to reduce tree invasion.
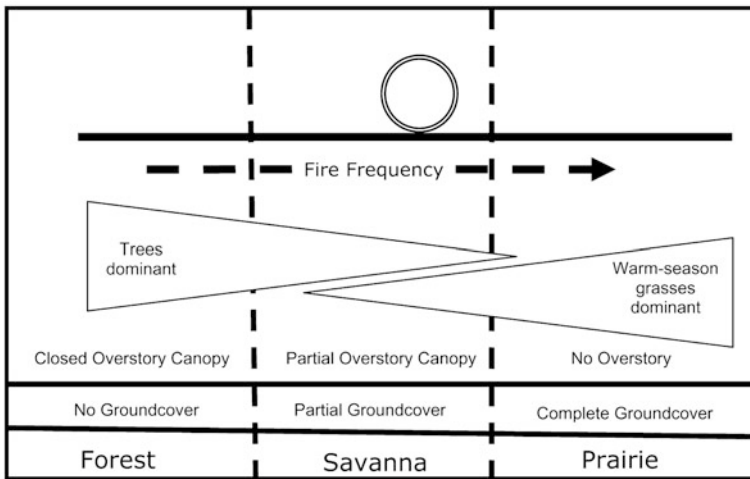
Figure 5.10. Hypothesized response of an ecosystem to fire frequency along a landscape gradient from forest to savanna to prairie. As fire frequency increases, relative dominance shifts from trees to warm-season grasses, with savanna occupying the middle ground. This is a neutral model, as indicated by the horizontal line below the circle (which represents the ecosystem); hence, a unit change in fire frequency moves the ecosystem with equal ease in either direction. With a fire regime typical of central Florida, an ecosystem is most likely to be in the central (savanna) position. From Platt et al. (2006).
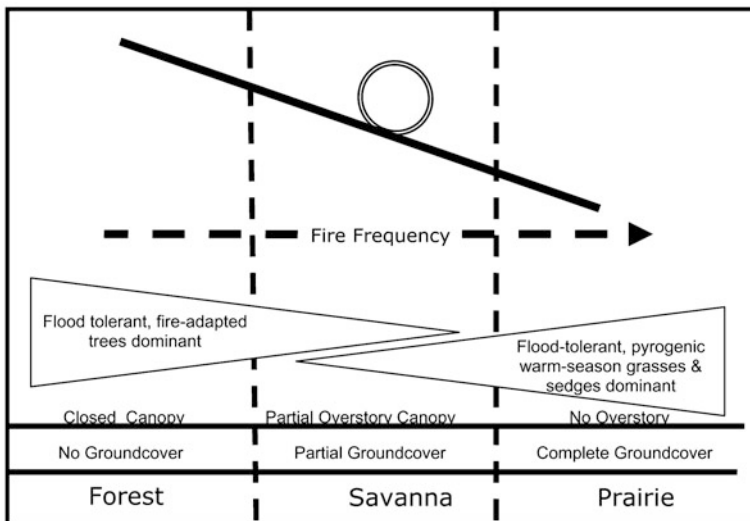
Figure 5.11. Predicted effects of frequent flooding combined with fire on the position of an ecosystem along the forest–prairie continuum. In contrast to fig. 5.10, this is not a neutral model. Rather, the slope of the line to the right indicates the effect of frequent flooding, which stresses even fire-adapted trees and shifts the ecosystem to a prairie state. From Platt et al. (2006).

THE ENIGMATIC CANEBRAKES

I close this chapter with a short account of one of the most enigmatic grass-lands of the South: canebrakes (fig. 5.12). The term *canebrake* usually refers to tall (historically up to twelve meters or nearly forty feet), dense monotypic thickets of the American bamboo or giant cane (*Arundinaria gigantea*), although it is sometimes applied to stands of the smaller switch cane (*A. tecta*). *Arundinaria* is a member of Poaceae, the grass family, so canebrakes are legitimate grasslands, though unlike any other in North America. Canebrakes, as an extensive eco-system, are nearly extinct. Why? To answer this question, we must consider potential combinations of factors that formed and maintained canebrakes.

Botanist Thomas Nuttall, descending down the Ohio River on his trip to the Arkansas Territory in 1819, first found cane by the mouth of Big Sandy Creek, on the Kentucky border. He wondered whether some change in cli-mate or soil explained its sudden appearance. Further downriver, cane became taller and more abundant. At the mouth of the Ohio River, Nuttall com-mented in his journal:

Figure 5.12. Canebrake, Pecano Plantation, 1905 or 1906, near current-day Waterproof, Louisiana, in Tensas Parish. USDA photograph (Bureau of Plant Introduction, negative no. 3208).

The summit of the bank, at the foot of which we had landed, was surmounted by an almost impenetrable and sempervirent cane brake; we measured several canes upwards of 30 feet in height. These wilds afford but little gratification to the botanist, their extreme darkness excluding the existence of nearly [every] herbaceous plant…the whole country here, on both sides of the Mississippi and the Ohio, remains uninhabited in consequence of inundation, and abounds with various kinds of game, but particularly deer and bear, turkeys, geese, and swans, with hosts of other aquatic fowls.

Canebrakes are part of the deep history of the South. Just how deep was made poignantly clear to me while visiting the Gray Fossil Site in east Tennessee, where bones of an ancient red panda were discovered. Its teeth indicate that it fed on bamboo, like the modern red panda (see chap. 2). It was evidently a canebrake specialist. Long after the American red panda went extinct, Native Americans, going back at least to the Mississippian period, promoted and made extensive use of cane, for example for house construction, fences, and a variety of weapons (knives, arrows, spears, blow-guns, darts, body armor, etc.) and personal items. Cane also was food. Shoots were collected in the spring and early summer, boiled, and eaten; seeds were pounded into flour. Steven Platt and coauthors describe southern tribes as a "bamboo culture."

The Indians observed that cane grew on the most fertile soils in the alluvial bottomlands. Hence, they cut down canebrakes to plant their crops (chiefly corn). Abandoned agricultural lands then often reverted to canebrakes. This is one common explanation for the occurrence of extensive canebrakes, and numerous historic accounts report invasion of fallow Indian agricultural fields by cane. This explanation begs the question, however, of how a species such as cane, which reproduces rarely (in mass flowering events every forty to fifty years) and is a poor colonizer, could rapidly invade disturbed areas. The reproductive biology of cane remains poorly understood. It is clear, however, that most reproduction is vegetative (asexual). Steven Platt and Christopher Brantley surmise that regrowth from preexisting rhizomes would have been rapid in abandoned fields; indeed, rhizome growth of six meters (twenty feet) within a single season has been reported. Indians also actively managed and maintained cane through burning, in part to favor bison, for which cane is one of the highest quality forage plants. Early white settlers regularly reported bison in canebrakes, as well as bear and other wildlife.

Some canebrakes, then, were partly anthropogenic, and their decline followed the decline of Native American populations. Nevertheless, as the red

panda fossils show, canebrakes inhabited the South long before humans arrived. Also, several nonhuman disturbances are known to favor cane. As noted by Nuttall, canebrakes occurred almost entirely within active floodplains, where floods would have encouraged frequent vegetative regeneration and reduced tree invasion. Now that most rivers have been dammed and otherwise controlled, this process has abated. As known by the Indians, fire also promotes canebrakes; today, fire is much less common than historically. Paul Gagnon and Bill Platt studied giant cane growing under a forest canopy and within a tornado-created gap, with and without experimental burning. The combined disturbance of windstorm followed by fire nearly doubled the growth of ramets (i.e., individual stems of the clone). Gagnon and Platt proposed that a combination of disturbances, especially fire following a canopy-opening event such as windstorm, ice storm, or flood, promotes canebrake development. Under these conditions canebrakes can exist as an alternative stable state to bottomland forest.

I suspect that passenger pigeons (*Ectopistes migratorius*) also created appropriate conditions for canebrakes. Their huge flocks, up to an estimated one billion individuals, broke apart tree canopies, which would have favored sun-loving cane. Their abundant excrement would have provided the high nutrient conditions with which extensive canebrakes were invariably associated. Such a scenario is consistent with the ecological effects of passenger pigeon flocks described by Joshua Ellsworth and Brenda McComb: "The activities of roosting and nesting Passenger Pigeons caused widespread, frequent disturbances in presettlement eastern forests through tree limb and stem breakage and nutrient deposition from pigeon excrement. We suspect that the deposition of fine fuels resulting from such disturbances may have influenced fire intensity and frequency." With the passenger pigeon extinct in the wild by the end of the nineteenth century (after being the most abundant landbird in the world just a century earlier), Native American agriculture and burning eliminated, and flooding greatly reduced by dams, the combination of disturbances and nutrient inputs that canebrakes require became exceedingly rare. Thus, truly large, tall canebrakes no longer occur anywhere. With their demise has come the extinction of Bachman's warbler (*Vermivora bachmanii*) and the decline of Swainson's warbler (*Limnothlypis swainsonii*), both known to prefer canebrakes. Restoring large canebrakes is a possibility that should be aggressively pursued.

REFERENCES

Bottom-up regulation: Cardinale et al. 2011

Top-down regulation, large carnivores, keystone and strongly interacting species, trophic cascades: Hairston et al. 1960, Paine 1966, Soulé et al. 1988, Koehler and Hornocker 1991, McLaren and Peterson 1994, Power et al. 1996, Maehr 1997, Hulbert 2001, Nowak 2002, Soulé et al. 2003, Thornton et al. 2004, Soulé et al. 2005, Beschta and Ripple 2009, Ripple and Van Valkenburgh 2010, Soulé 2010, Terborgh and Estes 2010, Estes et al. 2011, Dorcas et al. 2012

Fox squirrels: Weigl et al. 1989

Fire and fire surrogates: Harper 1911, 1914, 1927; Small 1927, Wahlenberg 1946, Komarek 1964, Mutch 1970, Myers 1985, Platt et al. 1988, Platt and Schwartz 1990, Bond and Midgley 1995, Glitzenstein et al. 2003, Varner et al. 2003, Duncan and Schmalzer 2004, Bond et al. 2005, Bond and Keeley 2005, Mann 2005, Brockway et al. 2006, Huffman 2006, Anderson 2007, Way 2008, Bowman et al. 2009, Gill 2009, Keeley et al. 2009, Gagnon et al. 2010, Menges and Gordon 2010, Slapcinsky et al. 2010, Willcox and Giuliano 2010, Duever 2011, Myers and Harms 2011, Staver et al. 2011a and 2011b

Insects: Tschinkel 2002, Earley 2004, King and Tschinkel 2008, Tucker et al. 2010

Large herbivores (including livestock), grazing, fire-herbivore interactions, grassy balds: Rostlund 1960, Jakle 1968, Owen-Smith 1987 and 1989, Weigl and Knowles 1995, Belue 1996, Giuliano et al. 1996, Knapp et al. 1999, Wiser and White 1999, Hulbert 2001, Morrison and Humphrey 2001, Mullahey et al. 2002, Main et al. 2004, Frost 2006, Means 2006, Barnes et al. 2008, Fuhlendorf et al. 2008, King and Tschinkel 2008, Barrow 2009, Staver et al. 2009, Tucker et al. 2010, Willcox et al. 2010, Allred et al. 2011, Pillsbury et al. 2011

Florida dry prairie and Florida grasshopper sparrow: Bridges 2006a and 2006b, Orzell and Bridges 2006b, Platt, Huffman, et al. 2006, Pranty and Tucker 2006, Noss et al. 2008

Canebrakes: Nuttall (1819) 1980, Platt and Brantley 1997, Brantley and Platt 2001, Ellsworth and McComb 2003, Gagnon and Platt 2008, Platt et al. 2009

The Future of Southern Grasslands: Outline of a Strategy

> Humanity is exalted not because we are so far above other living creatures, but because knowing them well elevates the very concept of life.
>
> Edward O. Wilson (1984)

I rode with Ann Johnson, plant ecologist with the Florida Natural Areas Inventory (FNAI), and Wilson Baker, one of the finest all-round naturalists in north Florida, in Wilson's pickup truck. The truck was loaded with books, boots, nets, binoculars, plant press, and other tools of the naturalist's trade. It was late October 2010, deep in Jackson County in the Florida Panhandle. We traveled the dirt road up the hill, around the edge of large quarry, and then up a steeper hill through dense second-growth woods until the road became a narrow jeep trail and the trees that had fallen across it were too big to move out of the way. A chain saw was one tool Wilson hadn't brought along. We parked and continued up the hill on foot, identifying plants along the way. It was cool enough for jackets, the early morning sun casting diagonal rays through the many layers of leaves. We were headed uphill to visit the largest and best remaining example of a Jackson glade, one of two subtypes of the upland glade natural community (the other is Gadsden glades, in Gadsden County). Wilson and Ann are experts on upland glades, one of the rarest natural communities in North America.

We hadn't walked long when we saw the opening ahead. I was excited. I had always wanted to visit Florida upland glades since first hearing about them years ago and then reading about them in the *Guide to the Natural Communities*

of Florida on FNAI's website. This is an endemic community, containing a mixture of plants distinct from any other. Most Jackson glades are dominated by black bogrush (*Schoenus nigricans*) in a mosaic with the much lower-growing poverty dropseed (*Sporobolus vaginiflorus*). Different sets of plant species are associated with black bogrush versus poverty dropseed. It is unexplained how black bogrush thrives on these dry upland sites; as noted in chapter 4, this is a wetland plant everywhere else across its unusual distribution.

As we reached the clearing, we immediately knew something was wrong. My heart sank as walked into the sunlight. Fresh bulldozer tracks criss-crossed a large portion of the glade, exposing the shrink-swell clay, now dry and powdery from drought. In a small clump of plants remaining in the bulldozed area, we found an individual basal rosette of *Coreopsis* sp. *nova*, a species of *Coreopsis* (coreopsis or tickseed, in the family Asteraceae) new to science. Ann discovered this local endemic, which is somewhat similar to *C. lanceolata*; it has been found nowhere else but in a couple of these Jackson glades. Looking at this little plant surrounded by devastation, I realized that it could be driven extinct in the wild before it even gets a proper scientific name. This kind of tragedy occurs routinely in developing countries, for example as endemic-rich rainforest is cleared for cattle pasture or oil palm plantations. But here in the United States? In Florida, which has one of the largest concentrations of wealth in the world? Can't we afford to behave more ethically?

Most people, detached from natural history, couldn't care less about this *Coreopsis* or the upland glade community. The landowner, who had given Wilson and Ann permission to visit, runs the adjacent quarry operation. He had been informed of the significance of this site and had verbally agreed to protect it. Voluntary protection, championed by some conservationists as an alternative to acquisition or regulation, has little substance. This act of destruction is entirely within the law. The land is his property. Even if this *Coreopsis* had already been listed under the US Endangered Species Act, he could bulldoze the entire population to extinction with impunity, because plants on private lands are not protected by the act.

About a year after our visit, I mustered the courage to ask Ann if she had returned to the bulldozed glade and if it were now completely destroyed. She replied that she had recently visited and—good news—the site had not been damaged further since we had been there. Glade species were even beginning to grow back in the denuded area, demonstrating resilience of this tough community. Wilson had talked to the landowner about the damage. He said it was not intentional; it was just some of the "boys" joyriding with the heavy equipment. I've seen this before—if you give a man a piece of powerful equipment,

he will play with it just like a little boy with toy trucks in a sandbox. For better or worse, rednecks never grow up (to be fair, nor do naturalists, and I'm proud of it). Ann also gave me some unwelcome news. Two smaller glades belonging to the same landowner, which he had *not* agreed to protect, were recently mined and are unrecognizable. As of this writing, no high-quality upland glade has been afforded protection. A small degraded glade exists within Florida Caverns State Park. Two Gadsden glades are on Department of Corrections land, but are being managed poorly.

During our visit, Wilson and Ann explained how, for years, they had tried to interest The Nature Conservancy (TNC) in protecting these upland glades, to no avail. With some notable exceptions, TNC has been more interested recently in the conservation of large landscapes, usually "working landscapes" with active cattle ranches, silviculture, or other economic activities. Many of these landscapes contain nothing highly imperiled. I felt a sharp pang of guilt. Beginning in the early 1980s I published a series of papers arguing that conservationists have focused too narrowly on saving small sites with rare species, many of which are climatic relics that are much more common elsewhere. Conservationists, I argued, should emphasize the protection and restoration of large landscapes and "functional mosaics" of communities, which compose the characteristic natural vegetation of a biogeographic region, rather than concentrating on quirky "museum pieces" that are too small to contain viable populations of many species and are difficult to protect and manage.

Slowly but surely, my ideas caught on all too well. TNC and many other conservation groups jumped on the landscape bandwagon and now have come perilously close to abandoning the protection of inherently small communities and sites with concentrations of endemics and other imperiled species. This rather radical switch parallels a growing infatuation of conservationists with ecosystem services. It is quite easy to see how large landscapes could provide ecosystem services to human society, such as protecting water quality and supply. To imagine how tiny patches of grassland and obscure little plants or bugs found nowhere else in the world could benefit humans is quite a strain. You have to learn to love these crazy little places and unassuming species for reasons totally apart from their direct utility to humans. You have to appreciate them for what they are, for themselves, as places and as creatures every bit as worthy of respect as we are. Naturalists tend not to talk much about intrinsic value, leaving such esoteric concepts to the philosophers. Yet, by seeing each species and community as inherently interesting and important, naturalists intuitively recognize this value.

Especially since engaging in this book project, I recognize that, collectively,

the small, weird sites contain a substantial fraction of a region's biodiversity and often the majority of its truly distinctive and endemic taxa. Their conservation value is complementary to that of large, functional landscapes. As for climatic relicts and other disjuncts, even if these species are common a few hundred miles away, they tell fascinating stories about the biogeographic history of a region; furthermore, they are likely distinct genetically and on the cutting edge of evolution. Today I strongly urge reconciliation of small-site and large-landscape conservation.

A CONSERVATION STRATEGY FOR SOUTHERN GRASSLANDS

This is a short chapter, relative to the previous few. I have been writing about conservation strategy, methods, and tactics for decades, and I do not want to be redundant (or bore myself). A conservation strategy for southern grasslands should encompass several iterative and overlapping phases: prioritization, protection, restoration, and management. By "protection" I do not mean closing an area to all human uses (although this is sometimes necessary for extremely sensitive sites), but rather prohibition of uses that are incompatible with biodiversity conservation objectives. Compatible uses, such as hiking, natural history study, many types of research, and even some direct economic uses, should be encouraged because people will want to protect what they know and appreciate.

Conservation planning for southern grasslands should be coordinated with planning for all other ecosystem types and their associated species across a region. Each major ecosystem (e.g., at the ecological systems level of classification) deserves its own conservation plan, and the most highly imperiled taxa warrant individual recovery plans. This tiered strategy is consistent with the philosophy and methodology of the generally successful coarse/fine-filter approach to conservation developed by Bob Jenkins of TNC in the 1970s and refined by many ecologists since then.

Prioritization

Prioritization is fundamental to conservation planning. It is best pursued boldly, based on what the best available science suggests is needed to fulfill biological goals, rather than timidly, constrained by theories of what is politically feasible. The following principles can guide prioritization of grasslands and other ecosystems for conservation.

No more development on natural or seminatural lands

It is best to start out ambitious rather than come to the bargaining table meekly begging for a few scraps. Conservationists must articulate a simple message: no more development on the remaining natural and seminatural lands. Paul Ehrlich and several other biologists, including me, have recommended a policy of this sort for many years. Such a policy will not be achieved overnight, but with scientifically informed land-use planning, accompanied by economic and social incentives to reduce population growth (immigration as well as births) and move to a sustainable steady-state economy, this seemingly impractical objective could someday evolve into political reality. It must, if we are to reduce the magnitude of the current mass extinction event. During a period when growth continues but slows, refraining from development on natural and semi-natural lands will seldom impose hardships. There is plenty of space to build within urban cores and on some surrounding lands that are already degraded and can accommodate additional development with few new impacts on species and ecosystems.

Argument will arise about what constitutes seminatural land; a science advisory committee could assist states or counties in making such determinations. Where I live, seminatural lands include mostly undeveloped ranches (rangelands) and dilapidated citrus groves, as well as some pine plantations and other types of relatively low-intensity agriculture. Many of these lands warrant increased protection and restoration, but let's at least safeguard them from urban development or other further degradation for the time being. The status quo is not so bad when compared to high-growth future scenarios. Virtually everyone except developers and their political cronies would benefit, in terms of physical and emotional health, aesthetics, recreation, and property values, if we simply stopped building unnecessary subdivisions and other developments in exurban areas or anyplace else where reasonably high-quality habitat for native species still exists. Who needs one more vacant strip mall? Who needs neighborhoods like mine, half full of foreclosed and empty homes, while brand new subdivisions spring up nearby?

Every rule must allow for exceptions. Besides the first and second laws of thermodynamics, and a few other physical laws, I'm hard pressed to come up with absolutes in nature. Cases will arise where, for example, a road needs to be widened, a pipeline built or replaced, or a new school building constructed on natural or seminatural land. Such developments should proceed if they are truly mitigated by habitat improvement on-site or off-site, not the fake mitigation we see in most projects—"protecting" habitat, such as jurisdictional wetland,

which is unlikely to be developed within the foreseeable future. The result of these shady deals is inevitably a net loss of habitat. What makes true ecological mitigation possible is that habitat for a species or a set of species is not merely quantitative; it is also qualitative. It is measureable not only in acres, but also in its carrying capacity or potential population growth rate for species of concern. For example, we could lose five hundred acres to development if another two thousand acres are dramatically improved in quality for the species in question through prescribed burning, control of invasive nonnative species, or other legitimate restoration and management actions.

Prioritize using multiple criteria at several spatial scales

Protecting all undeveloped natural and seminatural habitat is the most defensible course, but even with the best intentions it cannot be implemented immediately. During the transition to a no-growth, steady-state economy (the only viable option for sustaining life on earth), we must identify and rapidly protect the lands and elements of biodiversity of highest conservation value and vulnerability. The following are some key steps:

1. Identify, map, and protect hotspots of biodiversity. As reviewed in chapter 3, endemism is the most robust measure for geographic prioritization and has many spinoff benefits. Prioritization focused on endemic taxa may protect more total species and more threatened species than a strategy focused on species richness or threatened species. Centers of endemism are often hotspots of evolution and refugia within which species persist during climate change. The rarity-weighted richness hotspots identified by NatureServe represent concentrations of range-restricted imperiled and critically imperiled taxa (plate 1). Protecting as much as possible of these irreplaceable landscapes provides a foundation (albeit incomplete) for a regional conservation plan. Site-selection algorithms and other prioritization methods and principles, as reviewed in a 2009 book edited by Atte Moilanen, Hugh Possingham, and Kerrie Wilson, allow the conservation planner to set quantitative targets for protecting designated elements of biodiversity and arrive at efficient mapped solutions (e.g., reserve networks).

2. Employ prioritization methods hierarchically at several geographic scales, because patterns in distributions of species vary across scales and levels of spatial resolution, and because planning at several geographical extents (e.g., counties, states, ecoregions, floristic provinces) allows

for more comprehensive protection. For example, plate 1 shows many regions as predominantly blue or white, hence lacking in conservation value by the rarity-weighted richness criterion at this spatial extent. A finer-resolution investigation within these blue and white areas would reveal smaller hotspots for some taxa that are legitimate priorities on a local, state, or subregional scale, if not more broadly. For example, a map of rarity-weighted richness for plants in Florida (fig. 6.1) reveals several hotspots that do not show up in a national multitaxa analysis (plate 1).
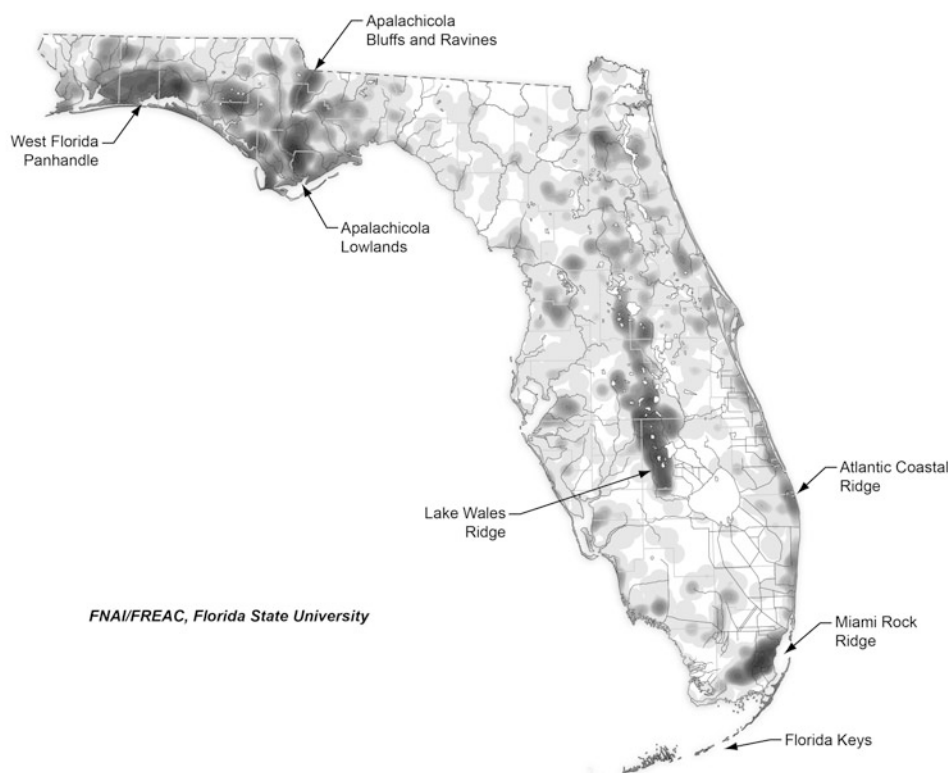
Figure 6.1. Rare plant hotspots in Florida, based on rarity-weighted richness of restricted range (endemic) plant species. This analysis applied a 100 × 100 meter cell size (1 hectare = 2.47 acres) and an approximately ten-kilometer search radius. Compare this map to plate 1, produced at lower resolution (ca. 160,000 acre cell size) for all inventoried taxonomic groups combined. Adapted from Knight et al. (2011).

3. Represent all ecosystem types across their natural range of variation. Representation has been a dominant theme of conservation planning in North America since the early twentieth century (among ecologists, at least). The idea is that protecting the full suite of ecosystem types (plant

communities, physical features such as landforms, geological and soil types, etc.) serves as a coarse filter that protects large numbers of species associated with these ecosystems. By protecting a natural community, such as shale barrens or mesic flatwoods, across its range of variation in sufficiently large or connected patches, and managing it to perpetuate natural processes, we protect most species that live there. The coarse-filter assumption is difficult to test, especially for the poorly known taxa that might benefit most from it, but we have few other options for such species. A combination of abiotic (e.g., geophysical) features and biotic features (e.g., vegetation classes) in a site-selection process is optimal and, as noted earlier, will assist adaptation to climate change.

4. Base ecosystem representation goals (targets) on the historic distribution and extent of ecosystems, not just the current distribution (taking into account any shifts that can be traced to climate change). For instance, an ecosystem that has lost only 10 percent of its area since settlement might be considered very well represented if we set aside half of the remaining distribution in conservation areas. In contrast, every remaining acre of an ecosystem that has lost 90 percent or more of its area should be protected, with additional area restored to the greatest extent feasible.

5. Protect wild and intact landscapes. Many regions of North America would be considered of low conservation value on the basis of endemism or rarity-weighted richness. Nevertheless, some of these regions have other biological and ecological values, such as large tracts of undeveloped forest or vast areas of grassland or marginal farmland with low human population density (e.g., the Great Plains) where intact ecosystems replete with bison, elk, wolves, bears, puma, and other megavertebrates could be restored. Low road density is the clearest indicator of intactness. In the South many landscapes with surprisingly low human footprint still exist, including (outside cities) much of the Appalachians; the Cumberland Plateau and Highland Rim of Tennessee, Kentucky, and northern Alabama; south and central Florida; the Florida Panhandle; northeastern Florida and adjacent Georgia (Okefenokee Swamp and surroundings); portions of the Piedmont; western Alabama and adjacent Mississippi; western Mississippi and adjacent Louisiana; western and northern Louisiana; and a large part of Arkansas.

     Cindy Thatcher and colleagues identified suitable reintroduction sites for the Florida panther across the Southeast (south of Kentucky and

Virginia), which in the first cut are essentially the wildest parts of their study area. They note that "anthropogenic factors heavily influenced our landscape model." Thus, areas suitable for reintroduction have low human population and road densities and largely natural land cover (fig. 6.2). Besides the potential reintroduction sites (A-I) identified in figure 6.2, many other areas (i.e., moderate to dark shades of gray in the map) should be considered for wilderness recovery (rewilding). The rewildling process would include closing unnecessary roads, reintroducing native large herbivores and carnivores and other extirpated species, removing dams, and allowing wildfires to burn unconstrained wherever feasible.
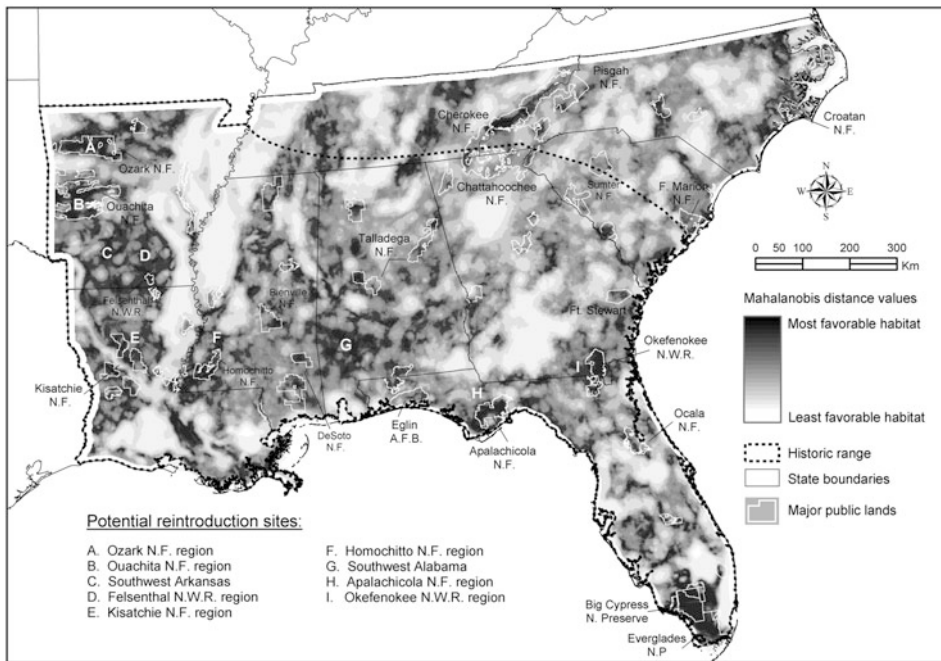
Figure 6.2. Potential reintroduction sites of Florida panthers in the southeastern United States. Areas in darker shades of gray have lower human population density, lower road density, more natural vegetation cover, and more aggregated patches of natural vegetation. Hence, these are the wildest landscapes in the region. Road closures and other "rewilding" can make them still more suitable for wilderness-associated species and restoration of a full suite of natural processes and vegetation mosaics. © 2006 by The Wildlife Society. Reprinted from Thatcher et al. (2006) with the permission of the publisher.

6. Identify, map, protect, and restore landscape connectivity on many spatial scales, including species-specific movement corridors, landscape link-ages between conservation areas and other areas of high conservation

value, and overall landscape permeability provided by a well-managed matrix. Recognize, however, that dispersal-limited species (e.g., gravity- or ant-dispersed plants) may not be able to recolonize even marginally isolated grassland patches on their own; active introduction of propagules may be necessary. Assisted colonization, applied cautiously, will be needed to help some species adjust their distributions in response to climate change and sea-level rise, especially in fragmented landscapes. It is important to remember that many grassland types and other imperiled communities exist naturally as small, isolated patches; artificially connecting these would not be prudent.

7. Consider landscape context in prioritization decisions. In particular, if there is a choice and all else is about equal, select sites and landscapes that are minimally fragmented by human land uses or where habitat connectivity for species of interest can be feasibly maintained or restored. A small scrap of seminatural habitat surrounded by subdivisions could be sacrificed (albeit with potential loss in natural history education value to the human community) in favor of protecting a parcel adjacent to an existing conservation area or one that may function as a landscape linkage between two conservation areas. Nevertheless, if a site, however small or isolated, holds potentially viable populations of endemic or other imperiled taxa, it must never be sacrificed. Another key point is to pursue every opportunity to conserve grasslands within their natural landscape context, that is, in a functional mosaic with other vegetation.

8. Identify the critical abiotic and biotic processes (including bottom-up, top-down, and sideways processes; see chap. 5) that maintain southern grassland ecosystems, and design protected area networks explicitly to assure optimal operation of these processes. Sites and species vary in their importance for ecological processes. For example, groundwater recharge areas (e.g., sandhills) and discharge areas (springs and seeps) are of high hydrological value, and sites where natural disturbances are initiated (e.g., a ridge that attracts lightning strikes) may be critical for the operation of disturbance regimes on a landscape extent. Ecologically pivotal species should be a priority for protection as ecologically effective populations.

9. Give individual attention to the most highly imperiled and ecologically and evolutionarily most distinctive taxa, natural communities, and sites.

Species that often require this attention include narrow endemics, ecologically pivotal (strongly interactive) species, species highly sensitive to human impacts, and phylogenetically distinct taxa.

Don't fall into the trap of triage

Prioritization is not the same as triage, although some conservationists have attempted to equate the two. Triage is an emergency strategy developed by French medics during World War I to address the quandary of too many wounded soldiers being hauled out of the battlefield to treat them all. Each wounded soldier is assigned to one of three categories: (1) those who are likely to live, even with no medical care; (2) those who will probably die, regardless of what the medics do; and (3) those for whom immediate care might make all the difference between life and death. Medics would focus their attention on the last category.

Conservationists have recently latched onto the triage idea. In the context of conservation, triage would "write off" some sites, species, and natural communities as too expensive, too close to extinction, or otherwise impractical to save. Many of the same conservationists who endorse triage are champions of the ecosystem services argument for conservation. Therefore, species, communities, and places that have no apparent economic or other utilitarian value to humans—such as the many amazing endemic species, disjunct populations, and unique natural communities whose stories fill the pages of this book—could be considered unworthy of conservation effort, especially if such effort were costly. Species on the brink of extinction or places about to be bulldozed would be dismissed as hopeless. By placing these elements in the category of lost causes, we effectively preclude further consideration of them even if more money or new technologies become available, or if species new to science are discovered in an area that previously was written off as unimportant.

Perhaps, if conservation biologists were the decision makers, they would exercise flexibility in the application of a triage strategy, for example by broadening the scope of species and places to be protected if politics change or if more money becomes available. We would apply what I've called "informed opportunism." In the real world, developers, industries, banks, and their politician friends call the shots. Do we really think a state or county agency will revoke the development permits for a new "big box store" in a prairie when conservationists suddenly tell them to ignore their previous advice, because a snail new to science has just been discovered there?

Triage supports the status quo by assuming implicitly that radical change, or even new knowledge, is impossible. Writing species and places off as imprac-

tical to protect violates the widely held ethical principle that nature, and every single species, is valuable for its own sake. As opposed to triage, conservation prioritization identifies the most critical sites to protect in the near term: those that have the most to lose biologically if we do not act quickly, and those that can be acquired relatively cheaply at present and offer high long-term benefits. Prioritization in this sense does not write off anything. Species, communities, and places of lower priority, for example because they are not endemic, not highly threatened or vulnerable (or, conversely, are right on the brink), or too expensive to protect in the short term, are not abandoned. Rather, conservation action on their behalf is postponed until we address the more urgent and promising cases and generate the political will and funds necessary to protect everything in need. While lingering on the waiting list, inevitably some species, communities, and places will be lost. That will be tragic, but at least we are not complicit in their extinction. We did not callously place them in a category of lost causes, even if they ended up being so. We did our best, but failed to get to them in time. We can avoid such tragedies only by changing human attitudes and politics to a point where conservation gets the funding and other attention it deserves.

Protection

Some conservationists today consider *protection* an antiquated and culturally biased idea. Evidence of rapid climatic change, in the past as well as today and for the foreseeable future, is used to argue against protected areas, which are assumed to have fixed boundaries. There is no inherent reason why protected areas must be static. I trust, for example, that most Americans would agree that Everglades National Park is a special place worth saving. Given that assumption, the northern boundary of the park will have to be moved northward as most of the park goes underwater due to sea-level rise over the next century or so. The park will remain valuable as a protected area, but it must be expanded into less than pristine habitat in order to facilitate shifts in species distributions inland and northward. Habitat restoration, and even creation of new habitat (for instance, converting abandoned sugar cane fields to marl prairie, if we can figure out how to do it), becomes increasingly necessary in such a dynamic environment. Without the park, whatever its future configuration and conditions, plus other protected areas in south Florida, all land would be open to development and biodiversity would plummet. Just look at Miami, Ft. Lauderdale, or Naples for a horror story of what a future south Florida, devoid of protected areas, would hold.

    I define a protected area as a legally designated area where the conservation

of biodiversity is a primary goal. Depending on its sensitivity, a protected area may be open to a variety of uses that are deemed compatible with its conservation goals. My colleagues and I presented arguments for why protected "core areas" remain a cornerstone of conservation in a 1999 book edited by Michael Soulé and John Terborgh, *Continental Conservation*. Yet, as other chapters in that book and the literature in conservation biology make clear, strictly protected areas are not sufficient to maintain biodiversity. They probably will never be big, numerous, or representative enough to do the job. Most have been situated in areas of low economic value, such as at high elevations or on poor soils.

Another limitation of a protected areas strategy is that it sometimes encourages black-and-white thinking by implying that everything outside of protected areas is useless for conservation. The landscape is visualized as binary: protected habitat versus unprotected nonhabitat. In truth, many landscapes have become binary as a result of intensive agricultural or urban development. In such landscapes the area and isolation of remaining patches of natural habitat are central determining factors for species persistence and overall biodiversity. Most landscapes, thankfully, are not yet that dichotomous—they are complex, with considerable variation in habitat suitability for many species.

Laura Prugh and colleagues conducted a synthesis of patch occupancy data from eighty-nine studies of terrestrial animals, involving 785 species. They found that patch area and isolation are important factors affecting occupancy of many species, but nevertheless poor predictors for most species. Hence, the habitat/nonhabitat dichotomy is an oversimplification, even in fragmented landscapes. For many amphibians, for example, habitat quality (which is not considered in simplistic fragmentation analyses) proved to be better than patch area as a predictor of population size and extinction risk. The authors reasoned that improving the quality of the landscape matrix outside protected areas "may lead to higher conservation returns than manipulating the size and configuration of remnant patches." Jerry Franklin and David Lindenmayer are articulate spokesmen for the importance of the landscape matrix. Commenting on the study by Prugh et al., they advise that "the future of the vast majority of the earth's species will depend on how the matrix is managed—including not only the human-perceived habitat patches, but also the extensive areas that surround them."

Southern grasslands occur within a wide range of landscape contexts. In some cases, such as the pine rocklands of the Miami Rock Ridge, the landscape is strongly binary. Very few of the specialized endemic and characteristic species of pine rocklands could persist within the urban environment of Miami. Remnant cedar glades within the metropolitan area of Nashville are in a similar situation. In these cases, a primary focus on protected habitat patches makes

sense. Most of the grasslands considered in this book, however, exist within a softer and more variegated matrix. Some endemic grassland species today find their primary habitat in such places as powerline rights-of-way and roadsides. In other situations, as discussed in chapter 5, seminatural grasslands and even monoculture pastures support species of high conservation concern. The large cattle ranches of Florida, although they could be managed better, fulfill crucial ecological and biodiversity-maintenance functions. The main limitation I see in concentrating on matrix management for conservation is that this approach cannot be assumed to meet conservation goals unless legally binding and enforced regulations keep land use in the matrix fully compatible with these goals. This is usually not the case; with increasing human population and development, matrix quality declines over time. Hence, there is a continuing need for strictly protected areas.

Strictly protected areas and a well-managed landscape matrix are not mutually exclusive. They are both more effective when combined with the other into a fully integrated approach to landscape-scale conservation. A comprehensive strategy should, wherever feasible, encompass a gradient from strictly protected areas, through a variety of multiple-use buffer and transition zones, to a more or less intensively used matrix (fig. 6.3). Designated corridors connecting core areas and spanning environmental (e.g., climatic) gradients should be included in cases where the matrix does not offer sufficient permeability for dispersal and other movements of fragmentation-sensitive species (again, however, some grassland communities and populations are naturally isolated). An ideal reserve network would contain core areas large enough to represent many natural communities as functional mosaics and to "manage themselves" with a natural disturbance regime. Few such opportunities remain in the South, but there are some. More commonly, in situations where core areas are small and where optimal buffer zone and matrix conservation is precluded by development, we must resign ourselves to intensive management of protected patches.

Restoration and Management

Restoration ecologists have been in a soul-searching mode recently, after being confronted with incontrovertible evidence that the pre-European settlement baseline, on which they had founded their restoration targets, is something that cannot—and perhaps should not—be returned to. Nature is dynamic, not static. Few ecosystems, as we know them today, have existed for more than around twelve thousand years, and some are only a few centuries old. The logical conclusion is that a fixed target for preservation or restoration is no longer defensible. Conservationists and restorationists have a moving target. As Stephen

Human-Dominated Matrix
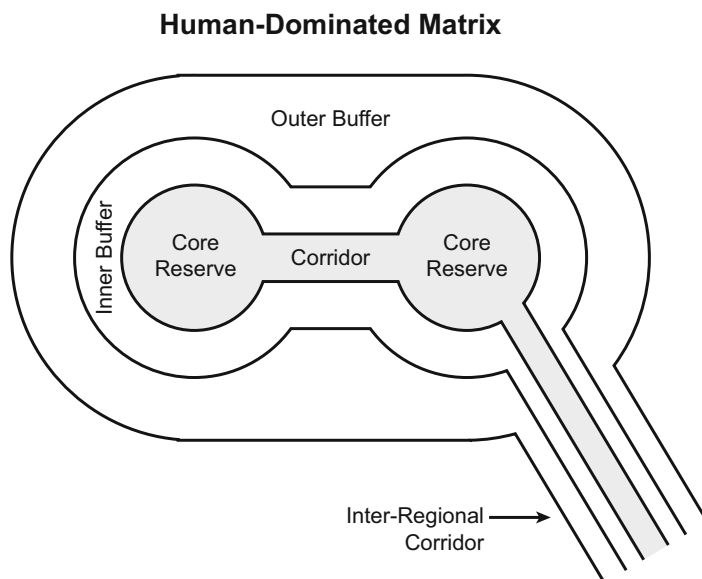
Figure 6.3. A conceptual network of core reserves, buffer zones, and connecting corridors (connectivity) within a human-dominated landscape. The network could vary in spatial scale from core areas a few acres in size to more than a million acres. The network model would be turned inside out in a wildland landscape, where the core areas are towns or other human developments, the corridors are transportation corridors, and the matrix is wildland. After Noss (1992).

Jackson and Richard Hobbs observed in a 2009 article, "In the long run, no inherent natural ecosystem or landscape configuration exists for any region."

Richard Hobbs and coauthors (2011) advocate a shift from restoration ecology and conservation biology to "intervention ecology." Given my prowilderness inclinations, I tend to distrust human intervention, which often displays the hubris that we can manage the land better than nature can. I have seen too many examples of intervention gone wrong. In chapter 5, I addressed the fallacy of managers believing that prescribed fire is superior to wildfire. As another example, human interventions that increase habitat diversity on a local scale usually increase species richness in that local landscape—sometimes markedly—but most of the added species are weedy, exotic, or otherwise thrive with human disturbance. As the more sensitive and endemic species are lost from one landscape after another, the consequence is reduced diversity and distinctiveness on a regional and ultimately global scale—what ecologist Hal Mooney has called "biotic homogenization."

Interventionist thinking is blossoming in crazy directions within the environmental movement. Author Mark Lynas writes in his book, *The God Species:*

Saving the Planet in the Age of Humans, "Nature no longer runs the earth. We do. It is our choice what happens from here." Such sentiments are as naïve as they are arrogant. Modern humans (*Homo sapiens*) have been around for no more than 250,000 of the 4.6 billion years of earth history. We may temporarily hold the reins of power, but we could be bucked off in a geological instant by a pandemic, global nuclear war, or the next big meteorite that strikes the earth. Megalomania has no legitimate place in conservation. More sensible is the plea by Emma Marris in *Rambunctious Garden*: "We've forever altered the Earth, and so now we cannot abandon it to a random fate. It is our duty to manage it." Yet, sooner or later, the global human population will crash and we will eat the ultimate humble pie. I am reminded of my favorite bumper sticker: "Nature Bats Last." Our challenge is to minimize damage to the earth while we are here, which can be accomplished only by reducing our population and consumption, while managing ecosystems with utmost care and respect.

I accept that conservation and restoration, as conventionally defined and implemented, are not up to the task of maintaining biodiversity during the current and near-future chaos of human overpopulation, massive habitat transformation, and rapid climate change. As Jackson and Hobbs put it, "Past and ongoing environmental changes ensure that many historical restoration targets will be unsustainable in the coming decades." The extinction of many species, including ecologically pivotal ones, makes it impossible to return to what wilderness purists might consider the ideal historic state. We are forced to be more proactive and interventionist, and accepting of novel ecosystems, if we want to reduce extinctions and keep a rich natural history around us.

Some advocates of novel ecosystems and the engineering of nature suggest that looking to the past for guidance is not helpful, since past conditions were historic quirks that will not carry on to the future. This is a blatant non sequitur—we simply need to look further into the past than the time of European settlement. Knowledge of geologic history and paleoecology is necessary precisely because it informs us of the ranges of variability in natural processes and ecosystem structure and composition well beyond a human time scale. Geologist Joe Donoghue of Florida State University determined that, since the Last Glacial Maximum 20,000 years ago, rates of sea-level rise on the geologically stable Gulf of Mexico coast have sometimes exceeded forty-five millimeters a year—that's equivalent to nearly fifteen feet in a century—twenty times faster than today's rate and faster than all but the most extreme estimates for the next century. This knowledge should not make us complacent about modern sea-level rise, but it shows that coastal ecosystems have had to cope, and change, with such stresses over many thousands of years. The fossil (includ-

ing fossil pollen) record indicates that many species that coexist in communities today were separated at various times in the past and vice versa. On the other hand, vegetation similar to today's existed up to millions of years ago in parts of the Coastal Plain, especially peninsular Florida, and some edaphic grasslands (e.g., cedar glades in Middle Tennessee) may have persisted relatively unchanged through major swings in regional climate and vegetation during the Pleistocene and Holocene. With the rapidity of climate change today, we will soon find ourselves surrounded by "no-analog communities," combinations of species that do not coexist today and perhaps never did in the past. Insights from deep history will help us prepare for a no-analog future, while protecting climatic refugia will allow at least some local hotspots of endemism to persist through a changing climate.

The concept of "historic range of variability" (HRV), as opposed to fixed historic targets, encourages ecologically informed flexibility in conservation and restoration planning. Most applications of the HRV concept have considered variability on temporal scales ranging from a few decades to a couple millennia. Our increasing knowledge of past and likely future climate and vegetation change suggests that our concept of HRV be expanded to a temporal scale of tens of thousands to even a few million years, because this is the time span over which many or most extant species have evolved and have had to cope with continuously shifting climatic conditions. Environmental change threatens species with extinction when it falls outside the range of variation that they have experienced over their evolutionary histories, assuming relative constancy in genetic diversity and evolutionary potential.

An additional consideration is that various kinds of environmental change interact and are often synergistic. For example, the current rate of climate change would pose much less threat to biodiversity, were it not played out on landscapes highly fragmented, simplified, and otherwise degraded by human activity. A degraded landscape makes it much more challenging for species to shift distributions or otherwise adapt to change. The collapse of many species to small populations has reduced their genetic variability and their potential responsiveness to natural selection imposed by climate change and other environmental disruption. All of this makes human intervention more necessary if we want to forestall, or at least reduce, mass extinction.

We know the earth is changing rapidly, climatologically and biologically, but we have little idea of what the novel ecosystems and no-analog communities of the future will look like. In line with the "shifting baseline syndrome" defined by Daniel Pauly, our perception of what is "natural" keeps shifting toward more and more degraded ecosystems with each new human generation. We find ourselves

satisfied with less and less, and we set our ambitions continually lower. This must change. Through consideration of the past, the present, and potential future scenarios, we know that (1) native grasslands have declined tremendously in the South since EuroAmerican settlement; (2) some species and natural communities continue to decline rapidly and are on the verge of extinction; (3) historic, species-rich grasslands appear to have been more resilient to environmental change than impoverished human-altered grasslands; and (4) grassland ecosystems that operate within the range of variability (e.g., in disturbance regimes) that their native species experienced during their evolutionary histories are likely to retain more species and resilience than ecosystems widely outside of historic bounds. Prudence suggests protecting as much grassland area as we can, restoring ecosystems to something resembling their natural historic conditions, and trying to figure out how to hang on to this diversity as the world changes.

Hanging on to dynamic biodiversity in the face of uncertainty about the future requires a flexible and learning-oriented management approach—what is usually called "adaptive management," but some call "results-based management" or other things. A simple definition of adaptive management was offered in a 2010 paper by Alison Howes and colleagues as "an iterative process of gathering new knowledge regarding a system's behavior and monitoring the ecological consequences of management actions to improve management decisions." In practice, adaptive management often has been an abysmal failure, but the defect is in the implementation (i.e., politics getting in the way), not in the soundness of the concept. Some basic and sensible components of adaptive management of grasslands and other systems are

- recognition that the system being managed will never be understood completely, which is reflected in uncertainty about the ecological model chosen to represent the system;
- acknowledgment of uncertainty about what policy or practice is "best" for the particular management problem, which is reflected in multiple competing hypotheses about the effects of management practices;
- implementation of a plan of action designed to reveal critical knowledge about the system and its response to management that is currently lacking;
- acknowledgment of the trade-off between gaining the most knowledge about the system versus achieving the best short-term results, and attempting to balance these often competing objectives;
- monitoring of carefully chosen response indicators to evaluate the outcome of alternative policies or management treatments;

- analysis of management outcomes in consideration of the original objectives;
- incorporation of the results of management experiments and other learning into decisions about new policies and management strategies and actions.

To be useful to managers, adaptive management must be linked to a decision-support framework. Managers should be able to evaluate the probabilities of effects of different policies or actions and, from there, make well-informed and defensible decisions. The entire process must be highly transparent, so that members of the public (including naturalists!) who care about such decisions can contribute their knowledge and advice and serve as watchdogs of the agencies.

EXAMPLES OF RESTORATION PROJECTS

I discussed specific restoration and management issues in chapter 5, in relation to fire, mechanical surrogates for fire, livestock, and hydrology. The following brief case studies provide snapshots of approaches that managers are applying to restore grasslands across the South today. They are quite encouraging.

May Prairie, Tennessee

May Prairie is a 250-acre natural area near Manchester, Tennessee. I visited here twice during this project, first with Brian Bowen of the Tennessee Natural Areas Program and later with my family. May Prairie was discovered botanically by A. J. Sharp and colleagues from the University of Tennessee in 1947, after they had lunch at the adjacent Prairie Café, where they were informed of a prairie just behind the restaurant. The site includes a little bluestem community, a tallgrass prairie, sedge meadows in wet depressions, and post oak woodland. During my July visit, I was lucky to find in bloom the only Tennessee population of the snowy orchid (*Platanthera nivea*), disjunct from the Coastal Plain. Another Coastal Plain disjunct, coastal plain bog asphodel (*Triantha racemosa*), also occurs here, as well as many species typical of midwestern prairies. Tennessee botanist Dwayne Estes, of Austin Peay State University, tells me that a species of aster (*Symphyotrichum*) new to science, with its closest relative in Florida, will soon be described from May Prairie.

When Sharpe first visited May Prairie, it had been subject to annual burning and grazing. In the 1960s the landowner built a pond in the middle of

the prairie, put in lateral drains, and planted fescue. The State of Tennessee purchased the first hundred acres here in the 1970s and most of the rest in the late 1990s. In 1995 the grassland was mostly fescue, but after fire and some herbicide (glyphosate) treatments, big bluestem and other native species exploded, illustrating the resilience of native grassland. Woody invasion remains a problem, with red maple (*Acer rubrum*) and sweetgum (*Liquidambar styraciflua*) the major invaders. The management goal is to maintain the open prairie and restore the post oak woodland.

Sod Prairie, Arkansas

One of the more innovative (and extreme) grassland restoration projects I know of was overseen by Tom Foti in Arkansas. Sod Prairie is part of the Grand Prairie landscape, a complex of prairies on Quaternary (mostly Pleistocene, some Holocene) terraces of the Mississippi River Embayment. Given its species composition, Grand Prairie is best considered an outlier of the coastal prairies of Louisiana and Texas, rather than an outlier of midwestern prairies. At the time of EuroAmerican settlement, there were ca. 500,000 acres of prairie here. Today less than one-tenth of 1 percent remains. The US Army Corps of Engineers agreed to mitigate loss of uplands as well as wetlands in the Grand Prairie region. A few years ago, a farmer proposed to develop an irrigation reservoir on a small remnant prairie. She said if they wouldn't let her build the reservoir, she would plow up the prairie anyway. Tom Foti proposed to use sod-cutting equipment to "roll up" the top one to two inches of prairie in winter, after mowing, and move the prairie to a new site. People said it wouldn't work because prairie plants are deep-rooted, but the prairie relocation went forward.

After the prairie sod was rolled up, it was loaded onto trucks, transported to a recipient site, unrolled, laid out, and watered. An inventory later that year documented 170 species of native plants on Sod Prairie. White wild indigo (*Baptisia alba*) and compass plant (*Silphium laciniatum*) did not survive the translocation, but compass plant subsequently moved in on its own, as did white prairie-clover (*Dalea candida*). Other prairie plants actually benefited from the disturbance and sprang up from the seed bank. I visited Sod Prairie with Tom Foti and Theo Witsell, and it looks authentic. The experiment worked so well that it has been repeated in northwestern Arkansas, where it was also successful.

Ouachita National Forest Shortleaf Pine–Bluestem Woodland, Arkansas

The center of distribution of the shortleaf pine–bluestem woodland is the northern and western Ouachita Mountains of Arkansas and adjacent Oklahoma. Shortleaf pine is the canopy dominant, with an understory characterized

by big and little bluestem and other prairie plants. This community is strongly reminiscent of longleaf pine savannas, replete with red-cockaded woodpeckers, brown-headed nuthatches, Bachman's sparrows, and other birds in common—but then a greater roadrunner (*Geococcyx californianus*) streaks by, and you know this place is a bit different. The largest remaining expanse of shortleaf pine–bluestem woodland is on the Ouachita National Forest, where the US Forest Service has been aggressively restoring this community. Forest Service biologists Larry Hedrick and Jerry Davis showed me what they are doing here.

By 1970 the woodland had declined precipitously, largely due to heavy logging followed by fire exclusion. Red-cockaded woodpeckers were almost gone. The Forest Service is conducting the restoration mostly through prescribed fire and thinning. The project won the Ecosystem Management Recognition Award from the chief of the Forest Service in 1999, when about 150,000 acres were in the process of restoration. In 2007, the year before my visit, 67 young red-cockaded woodpeckers were fledged on the national forest. The plan now calls for restoring at least 300,000 acres of shortleaf pine–bluestem to open woodland conditions, out of approximately one million acres of shortleaf pine on the forest, and reaching a population of 420 red-cockaded woodpeckers. Ouachita National Forest staff determined that conditions similar to those depicted in historic photographs can be achieved through thinning, midstory reduction treatments, and prescribed fires at three- to four-year intervals.

South Carolina Longleaf Pine

Johnny Stowe, a preserve manager in South Carolina, describes a spectrum from reactive management (dealing with unforeseen day-to-day problems) to visionary, strategic conservation planning. Many people work on the two ends of the spectrum, but few in the middle, which would require true integration. Johnny wants to provide that middle ground. He uses fairly intense fire to prune and thin stands of longleaf pine. With "thermal pruning," the lower limbs of smaller adult pines are killed. Johnny showed me the positive results of this technique at Lynchburg Savanna Heritage Preserve in April 2008; it was readily apparent how the technique allowed more sunlight to reach the herbaceous layer. Fire also thins stands of longleaf pine, producing the same favorable conditions for the species-rich groundcover.

For landowners interested in saw-timber production, thermal pruning and thinning increase valuable timber volume, while also fostering biodiversity and wildlife habitat. A problem in restoring long-unburned sites is that the litter on the ground becomes deep enough to turn to duff and humus. Longleaf roots run into this duff, and then it is difficult to reintroduce fire without killing the

pines. Smoldering around the bases of trunks can also girdle trees. In such cases labor-intensive management, such as raking away and removing part of the top organic layers, or spraying water around the base of trees, is sometimes necessary to prevent excessive mortality of adult pines.

Apalachicola Bluffs and Ravines, Florida

One of the showcase TNC preserves nationally is Apalachicola Bluffs and Ravines along the Apalachicola River in the Florida Panhandle. At 135 feet above the river, Alum Bluff provides the greatest topographic relief in the state. This preserve was established primarily to protect the "steephead" ravines, which harbor numerous relict taxa, including two of the world's rarest conifers, the Florida torreya (*Torreya taxifolia*, whose closest relatives are in California and eastern Asia) and Florida yew (*Taxus floridana*). Several plants more common in the Appalachians, such as mountain laurel (*Kalmia latifolia*), reach the southern teminus of their ranges here. The preserve also features longleaf pine sandhills, most of which had been clear-cut, intensively site-prepared (including windrowing, i.e., piling logging debris in long strips), and converted to pine plantations before TNC purchased the area. Restoring these sites required clear-cutting the plantations and planting longleaf pine and native groundcover species on virtually bare sand.

Preserve manager David Printiss provided me a fascinating tour of the sandhills restoration project here. This project has proceeded for over a decade, with its ups and downs. For example, wiregrass was originally planted in rows, but it stayed in those rows, rather than spreading out. Recently, David has employed a machine called the "Grasslander," modified to deal with the many stumps, to lightly scarify the soil in front and plant collected seeds of wiregrass and other grassland plants behind the machine. Longleaf seeds, as opposed to the more expensive "plugs" (seedlings) used earlier in the project, are then planted on the site—about 250 per acre. David told me that his motto is "bare mineral soil to functional sandhill in 40 months," and I am impressed with his progress toward this goal. David tries to eliminate virtually all hardwoods from the restoration sites, with a few exceptions. We had an interesting discussion about this. Many longleaf pine restorationists in the Coastal Plain want to eliminate tree-sized hardwoods. My inclination is to leave some, with the assumption that natural heterogeneous fires would, by chance, leave some small patches unburned through multiple fires, long enough to allow a few savanna oaks and some other hardwoods to grow big and resistant to fire. The presence of hardwood-dependent animals, such as fox squirrels, in this landscape suggests that some low density of hardwoods is perfectly natural in many longleaf pine sandhills.

THE FUTURE?

If I did not believe that southern grasslands have a future, I would not have written this book. It would be nice to conclude by stating that I am absolutely convinced that a renaissance in natural history is under way and that this will culminate in the conservation philosophy and body of knowledge that we need to fully protect and restore southern grasslands and other endangered ecosystems. Unfortunately, I am not convinced just yet. Natural history does seem to be on the upswing, at least among many scientists, writers, artists, and other professionals. For example, we have a new nonprofit organization, the Natural History Network, and a new Natural History Section of the century-old Ecological Society of America. There is a new section of the esteemed journal *American Naturalist* called "Natural History Miscellany," which implies a partial return to its roots for this journal that had drifted almost entirely to theoretical and mathematical ecology and evolutionary biology.

Natural history provides the most defensible foundation for conservation science, action, and education. By knowing nature well, we learn what it might take to keep species and communities going through rough times. Still, many forces work against the resurgence of natural history. For obvious reasons, natural history concentrates on biodiversity, and biodiversity, strangely enough, is out of vogue within the conservation establishment. When Peter Kareiva, the chief scientist for the world's largest land conservation organization, proudly proclaims in an article in the organization's magazine (*Nature Conservancy*) that he is "not a biodiversity guy" and that he prefers cities to natural areas—and is cheered on by the organization's president—then I think we have a problem. Although many wonderful staff committed to biodiversity conservation remain within the organization, we can no longer look to the leadership of TNC to support protection of biologically critical sites that do not provide palpable ecosystem services. Indeed, protection is no longer within the lexicon of this leadership. Chief scientist Kareiva asserts that "the message of protecting nature from humans is a losing message to most of the world. The alternative message is a goal of providing billions of people with a natural environment that is managed to meet their needs in perpetuity." Writing in the *Breakthrough Journal*, Kareiva and colleagues insist that "conservationists will have to jettison their idealized notions of nature, parks, and wilderness—ideas that have never been supported by good conservation science—and forge a more optimistic, human-friendly vision."

So much for natural history and biodiversity conservation in the newly declared "Age of the Anthropocene." Well, not necessarily. There is a grass-

roots countercurrent to this humanistic, antibiodiversity flood of rhetoric, and it is in the hearts, minds, and hands of naturalists—professionals and amateurs alike—who recognize the ethical and strategic limitations of purely theoretical science (which is what the "science" of ecosystem services mostly is) and human-centered conservation. As mentioned in chapter 3, TNC's own poll shows that essentially the same number of people in the United States value nature primarily for its own sake versus for what it provides to humans.

Appreciation of intrinsic value is something conservationists might want to encourage. A commentary in *Nature Climate Change* by Tom Crompton cites research showing that people who attach more importance to intrinsic values demonstrate more cooperative behavior in Prisoner's Dilemma games, have smaller personal environmental footprints, express more concern about social issues, and engage in more political activism. A growing body of empirical research shows that people prefer and appreciate species-rich sites and endemic taxa, and that their psychological well-being is enhanced by regular exposure to wild creatures and natural areas. Despite its detractors and many institutional obstacles in its way, natural history is being revived within academia, professional societies, and interest groups from native plant societies to birders. When individuals spend time in nature, they commonly develop aesthetic and intellectual appreciation of biodiversity, which spurs greater learning and a heartfelt commitment to conservation (fig. 6.4).

Natural history and public support for biodiversity conservation will grow because they must grow to confront the extinction crisis. Whether they will grow fast enough to be effective is anyone's guess. Even if the cause is hopeless, however, it is worth fighting for. As Michael Patten and Brenda Smith-Patten suggested in an essay in *BioScience*, "We do not need hope—only the courage to do what it right, regardless of whether we are rewarded."

I close with some conclusions and predictions about the future of southern grasslands:

1. Most of the South (especially the interior) is projected to become hotter and drier with global climate change. Because grassland taxa are drought-adapted, this shift may benefit grasslands at the expense of forest, as it did during the Hypsithermal and other historic dry periods. Increasing variability in temperature and precipitation within and among seasons will probably also favor grasslands.

2. The less drought-tolerant grassland species may be lost from some grasslands, especially extreme, shallow-soil sites such as glades and outcrops.
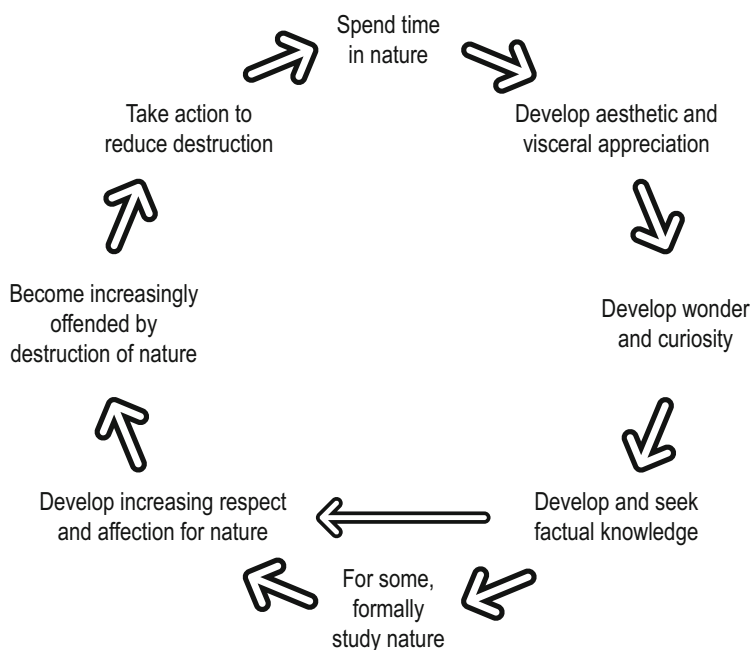
Figure 6.4. A hypothetical positive feedback loop (validated at least by the author). Spending time in nature leads to ever-increasing appreciation, wonder, knowledge, and respect for nature, and greater dedication to conservation. Continuing the loop, spending time in nature provides emotional breaks from the gloomy business of conservation.

Topographically and geologically more heterogeneous landscapes and regions hold more potential for adjustment of species distributions to environmental change.

3. A shift to grassier conditions with increased drought, and perhaps increased lightning activity with greater storminess, will promote more frequent fire, which might counteract to some extent the active and passive fire exclusion imposed by humans. If so, this will benefit many grassland communities.

4. Invasive nonnative species are generally predicted to benefit from global warming, because they typically are adaptable and good dispersers. Southern grasslands appear to vary substantially in their susceptibility to invasion, but this problem could be exacerbated by climate change.

5. Coastal grasslands and others in low-lying regions not far from the coast (e.g., pine rocklands and marl prairies of south Florida) may be the most

vulnerable grasslands in the face of climate change. Many of these communities will be inundated by sea-level rise, and many are also being squeezed from the other direction by development. As Larry Harris put it, these communities are caught "between the devil and the deep blue sea."

6. If natural history education and public interest in natural history truly resurge, support for grasslands and biodiversity conservation will increase and more land will be protected. If, on the other hand, the recovery of natural history is thwarted by other trends, such as continued population growth, population shifts to cities, new cities built in rural areas, economic woes, or technological toys, which distract or distance people from nature, the future will be bleak.

How humans treat southern grasslands will largely determine their fate. If we recognize grasslands, other natural communities, and species as respectable despite, in many cases, a lack of any plausible utilitarian value, we will protect them. We will intervene, as needed, to assure their survival in a world changed and damaged by industrial civilization. What we have messed up, we have a responsibility to fix, if we can. Participation in natural history, the oldest human tradition, almost inevitably instills a land ethic as described by Aldo Leopold, where mistreatment of natural areas is seen as fundamentally wrong. As we come to know wild places and nonhuman beings intimately, we care about them as friends and will act in their behalf at every possible opportunity.

> A song of the good green grass
> A song no more of the city streets
> > Walt Whitman (1882) *Leaves of Grass*

REFERENCES

Conservation planning and prioritization: Noss 1992, Noss and Cooperrider 1994, Noss et al. 1995, Noss et al. 1997, Noss et al. 1999, Soulé and Terborgh 1999, Margules and Pressey 2000, Groves 2003, Prugh et al. 2008, Franklin and Lindenmayer 2009, Moilanen et al. 2009

Functional landscape mosaics: Noss and Harris 1986, Noss 1987, Poiani et al. 2000

Hotspots: Myers et al. 2000, Stein et al. 2000, Knight et al. 2011

Rewilding and wilderness recovery: Noss 1985, Foreman and Wolke 1989, Soulé and Noss 1998, Donlan et al. 2005, Thatcher et al. 2006

Triage: Millar et al. 2007, Bottrill et al. 2008, Marris 2011

Sea-level rise: Donoghue 2011

Restoration, intervention, and adaptive management: Mooney 1988, Pauly 1995, Kirkman et al. 2004, Jackson and Hobbs 2009, Howes et al. 2010, Hobbs et al. 2011, Lynas 2011, Marris 2011

Natural History Network: http://naturalhistorynetwork.org/

The (new) Nature Conservancy: Fairbank, Maslin, Maullin, Metz & Associates 2010, Dunkel 2011, Kareiva 2011, Kareiva et al. 2011

Values and ethics: Leopold 1949, Wilson 1984, Crompton 2011, Patten and Smith-Patten 2011

Species List

Includes species, subspecies, and varieties mentioned in text, but not inclusive of tables

PLANTS (AND FUNGI AND CYANOBACTERIA)

acacia, prairie (*Acacia angustissima* var. *hirta* = *Acaciella hirta*)
adderstongue, limestone (*Ophioglossum engelmannii*)
alicia, Florida (*Chapmannia floridana*)
alligatorlily (*Hymenocallis palmeri*)
anemone, eastern prairie (*Anemone berlandieri*)
anise, yellow (*Illicium parviflorum*),
antelopehorn, green (*Asclepias viridis*)
ash, white (*Fraxinus americana*)
aster, barrens silky (*Symphyotrichum pratense*)
aster, Georgia (*Symphyotrichum georgianum*)
aster, late purple (*Symphyotrichum patens* var. *patens*)
aster, Rhiannon's (*Symphyotrichum rhiannon*)
aster, Stoke's (*Stokesia laevis*)
avens, Appalachian (*Geum radiatum*)
azalea, flame (*Rhododendron calendulaceum*)
bachelor's button, yellow (*Polygala rugelii*)
bahiagrass (*Paspalum notatum*)
Barbara's-buttons, Coosa (*Marshallia mohrii*)
Barbara's-buttons, southern (*Marshallia ramosa*)
Barbara's-buttons, spoonshape (*Marshallia obovata*)
barberry, American (*Berberis canadensis*)
beaksedge, spreading (*Rhynchospora divergens*)
beardtongue, dissected (grit) (*Penstemon dissectus*)

beardtongue, Cobaea (*Penstemon cobaea*)
beardtongue, longsepal (*Penstemon calycosus*)
beargrass, common (*Xerophyllum tenax*)
beech, American (*Fagus grandifolia*)
bentgrass, Elliott's (*Agrostis elliottiana*)
bitter-bloom (*Sabatia angularis*)
bitterweed (*Helenium amarum*)
black-eyed Susan, Little River (*Rudbeckia heliopsidis*)
blackroot (*Pterocaulon pycnostachyum*)
blazing-star, Chapman's (*Liatris chapmanii*)
blazing-star, cylindrical (*Liatris cylindracea*)
blazing-star, dense (*Liatris spicata*)
blazing-star, Sandhills (*Liatris cokeri*)
blazing-star, scaly (*Liatris squarrosa*)
blazing-star, slender (*Liatris gracilis*)
blazing-star, tall or rough (*Liatris aspera*)
blue curls (*Trichostema dichotomum*)
bluestar, Hubricht's (*Amsonia hubrichtii*)
bluestem, big (*Andropogon gerardii*)
bluestem, broomsedge (*Andropogon virginicus*)
bluestem, bushy (*Andropogon glomeratus*)
bluestem, chalky (*Andropogon capillipes*)
bluestem, Elliott's (*Andropogon gyrans*)
bluestem, Florida little (*Schizachyrium rhizomatum*)
bluestem, little (*Schizachyrium scoparium*)
bluestem, slender little (*Schizachyrium tenerum*)
bluestem, splitbeard (*Andropogon ternarius*)
bogrush, black (*Schoenus nigricans*)
breadroot, Dixie Mountain (*Pediomelum piedmontanum*)
breadroot, Nashville (*Pediomelum subacaule*)
buffalo nut (*Pyrularia pubera*)
bugbane, Carolina (tassle-rue) (*Trautvetteria caroliniensis*)
butterwort, small (*Pinguicula pumila*)
cactus, cockspur pricklypear (*Opuntia pusilla*)
cactus, devil's-tongue (prickly pear) (*Opuntia humifusa*)
cactus, semaphore (*Conseola corallicola*)
Cahaba torch (*Liatris oligocephala*)
camphorweed, rosy (*Pluchea rosea*)
campion, fringed (*Silene catesbaei*)
cane, giant (*Arundinaria gigantea*)
cane, hill (*Arundinaria appalachiana*)
cane, switch (*Arundinaria tecta*)
catchfly, royal (*Silene regia*)
celestial lily (*Nemastylis floridana*)
chaffheads (*Carphephorus corymbosus, C. paniculatus*)
chaffseed (*Schwalbea americana*)
chickweed, field (*Cerastium velutinum* var. *villosissimum*)

chinaberry (*Melia azedarach*)
cliffbreak, purple (*Pellaea atropurpurea*)
cloakfern, hybrid (*Astrolepis integerrima*)
clover, Kate's mountain (*Trifolium virginicum*)
clover, running buffalo (*Trifolium stoloniferum*)
columbine (*Aquilegia canadensis*)
compass plant (*Silphium laciniatum*)
coneflower, gray-headed (*Ratibida pinnata*)
coneflower, pale purple (*Echinacea pallida*)
coneflower, pinnate prairie (*Ratibida pinnata*)
coneflower, purple (*Echinacea purpurea*)
coneflower, smooth purple (*Echinacea laevigata*)
coneflower, Tennessee (*Echinacea tennesseensis*)
coneflower, Topeka purple (*Echinacea atrorubens*)
coral bean (*Erythrina herbacea*)
cordgrass, sand (*Spartina bakeri*)
cornsalad, Nuttall's (*Valerianella nuttallii*)
cornsalad, Palmer's (*Valerianella palmeri*)
crabgrass, two-spike (*Digitaria pauciflora*)
crossvine (*Bignonia capreolata*)
croton, Alabama (*Croton alabamensis*)
cup plant (*Silphium perfoliatum*)
cyanobacteria (*Nostoc commune*)
cypress, bald (*Taxodium distichum*)
cypress, pond (or dwarf) (*Taxodium ascendens*)
daisy, Engelmann's (*Engelmannia peristenia*)
dogwood, gray (*Cornus drummondi*)
draba, openground (*Draba aprica*)
dropseed, Carolina (*Sporobolus pinetorum*)
dropseed, composite (*Sporobolus compositus* var. *compositus*)
dropseed, poverty (*Sporobolus vaginiflorus* and *S. vaginiflorus* var. *vaginiflorus*)
dropseed, prairie (*Sporobolus heterolepis*)
dropseed, rough (*Sporobolus clandestinus*)
elf orpine (*Diamorpha smallii*)
elm, American (*Ulmus americanus*)
eupatorium, common roundleaf (*Eupatorium rotundifolium*)
eupatorium, Mohr's (*Eupatorium mohrii*)
evening primrose, bigfruit (*Oenothera macrocarpa*)
evening primrose, showy (pinkladies) (*Oenothera speciosa*)
false aloe (*Manfreda virginica*)
fir, balsam (*Abies balsamea*)
foxglove, combleaf yellow false (*Aureolaria pectinata*)
foxglove, earleaf (*Agalinis auriculata*)
foxglove, false (*Agalinis fasciculata*)
false indigo, Ouachita (*Amorpha ouachitensis*)
fameflower, largeflower (*Phemeranthus calycinus*)
fameflower, limestone (*Phemeranthus calcaricus*)

fameflower, Menges' (*Phemeranthus mengesii*)
fameflower, Piedmont (*Phemeranthus piedmontanus*)
fern, shoestring (*Vittaria lineata*)
fetterbush (*Lyonia lucida*)
fimbry, hairy (*Fimbristylis puberula*)
fir, Fraser (*Abies fraseri*)
fogfruit, southern (*Phyla stoechadifolia*)
fringetree, white (*Chionanthus virginicus*)
fungus, redheart (*Phellinis* [*Fomes*] *pini*)
gallberry (*Ilex glabra*)
gamagrass, eastern (*Tripsacum dactyloides*)
gaura, biennial (*Gaura biennis*)
gaywings (*Polygala paucifolia*)
gentian, prairie (downy) (*Gentiana puberulenta*)
gentian–pinkroot, Alabama (*Spigelia gentianoides* var. *alabamensis*)
Georgia plume (*Elliottia racemosa*)
ginseng, dwarf (*Panax trifolius*)
gladecress, Alabama (*Leavenworthia alabamensis*)
gladecress, long-styled (cedar) (*Leavenworthia stylosa*)
gladecress, Michaux's (*Leavenworthia uniflora*)
gladecress, necklace (*Leavenworthia torulosa*)
gladecress, Tennessee (*Leavenworthia exigua* var. *exigua*)
gladecress, Tennessee (*Leavenworthia exigua* var. *laciniata*)
goldenasters (*Chrysopsis linearifolia*, *C. scabrella*)
goldencrest (*Lophiola aurea*)
goldenrod, bush (*Chrysoma pauciflosculosa*)
goldenrod, Carolina (*Solidago pulchra*)
goldenrod, Nuttall's rayless (*Bigelowia nuttallii*)
goldenrod, seaside (*Solidago sempervirens*)
goldenrod, shale barren (*Solidago harrisii*)
goldenrod, Short's (*Solidago shortii*)
goldenrod, sticky (*Solidago simplex* var. *racemosa*)
grama, hairy (*Bouteloua hirsuta*)
grama, side-oats (*Bouteloua curtipendula*)
grass, cogon (*Imperata cylindrica*)
grass, Johnson (*Sorghum halepense*)
grass, Scribner's rosette (*Dichanthelium oligosanthes* var. *scribnerianum*)
grass, toothache (*Ctenium aromaticum*)
grasspink, manyflower (*Calopogon multiflorus*)
ground plum, Pyne's (*Astralagus bibullatus*)
gum, black (*Nyssa sylvatica*)
hackberry, dwarf (*Celtis tenuifolia*)
hairgrass, wavy (*Deschampsia flexuosa* var. *flexuosa*)
hartwrightia, Florida (*Hartwrightia floridana*)
hatpins, dwarf (*Eriocaulon koernickianum*)
hawkweed, shale barren (*Hieracium traillii*)
hawthorn, threeflower (*Crataegus triflora*)

heartleaf, Sandhills (*Hexastylis sorriei*)
hickory, pignut (*Carya glabra*)
hickory, sand (*Carya pallida*)
holly, Carolina (*Ilex ambigua*)
honeycombhead, coastalplain (*Balduina angustifolia*)
honeycup (*Zenobia pulverulenta*)
honeysuckle, Japanese (*Lonicera japonica*)
horsenettle, Carolina (*Solanum pumilum*)
Indiangrass (yellow) (*Sorghastrum nutans*)
Indiangrass, lopsided (*Sorghastrum secundum*)
Indiangrass, slender (*Sorghastrum elliottii*)
Indian paintbrush, scarlet (*Castilleja coccinea*)
Indian plantain, groovestem (*Arnoglossum plantagineum*)
indigo-bush, savanna (*Amorpha confusa*)
jessamine, yellow (*Gelsemium sempervirens*)
jewelflower, clasping (*Streptanthus maculatus* ssp. *obtusifolius*)
jewelflower, pine-oak (*Streptanthus squamiformis*)
Junegrass, prairie (*Koeleria macrantha*)
lady's slipper, greater yellow (*Cypripedium parviflorum* var. *pubescens*)
lady's slipper, white (*Cypripedium candidum*)
lady's tresses, Navasota (*Spiranthes parksii*)
lady's tresses, Texas (*Spiranthes brevilabris*)
larkspur, Alabama (*Delphinium alabamicum*)
larkspur, blue (*Delphinium carolinianum* ssp. *carolinianum*)
leatherflower, Addison's (*Clematis addisonii*)
leatherflower, Millboro (*Clematis viticaulis*)
leatherflower, whitehair (*Clematis albicoma*)
leatherflower, whiteleaf (*Clematis glaucophylla*)
leatherwood, eastern (*Dirca palustris*)
lespedeza, bicolor (shrub) (*Lespedeza bicolor*)
lily, Atamasco (*Zephyranthes atamasco*)
lily, Canada (*Lilium canadense* var. *editorum*)
lily, Gray's (*Lilium grayii*)
lily, swamp (*Crinum americanum*)
lipfern, chestnut (*Cheilanthes castanea*)
littlebrownjug, Ruth's (*Hexastylis arifolia* var. *ruthii*)
lobelia, palespike (*Lobelia spicata*)
locust, black (*Robinia pseudoacacia*)
locust, dwarf bristly (*Robinia nana*)
loosestrife, pocosin (*Lysimachia asperulifolia*)
lovegrass, Elliott's (*Eragrostis elliottii*)
magnolia, southern (*Magnolia grandiflora*)
maidenbush, Missouri (*Leptopus phyllanthoides*)
mangrove, red (*Rhizophora mangle*)
maple, red (*Acer rubrum*)
maple, sugar (*Acer saccharum*)
marbleseed, deceptive (*Onosmodium decipiens*)

marbleseed, eastern prairie (*Onosmodium hispidissimum*)
marbleseed, soft hair (*Onosmodium molle*)
May apple (*Podophyllum peltatum*)
meadowbeauty, Nuttall's (*Rhexia nuttallii*)
meadowbeauty, pale (*Rhexia mariana*)
meadowbeauty, tall (*Rhexia alifanus*)
meadowbeauty, white (*Rhexia mariana* var. *exalbida*)
meadowbeauty, yellow (*Rhexia lutea*)
meadowrue, Cooley's (*Thalictrum cooleyi*)
milkpea, downy (*Galactia volubilis*)
milkvetch, Tennessee (*Astragalus tennesseensis*)
milkweed, pineland (*Asclepias obovata*)
milkweed, southern (*Asclepias viridula*)
milkweed, whorled (*Asclepias verticillata*)
moss, highlands (lanceleaf) (*Schlotheimia lancifolia*)
moss, Keever's orthotrichum (*Orthotrichum keeverae*)
mountain laurel (*Kalmia latifolia*)
mountain mallow, Peter's (*Iliamna corei* or *I. rivularis*)
mountain–mint, narrow–leaved (*Pcynanthemum tenuifolium*)
muhly, cutover (*Muhlenbergia expansa*)
muhly, hairyawn (*Muhlenbergia capillaris, M. sericea*)
nailwort, yellow (*Paronychia virginica*)
New Jersey tea (*Ceanothus americanus*)
nutrush, slenderfruit (*Scleria georgiana*)
oak, bastard (*Quercus sinuata*)
oak, blackjack (*Quercus marilandica*)
oak, chinkapin (*Quercus muehlenbergii*)
oak, Georgia (*Quercus georgiana*)
oak, laurel (*Quercus laurifolia*)
oak, live (*Quercus virginiana*)
oak, northern red (*Quercus rubra*)
oak, Oglethorpe (*Quercus oglethorpensis*)
oak, post (*Quercus stellata*)
oak, rock chestnut (*Quercus montana*)
oak, sand laurel (*Quercus hemisphaerica*)
oak, sand live (*Quercus geminata*)
oak, sand post (*Quercus margarettae*)
oak, scarlet (*Quercus coccinea*)
oak, southern red (*Quercus falcata*)
oak, turkey (*Quercus laevis*)
oak, water (*Quercus nigra*)
oak, white (*Quercus alba*)
oatgrass, flattened (*Danthonia compressa*)
obedient plant (*Physostegia virginiana*)
olive, autumn (*Elaeagnus umbellata*)
olive, thorny (*Elaeagnus pugens*)
onion, nodding (*Allium cernuum*)

orchid, green fly (*Epidendrum magnoliae*)
osage orange (Bois d'Arc) (*Maclura pomifera*)
palm, cabbage (*Sabal palmetto*)
palm, Florida royal (*Roystonea elata*)
palmetto, dwarf (*Sabal minor*)
palmetto, saw (*Serenoa repens*)
panicgrass, slimleaf (*Dichanthelium linearifolium*)
panicum (rosette grass), needleleaf (*Dichanthelium aciculare*)
panicum, velvet (*Dichanthelium scoparium*)
partridge pea (*Chamaecrista fasciculata*)
partridge pea, Big Pine (*Chamaecrista lineata* var. *keyensis*)
persimmon (*Diospyros virginiana*)
phlox, blue (*Phlox divaricata*)
phlox, swordleaf (*Phlox buckleyi*)
pimpernel, shale barren (*Pseudotaenidia montana*)
pine, loblolly (*Pinus taeda*)
pine, longleaf (*Pinus palustris*)
pine, pitch (*Pinus rigida*)
pine, pond (*Pinus serotina*)
pine, sand (*Pinus clausa*)
pine, shortleaf (*Pinus echinata*)
pine, slash (*Pinus elliottii*)
pine, south Florida slash (*Pinus elliottii* var. *densa*)
pine, Virginia (*Pinus virginiana*)
pinkroot, woodland (*Spigelia marilandica*)
pinweed, San Saba (*Lechea san-sabeana*)
pixie-moss, common (*Pyxidanthera barbulata*)
pixie-moss, sandhills (*Pyxidanthera brevifolia*)
pleatleaf, Nuttall's (*Nemastylis nuttallii*)
poison ivy (*Toxicodendron radicans*)
pool sprite (*Amphianthus pusillus*)
poppymallow, woodland (*Callirhoe papaver*)
portulaca, grit (*Portulaca biloba*)
prairie-clover, Cahaba (*Dalea cahaba*)
prairie-clover, Feay's (*Dalea feayi*)
prairie-clover, Gattinger's (*Dalea gattingeri*)
prairie-clover, leafy (*Dalea foliosa*)
prairie-clover, purple (*Dalea purpurea*)
prairie-clover, white (*Dalea candida*)
prairie-dawn, Texas (*Hymenoxys texana*)
prairie dock (*Silphium terebinthinaceum*)
prairie dock, Lucy Braun (*Silphium terebinthinaceum* var. *lucy-brauniae*)
privet, Chinese (*Ligustrum sinense*)
pussytoes, shale barren (*Antennaria virginica*)
quillwort, blackspore (*Isoetes melanospora*)
quillwort, limestone (*Isoetes butleri*)
quillwort, mat-forming (Merlin's grass) (*Isoetes tegetiformans*)

quillwort, Piedmont (*Isoetes piedmontanum*)
ragweed, annual (*Ambrosia artemisiifollia*)
ragwort, shale barren (*Packera antennariifolia*)
ragwort, wooly (*Packera tomentosa*)
rattlesnake-master (*Eryngium yuccifolium*)
redbud (*Cercis canadensis*)
redcedar, eastern (*Juniperus virginianus*)
redroot, prairie (*Ceanothus herbaceus*)
rhododendron, Catawba (*Rhododendron catawbiense*)
rockcress, Georgia (*Arabis georgiana*)
rockcress, hairy (*Arabis hirsuta*)
rose, swamp (*Rosa palustris*)
rose-gentian, Bartram's (*Sabatia bartramii*)
rose-gentian, Cumberland (*Sabatia capitata*)
rose-gentian, largeflower (*Sabatia grandiflora*)
rose-gentian, Pelton's (*Sabatia arkansana*)
roseling (*Cuthbertia* [*Callisia*] *ornata*)
rosemary, Florida (*Ceratiola ericoides*)
rosepink (*Sabatia angularis*)
rose-rush (*Lygodesmia aphylla*)
rosinweed, Old Cahaba (*Silphium perplexum*)
rosinweed, sticky (*Silphium glutinosum*)
rosinweed, wholeleaf (*Silphium integrifolium*)
rosinweed, whorled (*Silphium trifoliatum* var. *latifolium*)
rush, Georgia (*Juncus georgianus*)
rush-featherling (*Pleea tenuifolia*)
saltbush, Texas (*Atriplex texana*)
sandweed, matted (*Hypericum reductum*)
sawgrass (*Cladium jamaicense*)
sea-pink, annual (*Sabatia stellaris*)
sedge, littletooth (*Carex microdonta*)
sedge, Pennsylvania (*Carex pensylvanica*)
sedge, Waterfall's (*Carex latebracteata*)
shooting star (pride of Ohio) (*Dodecatheon meadia*)
silkgrass, narrowleaf (*Pityopsis graminifolia*)
skullcap, Florida scrub (*Scutellaria arenicola*)
snakeweed, threeflower (*Thurovia triflora*)
Spanish moss (*Tillandsia usneoides*)
speargrass, blackseed (*Piptochaetium avenaceum*)
spikemoss, spiny (*Selaginella acanthonota*)
spleenwort, forked (*Asplenium septentrionale*)
spruce, red (*Picea rubens*)
spurge, rockland (deltoid) (*Chamaesyce deltoidea* ssp. *serpyllum*)
St. Peter's-wort (*Hypericum tetrapetalum*)
stargrass, yellow (*Hypoxis juncea*)
stitchwort, oneflower (*Minuartia uniflora*)
stitchwort, pine barren (*Minuartia caroliniana*)

sumac, fragrant (*Rhus aromatica*)
sumac, Michaux's (*Rhus michauxii*)
sundew, annual dwarf (*Drosera brevifolia*)
sunflower, Schweinitz's (*Helianthus schweinitzii*)
sunflower, Shinner's (*Helianthus occidentalis* ssp. *plantagineus*)
sunflower, whorled (*Helianthus verticillatus*)
sunnybells (*Schoenolirion croceum*)
sweetgum (*Liquidambar styraciflua*)
switchgrass (*Panicum virgatum*)
thistle, Sandhills (*Cirsium repandum*)
thistle, smooth (*Cirsium carolinianum*)
thoroughwort, roundleaf (*Eupatorium rotundifolium*)
threadwort, Appalachian (*Drepanolejeunea appalachiana*)
threeawn, arrowfeather (*Aristida purpurascens*)
threeawn, prairie (*Aristida oligantha*)
threeawn, slimspike (*Aristida longespica*)
Tiny Tim (*Geocarpon minimum*)
titi (*Cyrilla racemiflora*)
toadflax, Canada (*Nuttallanthus canadensis*)
toothwort, cutleaf (*Cardamine concatenata*)
torreya, Florida (*Torreya taxifolia*)
tread-softly (*Cnidoscolus stimulosus*)
tree of heaven (*Ailanthus altissima*)
tulip-tree, Coastal Plain (*Liriodendron tulipifera* var. 1)
turkeybeard, eastern (*Xerophyllum asphodeloides*)
Venus fly-trap (*Dionaea muscipula*)
Venus' looking-glass, clasping (*Triodanus perfoliata*)
Venus's pride (*Houstonia pupurea* var. *montana*)
violet, Appalachian (*Viola appalachiensis*)
violet, lance-leaved (*Viola lanceolata*)
violet, prairie (*Viola pedatifida*)
whitecedar, northern (*Thuja occidentalis*)
whitetop, starrush (*Rhynchospora colorata*)
wild-buckwheat, Harper's (*Eriogonum harperi*)
wild-buckwheat, shale barren (*Eriogonum allenii*)
wild indigo, glade (*Baptisia australis* var. *aberrans*)
wild indigo, white (*Baptisia alba*)
wild mercury, Blodgett's (*Argythamnia blodgettii*)
wild pine, reflexed (*Tillandsia balbisiana*)
wild quinine (*Parthenium integrifolium, P. auriculatum*)
willkommia, Texas (*Willkommia texana* var. *texana*)
windmill-grass, Texas (*Chloris texensis*)
wiregrass (*Aristida beyrichiana, A. stricta*)
witchgrass (*Panicum capillare*)
yellow-eyed grass, Carolina (*Xyris caroliniana*)
yellow-eyed grass, coastal plain (*Xyris ambigua*)
yellow-eyed grass, pineland (*Xyris stricta*)

yellow-eyed grass, Tennessee (*Xyris tennesseensis*)
yellow puff (*Neptunia lutea*)
yellowtops, narrowleaf (*Flaveria linearis*)
yew, Florida (*Taxus floridana)*
yucca (Adam's needle) (*Yucca filamentosa*)

INVERTEBRATES

ant, acrobat (*Crematogaster ashmeadi*)
ant, red imported fire (*Solenopsis invicta*)
azure, dusky (*Celastrina nigra*)
beetle, flightless ground (*Cyclotrechus hypherpiformis*)
beetle, May (*Phyllophaga davisi*)
butterfly, black swallowtail (*Papilio polyxenes*)
butterfly, Olympia marble (*Euchloe olympia*)
checkerspot, gorgone (*Chlosyne gorgone*)
copepod (*Stolonicyclops heggiensis*)
crayfish, Jackson Prairie (*Procambarus barbiger*)
crescent, Appalachian (*Phyciodes batesii maconensis*)
fritillary, cullasaja aphrodite (*Speyeria aphrodite cullasaja*)
giant-skipper, yucca (*Megathymus yuccae*)
moth, gopher tortoise shell (*Ceratophaga vicinella*)
spider, Carolina wolf (*Hogna carolinensis*)
trilobite (*Flexicalymene meeki*)

VERTEBRATES

alligator, American (*Alligator mississippiensis*)
armadillo, nine-banded (*Dasypus novemcinctus*)
bear, black (*Ursus americanus*)
bear, Florida black (*Ursus americanus floridanus*)
beaver (*Castor canadensis*)
bison, ancient (*Bison antiquus*)
bison, giant (*Bison latifrons*)
bison (modern) (*Bison bison*)
bobcat (*Lynx rufus*)
bobwhite, northern (*Colinus virginianus*)
bunting, snow (*Plectrophenax nivalis*)
caracara, crested (*Caracara cheriway*)
cat, house or feral (*Felis catus*)
cattle (*Bos taurus*)
condor (*Gymnogyps kofordi*)
coyote (*Canis latrans*)
coyote (ancestral) (*Canis lepophagus*)
crocodile, American (*Crocodylus acutus*)
deer, Florida Key (*Odocoileus virginianus clavium*)
deer, white-tailed (*Odocoileus virginianus*)

elk (*Cervus elaphus*)
frog, gopher (*Lithobates capito*)
glyptodont (*Glyptotherium arizonae*)
ground-dove, common (*Columbina passerina*)
ground sloth, Harlan's (*Paramylodon harlani*)
ground sloth, Jefferson's (*Megalonyx jeffersonii*)
hawk, white-tailed (*Buteo albicaudatus*)
hog, domestic or feral (*Sus scrofa*)
horse, ancient (*Equus* cf. *complicates*)
horse, modern (*Equus caballus*)
kestrel, southeastern American (*Falco sparverius paulus*)
leopard (*Panthera pardus*)
lizard, collared (*Crotaphytus collaris*)
mammoth (*Mammuthus columbi*)
marsh rabbit, Lower Keys (*Sylvilagus palustris hefneri*)
mastodon (*Mammut americanum*)
mole skink, Florida Keys (*Plestiodon egregius egregius*)
moose (*Alces alces*)
moose, stag (*Cervalces scotti*)
mosquitofish (*Gambusia holbrooki*)
musk-ox, Harlan's (*Bootherium bombifrons*)
nuthatch, brown-headed (*Sitta pusilla*)
opossum, Virginia (*Didelphis virginiana*)
owl, barred (*Strix varia*)
owl, burrowing (*Athene cunicularia*)
pampathere (*Holmesina floridanus*)
panda, red (*Pristinailurus bristoli*)
panther, Florida (*Puma concolor coryi*)
pigeon, passenger (*Ectopistes migratorius*)
prairie-chicken, Attwater's (*Tympanuchus cupido attwateri*)
puma (*Puma concolor*)
python, Burmese (*Python molurus bivittatus*)
raccoon (*Procyon lotor*)
racerunner, six-lined (*Aspidoscelis sexlineatus*)
rattlesnake, eastern diamondback (*Crotalus adamanteus*)
roadrunner, greater (*Geococcyx californianus*)
silverside, Key (*Menidia conchorum*)
snail, Stock Island tree (*Orthalicus reses reses*)
snake, eastern indigo (*Drymarchon couperi*)
snake, pine (*Pituophis melanoleucus*)
sparrow, Bachman's (*Peucaea aestivalis*)
sparrow, Cape Sable seaside (*Ammodramus maritimus mirabilis*)
sparrow, Florida grasshopper (*Ammodramus savannarum floridanus*)
sparrow, Henslow's (*Ammodramus henslowii*)
squirrel, fox (*Sciurus niger*)
squirrel, Sherman's fox (*Sciurus niger shermani*)
tortoise, gopher (*Gopherus polyphemus*)

treefrog, pine barrens (*Hyla andersonii*)
warbler, Bachman's (*Vermivora bachmanii*)
warbler, pine (*Setophaga pinus*)
warbler, Swainson's (*Limnothlypis swainsonii*)
waxwing, cedar (*Bombycilla cedrorum*)
wolf, gray (*Canis lupus*)
wolf, red (*Canis lupus rufus*)
woodpecker, ivory-billed (*Campephilus principalis*)
woodpecker, red-cockaded (*Picoides borealis*)
woodrat, Key Largo (*Neotoma floridana smalli*)

Literature Cited

Ahrends, A., C. Rahbek, M. T. Bulling, N. D. Burgess, P. J. Platts, J. C. Lovett, V. W. Kindemba et al. 2011. "Conservation and the Botanist Effect." *Biological Conservation* 144:131–40.

Allison, J. R., and T. E. Stevens. 2001. "Vascular Flora of Ketona Dolomite Outcrops in Bibb County, Alabama." *Castanea* 66:154–205.

Allred, B. W., S. D. Fuhlendorf, and R. G. Hamilton. 2011. "The Role of Herbivores in Great Plains Conservation: Comparative Ecology of Bison and Cattle." *Ecosphere* 2(3): 1–17.

Anderson, D. M. 1982. *Plant Communities of Ohio: A Preliminary Classification and Description*. Ohio Department of Natural Resources, Division of Natural Areas and Preserves, Columbus.

Anderson, M. G., and C. E. Ferree. 2010. "Conserving the Stage: Climate Change and the Geophysical Underpinnings of Species Diversity." *PLoS One* 5(7): e11554.

Anderson, M. K. 2007. "Native American Uses and Management of California's Grasslands." In M. R. Stromberg, J. D. Corbin, and C. M. D'Antonio, eds., *California Grasslands—Ecology and Management*. Berkeley: University of California Press, 57–66.

Anderson, R. C., and M. L. Bowles. 1999. "Deep-Soil Savannas and Barrens of the Midwestern United States." In R. C. Anderson, J. R. Fralish, and J. M. Baskin, eds., *Savannas, Barrens, and Rock Outcrop Plant Communities of North America*. Cambridge, UK: Cambridge University Press, 155–70.

Anderson, R. C., J. R. Fralish, and J. M. Baskin, eds. 1999. *Savannas, Barrens, and Rock Outcrop Plant Communities of North America*. Cambridge, UK: Cambridge University Press.

Axelrod, D. I. 1985. "Rise of the Grassland Biome, Central North America." *Botanical Review* 51:163–201.

Barbour, M. G., and W. D. Billings, eds. 2000. *North American Terrestrial Vegetation*, 2nd ed. Cambridge, UK: Cambridge University Press.

Barden, L. S. 1997. "Historic Prairies in the Piedmont of North and South Carolina, USA." *Natural Areas Journal* 17:149–52.

Barnes, T. G., D. White, and M. Evans. 2008. *Rare Wildflowers of Kentucky*. Lexington: University Press of Kentucky.

Barone, J. A. 2005. "Historical Presence and Distribution of Prairies in the Black Belt of Mississippi and Alabama." *Castanea* 70:170–83.

Barone, J. A., and J. G. Hill. 2007. "Herbaceous Flora of Blackland Prairie Remnants in Mississippi and Western Alabama." *Castanea* 72:226–34.

Barrow, M. V., Jr. 2009. *Nature's Ghosts: Confronting Extinction from the Age of Jefferson to the Age of Ecology.* Chicago: University of Chicago Press.

Bartram, W. (1774) 1998. *The Travels of William Bartram. Naturalist Edition*. Edited by Francis Harper. Athens: University of Georgia Press.

Baskin, J. M., and C. C. Baskin. 1986. "Distribution and Geographical/Evolutionary Relationships of Cedar Glade Endemics in Southeastern United States." *ASB Bulletin* 33:138–54.

———. 1999. "Cedar Glades of the Southeastern United States." In R. C. Anderson, J. R. Fralish, and J. M. Baskin, eds., *Savannas, Barrens, and Rock Outcrop Plant Communities of North America*. Cambridge, UK: Cambridge University Press, 206–19.

———. 2003. "The Vascular Flora of Cedar Glades of the Southeastern United States and Its Phytogeographical Relationships." *Journal of the Torrey Botanical Society* 130:101–18.

———. 2004. "History of the Use of 'Cedar Glades' and Other Descriptive Terms for Vegetation on Rocky Limestone Soils in the Central Basin of Tennessee." *Botanical Review* 70:403–24.

Baskin, J. M., C. C. Baskin, and E. W. Chester. 1999. "The Big Barrens Region of Kentucky and Tennessee." In R. C. Anderson, J. R. Fralish, and J. M. Baskin, eds., *Savannas, Barrens, and Rock Outcrop Plant Communities of North America.* Cambridge, UK: Cambridge University Press, 190–205.

Baskin, J. M., C. C. Baskin, and P. J. Lawless. 2007. Calcareous Rock Outcrop Vegetation of Eastern North America (Exclusive of Nashville Basin), with Particular Reference to Use of the Term 'Cedar Glades.'" *Botanical Review* 73:303–25.

Beckage, B., and I. J. Stout. 2000. "Effects of Repeated Burning on Species Richness in a Florida Pine Savanna: A Test of the Intermediate Disturbance Hypothesis." *Journal of Vegetation Science* 11:113–22.

Beerling, D. 2007. *The Emerald Planet: How Plants Changed Earth's History*. New York: Oxford University Press.

Beier, P., and B. Brost. 2010. "Use of Land Facets to Plan for Climate Change: Conserving the Arenas, Not the Actors." *Conservation Biology* 24:701–10.

Belue, T. F. 1996. *The Long Hunt: Death of the Buffalo East of the Mississippi*. Mechanicsburg, PA: Stackpole.

Beschta, R. L., and W. J. Ripple. 2009. "Large Predators and Trophic Cascades in Terrestrial Ecosystems of the Western United States." *Biological Conservation* 142:2401–14.

Blevins, D., and M. P. Schafale. 2011. *Wild North Carolina: Discovering the Wonders of Our State's Natural Communities.* Chapel Hill: University of North Carolina Press.

Boettcher, S. E., and P. J. Kalisz. 1991. "The Prairies of the E. Lucy Braun Preserve, Adams County, Ohio: A Soil Study." *Ohio Journal of Science* 91:122–28.

Bond, W. J., and J. E. Keeley. 2005. "Fire as a Global 'Herbivore': The Ecology and Evolution of Flammable Ecosystems." *Trends in Ecology and Evolution* 20:387–94.

Bond, W. J., and J. J. Midgley. 1995. "Kill Thy Neighbor: An Individualistic Argument for the Evolution of Flammability." *Oikos* 73:79–85.

———. 2000. "A Proposed CO_2-Controlled Mechanism of Woody Plant Invasion in Grasslands and Savannas." *Global Change Biology* 6:865–69.

Bond, W. J., and C. L. Parr. 2010. "Beyond the Forest Edge: Ecology, Diversity and Conservation of the Grassy Biomes." *Biological Conservation* 143:2395–2404.

Bond, W. J., F. I. Woodward, and G. F. Midgley. 2005. "The Global Distribution of Ecosystems in a World without Fire." *New Phytologist* 165:525–38.

Bottrill, M. C., L. N. Joseph, J. Carwardine, M. Bode, C. Cook, E. T. Game, H. Grantham et al. 2008. "Is Conservation Triage Just Smart Decision-Making?" *Trends in Ecology and Evolution* 23:649–54.

Bowman, D. M. J. S, J. K. Balch, P. Artaxo, W. J. Bond, J. M. Carlson, M. A. Cochrane, C. M. D'Antonio et al. 2009. "Fire in the Earth System." *Science* 324:481–84.

Brantley, C. G., and S. G. Platt. 2001. "Canebrake Conservation in the Southeastern United States." *Wildlife Society Bulletin* 29:1175–81.

Braun, E. L. 1928a. "Glacial and Post-Glacial Plant Migrations Indicated by Relict Colonies of Southern Ohio." *Ecology* 9:284–302.

———. 1928b. "The Vegetation of the Mineral Springs Region of Adams County, Ohio." *Ohio Biological Survey* 3:375–517 (Bulletin no. 15).

———. 1950. *Deciduous Forests of Eastern North America.* Philadelphia: Blakiston.

Braunschweig, E., T. Nilsen, and T. F. Wieboldt. 1999. "The Mid-Appalachian Shale Barrens." In R. C. Anderson, J. R. Fralish, and J. M. Baskin, eds., *Savannas, Barrens, and Rock Outcrop Plant Communities of North America.* Cambridge, UK: Cambridge University Press, 83–98.

Bridges, E. L. 2006a. "Historical Accounts of Vegetation in the Kissimmee River Dry Prairie Landscape." In R. F. Noss, ed., *Land of Fire and Water: The Florida Dry Prairie Ecosystem.* Proceedings of the Florida Dry Prairie Conference, October 5–7, 2004. DeLeon Springs, FL: E. O. Painter, 43–63.

———. 2006b. "Landscape Ecology of Florida Dry Prairie in the Kissimmee River Region." In R. F. Noss, ed., *Land of Fire and Water: The Florida Dry Prairie Ecosystem.* Proceedings of the Florida Dry Prairie Conference, October 5–7, 2004. DeLeon Springs, FL: E. O. Painter, 14–42.

Bridges, E. L., and S. L. Orzell. 1986. "Distribution Patterns of the Non-Endemic Flora of Middle Tennessee Limestone Glades." *ASB Bulletin* 33:155–66.

Briles, C. E., C. Whitlock, C. N. Skinner, and J. Mohr. 2011. "Holocene Forest Development and Maintenance on Different Substrates in the Klamath Mountains, Northern California, USA." *Ecology* 92:590–601.

Britton, W., and A. Messenger. 1969. "Computed Soil Moisture Patterns in and around the Prairie Peninsula during the Great Drought of 1933–34." *Transactions of the Illinois State Academy of Science* 62:181–87.

Brockway, D. G., K. W. Outcalt, and W. D. Boyer. 2006. "Longleaf Pine Regeneration Ecology and Methods." In S. Jose, E. J. Jokela, and D. L. Miller, eds., *The Longleaf Pine Ecosystem: Ecology, Silviculture, and Restoration*. New York: Springer-Verlag, 95–133.

Brouillet, L., and R. D. Whetstone. 1993. "Climate and Physiography." In Flora of North America Editorial Committee, eds., *Flora of North America, North of Mexico*. Vol. 1. "Introduction." New York: Oxford University Press, 15–46.

Brown, R. L. 2003. "Paleoenvironment and Biogeography of the Mississippi Black Belt." In E. Peacock and T. Schauwecker, eds., *Blackland Prairies of the Gulf Coastal Plain: Nature, Culture, and Sustainability*. Tuscaloosa: University of Alabama Press, 11–26.

Burnham, K. P., and D. R. Anderson. 2002. *Model Selection and Multi-Model Inference: A Practical Information-Theoretic Approach*. New York: Springer.

Cabeza de Vaca, Alvar Núñez. (1542) 1993. *Castaways: The Narrative of Alvar Núñez Cabeza de Vaca*. Edited by Enrique Pupo-Walker. Translated by Franes M. López Morillas. Berkeley: University of California Press.

Capinera, J. L., C. W. Scherer, and J. M. Squitier. 2001. *Grasshoppers of Florida*. Gainesville: University Press of Florida.

Cardinale, B. J., K. L. Matulich, D. U. Hooper et al. 2011. "The Functional Role of Producer Diversity in Ecosystems." *American Journal of Botany* 98:572–92.

Carr, S. C., K. M. Robertson, and R. K. Peet. 2010. "A Vegetation Classification of Fire-Dependent Pinelands of Florida." *Castanea* 75:153–89.

Carr, S. C., K. M. Robertson, W. J. Platt, and R. K. Peet. 2009. "A Model of Geographical, Environmental and Regional Variation in Vegetation Composition of Pyrogenic Grasslands of Florida." *Journal of Biogeography* 36:1600–1612.

Cech, R., and G. Tudor. 2005. *Butterflies of the East Coast: An Observer's Guide*. Princeton, NJ: Princeton University Press.

Cerling, T. E., J. G. Wynn, S. A. Andanje, M. I. Bird, D. K. Korir, N. E. Levin, W. Mace, A. N. Macharia, J. Quade, and C. H. Remien. 2011. "Woody Cover and Hominin Environments in the Past 6 Million Years." *Nature* 476:51–56.

Chamberlin, T. C. 1890. "The Method of Multiple Working Hypotheses." *Science* 15:92–96. (reprinted in *Science* 148:754–59)

Christman, S. P. 1970. "HYLA ANDERSONII in Florida." *Quarterly Journal of the Florida Academy of Science* 33:80.

Collins, S. L., S. M. Glenn, and D. J. Gibson. 1995. "Experimental Analysis of Intermediate Disturbance and Initial Floristic Composition: Decoupling Cause and Effect." *Ecology* 76:486–92.

Comer, P., D. Faber-Langendoen, R. Evans, S. Gawler, C. Josse, G. Kittel, and S. Menard. 2003. *Ecological Systems of the United States: A Working Classification of U.S. Terrestrial Systems*. Arlington, VA: NatureServe.

Connell, J. H. 1978. "Diversity in Tropical Rain Forests and Coral Reefs." *Science* 199:1302–10.

Coupland, R. T., ed. 1991. *Ecosystems of the World 8A. Natural Grasslands: Introduction and Western Hemisphere.* Amsterdam: Elsevier.

Crompton, T. 2011. "Values Matter." *Nature Climate Change* 1:276–77.

Culver, M. 2010. "Lessons and Insights from Evolution, Taxonomy, and Conservation Genetics." In M. Hornocker and S. Negri, eds., *Cougar: Ecology and Conservation.* Chicago: University of Chicago Press, 27–40.

Dart, R. A. 1925. "*Australopithecus africanus*: The Man-Ape of South Africa." *Nature* 115:195–99.

Davis, J. E., Jr., C. McRae, B. L. Estep, L. S. Barden, and J. F. Matthews. 2002. "Vascular Flora of Piedmont Prairies: Evidence from Several Prairie Remnants." *Castanea* 67:1–12.

Davis, M. B. 1981. "Quaternary History and the Stability of Forest Communities." In D. C. West, H. H. Shugart, and D. B. Botkin, eds., *Forest Succession: Concepts and Application.* New York: Springer-Verlag, 134–53.

Davis, M. B., and R. G. Shaw. 2001. "Range Shifts and Adaptive Responses to Quaternary Climate Change." *Science* 292:673–79.

DeCoster, J. K., W. J. Platt, and S. A. Riley. 1999. "Pine Savannas of Everglades National Park—An Endangered Ecosystem." In D. T. Jones and B. W. Gamble, eds., *Florida's Garden of Good and Evil. Proceedings of the 1998 Joint Symposium of the Florida Exotic Pest Plant Council and Florida Native Plant Society.* West Palm Beach, FL: South Florida Water Management District, 81–88.

Delcourt, H. R. 1979. "Late Quaternary Vegetation History of the Eastern Highland Rim and Adjacent Cumberland Plateau of Tennessee." *Ecological Monographs* 49:255–80.

Delcourt, H. R., and P. A. Delcourt. 1997. "Pre-Columbian Native American Use of Fire on Southern Appalachian Landscapes." *Conservation Biology* 11:1010–14.

Delcourt, P. A., and H. R. Delcourt. 1981. "Vegetation Maps for Eastern North America: 40,000 yr B.P. to the Present." *Geobotany* 2:123–65.

———. 1984. "Late Quaternary Paleoclimates and Biotic Responses in Eastern North America and the Western North Atlantic Ocean." *Palaeogeography, Palaeoclimatology, Palaeoecology* 48:263–84.

———. 1993. "Paleoclimates, Paleovegetation, and Paleofloras during the Late Quaternary." In Flora of North America Editorial Committee, eds., *Flora of North America, North of Mexico.* Vol. 1. "Introduction." New York: Oxford University Press, 71–94.

———. 2004. *Prehistoric Native Americans and Ecological Change: Human Ecosystems in Eastern North America since the Pleistocene.* Cambridge, UK: Cambridge University Press.

Denevan, W. M. 1992. "The Pristine Myth: The Landscape of the Americas in 1492." *Annals of the Association of American Geographers* 82:369–85.

DeSelm, H. R., and N. Murdock. 1993. "Grass-Dominated Communities." In W. H. Martin, S. G. Boyce, and A. C. Echternacht, eds., *Biodiversity of the Southeastern United States. Upland Terrestrial Communities.* New York: Wiley, 87–141.

Deyrup, M. 1989. "Arthropods Endemic to Florida Scrub." *Florida Scientist* 52:254–70.

———. 1990. "Arthropod Footprints in the Sands of Time." *Florida Entomologist* 73:529–38.

———. 2003. "An Updated List of Florida Ants (Hymenoptera: Formicidae)." *Florida Entomologist* 86:43–48.

Deyrup, M., and J. Trager. 1986. "Ants of the Archbold Biological Station, Highlands County, Florida (Hymenoptera: Formicidae)." *Florida Entomologist* 69:206–28.

Dietz, T., E. A. Rosa, and R. York. 2007. "Driving the Human Ecological Footprint." *Frontiers in Ecology and the Environment* 5:13–18.

Donlan, J., H. W. Greene, J. Berger, C. E. Bock, J. H. Bock, D. A. Burney, J. A. Estes et al. 2005. "Re-Wilding North America." *Nature* 436:913–14.

Donoghue, J. F. 2011. "Sea Level History of the Northern Gulf of Mexico Coast and Sea Level Rise Scenarios for the Near Future." *Climatic Change* 107:17–33.

Dorcas, M. E., J. D. Willson, R. N. Reed, R. W. Snow, M. R. Rochford, M. A. Miller, W. E. Meshaka Jr. et al. 2012. "Severe Mammal Declines Coincide with Proliferation of Invasive Burmese Pythons in Everglades National Park." *Proceedings of the National Academy of Sciences* 10.1073/pnas.1115226109.

Duever, L. C. 2011. *Ecology and Management of Saw Palmetto*. Report to Florida Fish and Wildlife Conservation Commission. Gainesville, FL: Fish and Wildlife Research Unit.

Duncan, B. W., and P. A. Schmalzer. 2004. "Anthropogenic Influences on Potential Fire Spread in a Pyrogenic Ecosystem of Florida, USA." *Landscape Ecology* 19:153–65.

Dunkel, T. 2011. "Beyond Man vs. Nature: The Case for Reconciliation." *Nature Conservancy* Spring 2011: 31–37.

Earley, L. S. 2004. *Looking for Longleaf: The Fall and Rise of an American Forest*. Chapel Hill: University of North Carolina Press.

Echols, S. L., and W. B. Zomlefer. 2010. "Vascular Plant Flora of the Remnant Blackland Prairies in Oaky Woods Wildlife Management Area, Houston County, Georgia." *Castanea* 75:78–100.

Egler, F. E. 1952. "Southeast Saline Everglades Vegetation, Florida, and Its Management." *Vegetatio* 3:213–65.

Elliott, L. P., and B. E. Brook. 2007. "Revisiting Chamberlin: Multiple Working Hypotheses for the 21st Century." *BioScience* 57:608–14.

Ellsworth, J. W., and B. C. McComb. 2003. "Potential Effects of Passenger Pigeon Flocks on the Structure and Composition of Presettlement Forests of Eastern North America." *Conservation Biology* 17:1548–58.

Engstrom, R. T. 1993. "Characteristic Mammals and Birds of Longleaf Pine Forests." In S. M. Hermann, ed., *The Longleaf Pine Ecosystem: Ecology, Restoration, and Management. Proceedings of the 18th Tall Timbers Fire Ecology Conference*, 127-38.

Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter et al. 2011. "Trophic Downgrading of Planet Earth." *Science* 333:301–306.

Estill, J. C., and M. B. Cruzan. 2001. "Phytogeography of Rare Plant Species Endemic to the Southeastern United States." *Castanea* 66:3–23.

Fairbank, Maslin, Maullin, Metz & Associates. 2010. *Key Findings from Recent National Opinion Research on "Ecosystem Services."* Report to The Nature Conservancy, Los Angeles, CA.

Fleischner, T. L., ed. 2011. *The Way of Natural History*. San Antonio TX: Trinity University Press.

Florida Natural Areas Inventory (FNAI). 2010. *Guide to the Natural Communities of Florida: 2010 Edition.* Tallahassee: Florida Natural Areas Inventory.

Foreman, D., and H. Wolke. 1989. *The Big Outside.* Tucson, AZ: Ned Ludd Books.

Forterre, Y., J. M. Skotheim, J. Dumais, and L. Mahadevan. 2005. "How the Venus Flytrap Snaps." *Nature* 433:421–25.

Foti, T. L., S. Simon, D. Zollner, and M. Hattenbach. 2003. "Blackland Prairie Landscapes of Southwestern Arkansas." In E. Peacock and T. Schauwecker, eds., *Blackland Prairies of the Gulf Coastal Plain: Nature, Culture, and Sustainability.* Tuscaloosa: University of Alabama Press, 94–109.

Franklin, J. F., and D. B. Lindenmayer. 2009. "Importance of Matrix Habitats in Maintaining Biological Diversity." *Proceedings of the National Academy of Sciences* 106:349–50.

Frost, C. C. 1993. "Four Centuries of Changing Landscape Patterns in the Longleaf Pine Ecosystem." In S. M. Hermann, ed., *The Longleaf Pine Ecosystem: Ecology, Restoration, and Management. Proceedings of the 18th Tall Timbers Fire Ecology Conference,* 17–43.

———. 1995. "Presettlement Fire Regimes in Southeastern Marshes, Peatlands, and Swamps." In S. I. Cerulean and R. T. Engstrom, eds., *Fire in Wetlands: A Management Perspective. Proceedings of the 19th Tall Timbers Fire Ecology Conference,* 39–60.

———. 1998. "Presettlement Fire Frequency Regimes of the United States: A First Approximation." In Theresa L. Pruden and Leonard A. Brennan, eds., *Fire in Ecosystem Management: Shifting the Paradigm from Suppression to Prescription. Proceedings of the 20th Tall Timbers Fire Ecology Conference,* 70–81.

———. 2006. "History and future of the longleaf pine ecosystem." In S. Jose, E. Jokela, and D. Miller, eds., *The Longleaf Pine Ecosystem: Ecology, Silviculture, and Restoration.* New York: Springer-Verlag, 9–48.

Fuhlendorf, S. D., D. M. Engle, J. Kerby, and R. Hamilton. 2008. "Pyric Herbivory: Rewilding Landscapes through the Recoupling of Fire and Grazing." *Conservation Biology* 23:588–98.

Fuller, R. A., K. N. Irvine, P. Devine-Wright, P. H. Warren, and K. J. Gaston. 2007. "Psychological Benefits of Greenspace Increase with Biodiversity." *Biology Letters* 3:390–394.

Gagnon, P. R., K. E. Harms, W. J. Platt, H. A. Passmore, and J. A. Myers. 2012. "Small-Scale Variation in Fuel Loads Differentially Affects Two Co-Dominant Bunchgrasses in a Species-Rich Pine Savanna." *PLoS One* 7(1): e29674.

Gagnon, P. R., H. A. Passmore, W. J. Platt, J. A. Myers, C. E. T. Paine, and K. E. Harms. 2010. "Does Pyrogenicity Protect Burning Plants?" *Ecology* 91:3481–86.

Gagnon, P. R., and W. J. Platt. 2008. "Multiple Disturbances Accelerate Clonal Growth in a Potentially Monodominant Bamboo." *Ecology* 89:612–18.

Garland, B. 2008. "Bibb County Glades: Botanical Discovery of the Century." *Outdoor Alabama* April 2008: 6–11.

Gattinger, A. 1901. *The Flora of Tennessee and a Philosophy of Botany.* Nashville, TN: Gospel Advocate.

Gentry, A. H. 1986. "Endemism in Tropical versus Temperate Plant Communities." In M. E. Soulé, ed., *Conservation Biology: The Science of Scarcity and Diversity.* Sunderland, MA: Sinauer, 153–81.

———. 1988. "Tree Species Richness of Upper Amazonian Forests." *Proceedings of the National Academy of Sciences* 85:156–59.

Gentry, A. H., and C. Dodson. 1987. "Contribution of Nontrees to Species Richness of a Tropical Rain Forest." *Biotropica* 19:149–56.

Gill, J. L., J. W. Williams, S. T. Jackson, K. B. Lininger, and G. S. Robinson. 2009. "Pleistocene Megafaunal Collapse, Novel Plant Communities, and Enhanced Fire Regimes in North America." *Science* 326:1100–1103.

Giuliano, W. M., C. R. Allen, R. S. Lutz, and S. Demarais. 1996. "Effects of Red Imported Fire Ants on Northern Bobwhite Chicks." *Journal of Wildlife Management* 60:309–13.

Gleason, H. A. 1926. "The Individualistic Concept of the Plant Association." *Bulletin of the Torrey Botanical Club* 53:7–26.

Glitzenstein, J. S., D. R. Streng, and D. D. Wade. 2003. "Fire Frequency Effects on Longleaf Pine (*Pinus palustris* P. Miller) Vegetation in South Carolina and Northeast Florida." *Natural Areas Journal* 23:22–37.

Goldman, D. H., and S. L. Orzell. 2000. "Morphological, Geographical, and Ecological Re-evaluation of *Calopogon multiflorus* (Orchidaceae)." *Lindleyana* 15:237–51.

Gosse, P. H. 1859. *Letters from Alabama, Chiefly Relating to Natural History*. London: Morgan and Chase.

Grace, J. B., L. Allain, and C. Allen. 2000. "Factors Associated with Plant Species Richness in a Coastal Tall-Grass Prairie." *Journal of Vegetation Science* 11:443–52.

Graham, A. 1993. "History of the Vegetation: Cretaceous (Maastrichtian)—Tertiary." In Flora of North America Editorial Committee, eds., *Flora of North America, North of Mexico*. Vol. 1. "Introduction." New York, Oxford University Press, 57–70.

———. 1999. *Late Cretaceous and Cenozoic History of North American Vegetation, North of Mexico. 1999.* New York: Oxford University Press.

———. 2005. "Organisms in Nature as a Central Focus for Biology." *Trends in Ecology and Evolution* 20:23–27.

Griffin, D., III, R. C. Harris, and W. R. Buck. 1995. "The Bryophytes and Lichens of Rock Hill Preserve, Florida." *Evansia* 12:31–39.

Griffin, D., III, and F. Snow. 1998. "Broxton Rocks Ecological Preserve: Bryophyte Refugium of South Georgia." *Tipularia* 13:23–28.

Grimm, E. C., W. A. Watts, G. L. Jacobson Jr., B. C. S. Hansen, H. R. Almquist, and A. C. Dieffenbacher-Krall. 2006. "Evidence for Warm Wet Heinrich Events in Florida." *Quaternary Science Reviews* 25:2197–2211.

Groves, C. R. 2003. *Drafting a Conservation Blueprint: A Practitioner's Guide to Planning for Biodiversity*. Washington, DC: Island Press.

Guyette, R. P., M. C. Stambaugh, D. C. Dey, and R.-M. Muzika. 2012. "Predicting Fire Frequency with Chemistry and Climate." *Ecosystems.* doi: 10.1007 /s10021-011-9512-0.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. "Community Structure, Population Control and Competition." *American Naturalist* 94:421–25.

Hall, H. G., and J. S. Ascher. 2010. "Surveys of Bees (Hymenoptera: Apoidea: Anthophila) in Natural Areas of Alachua County in North-Central Florida." *Florida Entomologist* 93:609–29.

Hamer, T. L., C. H. Flather, and B. R. Noon. 2006. "Factors Associated with Grassland Bird Species Richness: The Relative Roles of Grassland Area, Landscape Structure, and Prey." *Landscape Ecology* 21:569–83.

Harper, R. M. 1906a. "A Phytogeographical Sketch of the Altamaha Grit Region of the Coastal Plain of Georgia." *Annals of the New York Academy of Sciences* 17:1–415.

———. 1906b. "Some Hitherto Undescribed Outcrops of Altamaha Grit and Their Vegetation." *Torreya* 6:241–46.

———. 1907. "Centers of Distribution of Coastal Plain Plants." *Science*, New Series 25:539–41.

———. 1911. "The Relation of Climax Vegetation to Islands and Peninsulas." *Bulletin of the Torrey Botanical Club* 38:515–25.

———. 1914. "Geography and Vegetation of Northern Florida." *Annual Report of the Florida State Geological Survey* 6:163–452.

———. 1927. "Natural Resources of Southern Florida." *Annual Report of the Florida State Geological Survey* 18:27–206.

Harrison, S. P., and J. H. Viers. 2007. "Serpentine Grasslands." In M. R. Stromberg, J. D. Corbin, and C. M. D'Antonio, eds., *California Grasslands: Ecology and Management*. Berkeley: University of California Press, 145–55.

Harrison, S., J. H. Viers, J. H. Thorne, and J. B. Grace. 2008. "Favorable Environments and the Persistence of Naturally Rare Species." *Conservation Letters* 1:65–74.

Hawkins, B. A., R. Field, H. V. Cornell, D. J. Currie, J.-F. Guégan, D. M. Kaufman, J. T. Kerr et al. 2003. "Energy, Water, and Broad-Scale Geographic Patterns of Species Richness." *Ecology* 84:3105–17.

Heatherington, A. L., and P. A. Mueller. 1997. "Geochemistry and Origin of Florida Crustal Basement Terranes." In A. F. Randazzo and D. S. Jones, eds., *The Geology of Florida*. Gainesville: University Press of Florida, 27–37.

Helzer, C. J., and D. E. Jelinski. 1999. "The Relative Importance of Patch Area and Perimeter-Area Ratio to Grassland Breeding Birds." *Ecological Applications* 9:1448–58.

Herkert, J. R., D. L. Reinking, D. A. Wiedenfeld, M. Winter, J. L. Zimmerman, W. E. Jensen, E. J. Finck, and R. R. Koford. 2003. "Effects of Prairie Fragmentation on the Nest Success of Breeding Birds in the Midcontinental United States." *Conservation Biology* 17:587–94.

Hickman, J. C., ed. 1993. *The Jepson Manual—Higher Plants of California*. Berkeley: University of California Press.

Hill, J. G., and J. L. Seltzer. 2007. "A Note on Additional Plants Found at Sixteenth Section (Osborn) Prairie." *Journal of the Mississippi Academy of Sciences* 52:295–96.

Hobbs, R. J., L. M. Hallett, P. R. Ehrlich, and H. A. Mooney. 2011. "Intervention Ecology: Applying Ecological Science in the Twenty-First Century." *BioScience* 61:442–50.

Hoekstra, J. M. , T. M. Boucher, T. H. Ricketts, and C. Roberts. 2005. "Confronting a Biome Crisis: Global Disparities of Habitat Loss and Protection." *Ecology Letters* 8:23–29.

Howes, A. L., M. Maron, and C. A. McAlpine. 2010. "Bayesian Networks and Adaptive Management of Wildlife Habitat." *Conservation Biology* 24:974–83.

Huang, Y., B. Shuman, Y. Wang, T. Webb III, E. C. Grimm, and G. L. Jacobson Jr. 2006. "Climatic and Environmental Controls on the Variation of C_3 and C_4 Plant Abundances in Central Florida for the Past 62,000 Years." *Palaeogeography, Palaeoclimatology, Palaeoecology* 237:428–35.

Hudson, C. 1976. *The Southeastern Indians*. Knoxville: University of Tennessee Press.

Huffman, J. 2006. "Historical Fire Regimes in Southeastern Pine Savannas." PhD diss. Louisiana State University, Baton Rouge.

Hulbert, R. C., Jr., ed. 2001. *The Fossil Vertebrates of Florida*. Gainesville: University Press of Florida.

Hunter, M. L., Jr., G. L. Jacobson Jr., and T. Webb III. 1988. "Paleoecology and the Coarse Filter Approach to Maintaining Biological Diversity." *Conservation Biology* 2:375–85.

Isbell, F., V. Calcagno, A. Hector, J. Connolly, W. S. Harpole, P. B. Reich, M. Scherer-Lorenzen et al. 2011. "High Plant Diversity Is Needed to Maintain Ecosystem Services." *Nature* 477:199–202.

Ives, A. R., and S. R. Carpenter. 2007. "Stability and Diversity of Ecosystems." *Science* 317:58–62.

Jablonski, D. 2001. "Lessons from the Past: Evolutionary Impacts of Mass Extinctions." *Proceedings of the National Academy of Sciences* 98:5393–98.

Jackson, S. T., and R. J. Hobbs. 2009. "Ecological Restoration in the Light of Ecological History." *Science* 325:567–68.

Jackson, S. T., E. S. Webb, K. H. Anderson, J. T. Overpeck, T. Webb III, J. W. Williams, and B. C. S. Hansen. 2000. "Vegetation and Environment in Eastern North America during the Last Glacial Maximum." *Quaternary Science Reviews* 19:489–508.

Jacobs, B. F., J. D. Kingston, and L. L. Jacobs. 1999. "The Origin of Grass-Dominated Ecosystems." *Annals of the Missouri Botanical Garden* 86:590–643.

Jakle, J. A. 1968. "The American Bison and the Human Occupance of the Ohio Valley." *Proceedings of the American Philosophical Society* 112:299–305.

James, C. W. 1961. "Endemism in Florida." *Brittonia* 13:225–44.

Janis, C. M., J. Damuth, and J. M. Theodor. 2002. "The Origins and Evolution of the North American Grassland Biome: The Story from the Hoofed Mammals." *Palaeogeography, Palaeoclimatology, Palaeoecology* 177:183–98.

Jenkins, R. E. 1985. "Information Methods: Why the Heritage Programs Work." *Nature Conservancy News* 35(6):21–23.

Jose, S., E. Jokela, and D. Miller, eds. 2006. *The Longleaf Pine Ecosystem: Ecology, Silviculture, and Restoration.* New York: Springer-Verlag.

Juras, P. 1997. "The Presettlement Piedmont Savanna." MS thesis, Landscape Architecture. University of Georgia, Athens.

———. 2011. *The Southern Frontier: Landscapes Inspired by Bartram's Travels*. Savannah, GA: Telfair Books.

Kareiva, P. 2011. "The Future of Conservation: Balancing the Needs of People and Nature." *Nature Conservancy* Spring 2011: 38–39.

Kareiva, P., R. Lalasz, and M. Marvier. 2011. "Conservation in the Anthropocene: Beyond Solitude and Fragility." *Breakthrough Journal* Fall 2011: 29–37.

Kauffman, G. L., G. L. Nesom, A. S. Weakley, and T. E. Govus. 2004. "A New Species of *Symphyotrichum* (Asteraceae: Astereae) from a Serpentine Barren in Western North Carolina." *Sida* 21:827–39.

Kay, C. E. 1994. "Aboriginal Overkill: The Role of Native Americans in Structuring Western Ecosystems." *Human Nature* 5:359–98.

Keeley, J. E., G. H. Aplet, N. L. Christensen, S. G. Conard, E. A. Johnson, P. N. Omi, D. L. Peterson, and T. W. Swetnam. 2009. *Ecological Foundations for Fire Management in North American Forest and Shrubland Ecosystems.* USDA Forest Service General Technical Report PNW-GTR-779. Pacific Northwest Research Station, Portland, OR.

Kesel, R. H. 1974. "Inselbergs on the Piedmont of Virginia, North Carolina, and South Carolina: Types and Characteristics." *Southeastern Geology* 16:1–30.

King, J. R., and W. R. Tschinkel. 2008. "Experimental Evidence that Human Impacts Drive Fire Ant Invasions and Ecological Change." *Proceedings of the National Academy of Sciences* 105:20339–43.

Kintsch, J. A., and D. L. Urban. 2002. "Focal Species, Community Representation, and Physical Proxies as Conservation Strategies: A Case Study in the Amphibolite Mountains, North Carolina, U.S.A." *Conservation Biology* 16: 936–47.

Kirkman, L. K., K. L. Coffey, R. J. Mitchell, and E. B. Moser. 2004. "Ground Cover Recovery Patterns and Life-History Traits: Implications for Restoration Obstacles and Opportunities in a Species-Rich Savanna." *Journal of Ecology* 92:40–21.

Knapp, A. K., J. M. Blair, J. M. Briggs, S. L. Collins, D. C. Hartnett, L. C. Johnson, and E. G. Towne. 1999. "The Keystone Role of Bison in North American Tallgrass Prairie." *BioScience* 49:39–50.

Knight, G. R., J. B. Oetting, and L. Cross. 2011. *Atlas of Florida's Natural Heritage—Biodiversity, Landscapes, Stewardship, and Opportunities.* Tallahassee: Florida State University.

Koehler, G. M., and M. G. Hornocker. 1991. "Seasonal Resources Use among Mountain Lions, Bobcats, and Coyotes." *Journal of Mammalogy* 72:391–96.

Komarek, E. V. 1964. "The Natural History of Lightning." *Proceedings of the Third Tall Timbers Fire Ecology Conference*, 139–83.

Krech, S., III. 1999. *The Ecological Indian: Myth and History*. New York: Norton.

Kruckeberg, A. R. 1984. *California Serpentines: Flora, Vegetation, Geology, Soils, and Management Problems.* Berkeley: University of California Press.

Küchler, A. W. 1964 (1985). *Potential Natural Vegetation of the Conterminous United States*. American Geographic Society Special Publication No. 36 (1964) and U.S. Geological Survey, Reston, VA (1985).

Kull, K., and M. Zobel. 1991. "High Species Richness in an Estonian Wooded Meadow." *Journal of Vegetation Science* 2:711–14.

Lamoreux, J. F., J. C. Morrison, T. H. Ricketts, D. M. Olson, E. Dinerstein, M. W. McKnight, and H. H. Shugart. 2006. "Global Tests of Biodiversity Concordance and the Importance of Endemism." *Nature* 440:212–14.

Landau, D., and D. Prowell. 1999. "A Partial Checklist of Moths from Longleaf Pine Savannas in Louisiana (Insecta: Lepidoptera)." *Transactions of the American Entomological Society* 125:127–38.

Laurance, W. F. 2008. "Theory Meets Reality: How Habitat Fragmentation Research Has Transcended Island Biogeographic Theory." *Biological Conservation* 141:1731–44.

Lawler, A. 2011. "America's Lost City." *Science* 334:1618–23.

Lawless, P. J., J. M. Baskin, and C. C. Baskin. 2006. "Xeric Limestone Prairies of Eastern United States: Review and Synthesis." *Botanical Review* 72:235–72.

Leakey, R. 1994. *The Origin of Humankind*. New York: Basic Books.

LeBlond, R. J. 2001. "Endemic Plants of the Cape Fear Arch Region." *Castanea* 66:83–97.

Leopold, A. 1949. *A Sand County Almanac*. New York: Oxford University Press.

Lerman, S. B., and P. S. Warren. 2011. "The Conservation Value of Residential Yards: Linking Birds and People." *Ecological Applications* 21:1327–39.

Lesica, P., and F. W. Allendorf. 1995. "When Are Peripheral Populations Valuable for Conservation?" *Conservation Biology* 9:753–60.

Lindemann-Mathiess, P., X. Junge, and D. Matthies. 2010. "The Influence of Plant Diversity on People's Perception and Aesthetic Appreciation of Grassland Vegetation." *Biological Conservation* 143:195–202.

Lockett, S. H. (1869) 1969. *Louisiana As It Is: A Geographical and Topographic Description of the State.* Edited by L. C. Post. Baton Rouge: Louisiana State University Press.

Lomolino, M. V., B. R. Riddle, and J. H. Brown. 2006. *Biogeography.* 3rd ed. Sunderland, MA: Sinauer.

Loreau, M., S. Naeem, and P. Inchausti, eds. 2002. *Biodiversity and Ecosystem Functioning: Synthesis and Perspectives.* Oxford, UK: Oxford University Press.

Lorenzen, E. D., D. Nogués-Bravo, L. Orlando, J. Weinstock, J. Binladen, K. A. Marske, A. Ugan et al. 2011. "Species-Specific Responses of Late Quaternary Megafauna to Climate and Humans." *Nature* 479:359–64.

Lubertazzi, D., and W. R. Tschinkel. 2003. "Ant Community Change across a Ground Vegetation Gradient in North Florida's Longleaf Pine Flatwoods." *Journal of Insect Science* 3:21. insectscience.org/3.21

Luck, G. W., P. Davidson, D. Boxall, and L. Smallbone. 2011. "Relations between Urban Bird and Plant Communities and Human Well-Being and Connection to Nature." *Conservation Biology* 25:816–26.

Ludwig, J. C. 1999. "The Flora of Dolomite and Limestone Barrens in Southwestern Virginia." *Castanea* 64:209–30.

Lynas, M. 2011. *The God Species: Saving the Planet in the Age of Humans*. London: Fourth Estate.

MacArthur, R. H. 1972. *Geographical Ecology: Patterns in the Distribution of Species*. Princeton, NJ: Princeton University Press.

MacArthur, R. H., and J. W. MacArthur. 1961. "On Bird Species Diversity." *Ecology* 42:594–98.

MacArthur, R. H., and E. O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton, NJ: Princeton University Press.

MacFadden, B. J. 1997. "Fossil Mammals of Florida." In A. F. Randazzo and D. S. Jones, eds., *The Geology of Florida*. Gainesville: University Press of Florida, 119–37.

Mackey, R. L., and D. J. Currie. 2001. "The Diversity-Disturbance Relationship: Is It Generally Strong and Peaked?" *Ecology* 82:3479–92.

MacRoberts, B. R., M. H. MacRoberts, C. S. Reid, and P. L. Faulkner. 2009. "Vascular Flora of a Saline Prairie in Winn Parish, Louisiana." *Journal of the Botanical Research Institute of Texas* 3:349–54.

MacRoberts, M. H., B. R. MacRoberts, and L. S. Jackson. 2003. "Louisiana Prairies." In E. Peacock and T. Schauwecker, eds., *Blackland Prairies of the Gulf Coastal Plain: Nature, Culture, and Sustainability*. Tuscaloosa: University of Alabama Press, 80–93.

Maehr, D. S. 1997. "The Comparative Ecology of Bobcat, Black Bear, and Florida Panther in South Florida." *Bulletin of the Florida Museum of Natural History* 40:1–176.

Main, M. B., M. E. Swisher, J. Mullahey, W. DeBusk, A. J. Shirar, G. W. Tanner, J. Selph, P. Hogue, P. Bohlen, and G. M. Allen. 2004. *The Ecology and Economics of Florida's Ranches*. Report WEC 187, Department of Wildlife Ecology and Conservation, Florida Cooperative Extension Service, University of Florida, Gainesville.

Mann, C. 2005. *1491: New Revelations of the Americas before Columbus*. New York: Knopf.

Mansberg, L., and T. R. Wentworth. 1984. "Vegetation and Soils of a Serpentine Barren in Western North Carolina." *Bulletin of the Torrey Botanical Club* 111:273–86.

Margules, C. R., and R. L. Pressey. 2000. "Systematic Conservation Planning." *Nature* 405:243–53.

Marris, E. 2011. *Rambunctious Garden: Saving Nature in a Post-Wild World*. New York: Bloomsbury.

Martin, W. H., and D. B. Means. 2000. "Distribution and Habitat Relationships of the Eastern Diamondback Rattlesnake (*Crotalus adamanteus*)." *Herpetological Natural History* 7:9–34.

Marye, W. B. 1955. "The Great Maryland Barrens." *Maryland Historical Magazine* 50:11–23, 120–142, 234–253.

Maschinski, J., M. S. Ross, H. Liu, J. O'Brien, E. J. von Wettberg, and K. E. Haskins. 2011. "Sinking Ships: Conservation Options for Endemic Taxa Threatened by Sea Level Rise." *Climatic Change* 107:147–67.

May, J. H., and A. G. Warne. 1999. "Hydrogeologic and Geochemical Factors Required for the Development of Carolina Bays along the Atlantic and Gulf of Mexico, Coastal Plain, USA." *Environmental & Engineering Geoscience* 5:261–70.

May, R. M. 1974. *Stability and Complexity in Model Ecosystems*. 2nd ed. Princeton, NJ: Princeton University Press.

McCoy, E. D., and H. R. Mushinsky. 1992. "Rarity of Organisms in the Sand Pine Scrub Habitat of Florida." *Conservation Biology* 6:537–48.

McLaren, B. E., and R. O. Peterson. 1994. "Wolves, Moose, and Tree Rings on Isle Royale." *Science* 266:1555–58.

McVaugh, R. 1943. "The Vegetation of the Granitic Flat-Rocks of the Southeastern United States." *Ecological Monographs* 13:119–66.

Means, D. B. 1983. "The Enigmatic Pine Barrens Treefrog." *Florida Wildlife* 37:16–19.

———. 2006. "Vertebrate Faunal Diversity of Longleaf Pine Ecosystems." In S. Jose, E. Jokela, and D. Miller, eds., *The Longleaf Pine Ecosystem: Ecology, Silviculture, and Restoration.* New York: Springer-Verlag, 157–213.

Means, D. B., and G. Grow. 1985. "The Endangered Longleaf Pine Community." *ENFO Report* 85(4):1–12.

Means, D. B., and C. J. Longden. 1976. "Aspects of the Biology and Zoogeography of the Pine Barrens Treefrog (*Hyla andersonii*) in Northern Florida." *Herpetologica* 32:117–30.

Means, D. B., and D. Simberloff. 1987. "The Peninsula Effect: Habitat-Correlated Species Declines in Florida's Herpetofauna." *Journal of Biogeography* 14:551–68.

Menges, E. S., and D. R. Gordon. 2010. "Should Mechanical Treatments and Herbicides Be Used as Fire Surrogates to Manage Florida's Uplands? A Review." *Florida Scientist* 73:147–74.

Meuser, E., H. W. Harshaw, and A. O. Mooers. 2009. "Public Preference for Endemism over Other Conservation-Related Species Attributes." *Conservation Biology* 23:1041–46.

Meylan, P. A. 1982. "The Squamate Reptiles of the Inglis IA Fauna (Irvingtonian: Citrus County, Florida)." *Bulletin of the Florida State Museum* 27:1–85.

Millar, C. I., N. L. Stephenson, and S. L. Stephens. 2007. "Climate Change and Forests of the Future: Managing in the Face of Uncertainty." *Ecological Applications* 17:2145–51.

Mohr, C. 1901. *Plant Life of Alabama.* Washington, DC: Government Printing Office.

Moilanen, A., H. Possingham, and K. Wilson, eds. 2009. *Spatial Conservation Prioritization: Quantitative Methods and Computational Tools.* Oxford, UK: Oxford University Press.

Mooney, H. A. 1988. "Lessons from Mediterranean-Climate Regions." In E. O. Wilson, ed., *Biodiversity.* Washington, DC: National Academy Press, 157–165.

Morgan, G. S., and S. D. Emslie. 2010. "Tropical and Western Influences in Vertebrate Faunas from the Pliocene and Pleistocene of Florida." *Quaternary International* 217:143–58.

Morrison, J. L., and S. R. Humphrey. 2001. "Conservation Value of Private Lands for Crested Caracaras in Florida." *Conservation Biology* 15:675–84.

Mullahey, J. J., G. W. Tanner, and S. Coates. 2002. *Range Sites in Florida.* Report CIR951, Department of Wildlife Ecology and Conservation, Florida Cooperative Extension Service, University of Florida, Gainesville.

Mutch, R. W. 1970. "Wildland Fire and Ecosystems—a Hypothesis." *Ecology* 51:1046–51.

Myers, J. A., and K. E. Harms. 2009. "Seed Arrival, Ecological Filters, and Plant Species Richness: A Meta-analysis." *Ecology Letters* 12:1250–60.

———. 2011. "Seed Arrival and Ecological Filters Interact to Assemble High-Diversity Plant Communities." *Ecology* 92:676–86.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. Fonseca, and J. Kent. 2000. "Biodiversity Hotspots for Conservation Priorities." *Nature* 403:853–58.

Myers, R. L. 1985. "Fire and the Dynamic Relationship between Florida Sandhill and Sand Pine Scrub Vegetation." *Bulletin of the Torrey Botanical Club* 112:241–52.

Nature Conservancy. 1994. "Standardized National Vegetation Classification System." *USGS/NPS Vegetation Mapping Program*. Arlington, VA: The Nature Conservancy.

Neill, W. T. 1957. "Historical Biogeography of Present-Day Florida." *Bulletin of the Florida State Museum* 2:175–220.

Noss, R. F. 1985. "Wilderness Recovery and Ecological Restoration: An Example for Florida." *Earth First!* 5(8):18–19.

———. 1987. "From Plant Communities to Landscapes in Conservation Inventories: A Look at The Nature Conservancy (USA)." *Biological Conservation* 41:11–37.

———. 1988. "The Longleaf Pine Landscape of the Southeast: Almost Gone and Almost Forgotten." *Endangered Species Update* 5(5):1–8.

———. 1989. "Longleaf Pine and Wiregrass: Keystone Components of an Endangered Ecosystem." *Natural Areas Journal* 9:211–13.

———. 1992. "The Wildlands Project: Land Conservation Strategy." *Wild Earth* (Special Issue): 10–25.

———. 1996a. "Ecosystems as Conservation Targets." *Trends in Ecology and Evolution* 11:351.

———. 1996b. "The Naturalists Are Dying Off." *Conservation Biology* 10:1–3.

———. 2006. "Introduction to the Florida 'Dry' Prairie." In R. F. Noss, ed., *Land of Fire and Water: The Florida Dry Prairie Ecosystem*. Proceedings of the Florida Dry Prairie Conference, October 5–7, 2004. DeLeon Springs, FL: E.O. Painter, 1-2.

———. 2011. "Between the Devil and the Deep Blue Sea: Florida's Unenviable Position with Respect to Sea Level Rise." *Climatic Change* 107:1–16.

Noss, R. F., C. Carroll, K. Vance-Borland, and G. Wuerthner. 2002. "A Multicriteria Assessment of the Irreplaceability and Vulnerability of Sites in the Greater Yellowstone Ecosystem." *Conservation Biology* 16:895–908.

Noss, R. F., and A. Cooperrider. 1994. *Saving Nature's Legacy: Protecting and Restoring Biodiversity*. Washington, DC: Island Press.

Noss, R. F., B. Csuti, and M. J. Groom. 2006. "Habitat Fragmentation." In M. J. Groom, G. K. Meffe, and R. C. Carroll, eds., *Principles of Conservation Biology*. 3rd ed. Sunderland, MA: Sinauer, 213–51.

Noss, R. F., E. Dinerstein, B. Gilbert, M. Gilpin, B. Miller, J. Terborgh, and S. Trombulak. 1999. "Core Areas: Where Nature Reigns." In M.E. Soulé and J. Terborgh, eds., *Continental Conservation: Scientific Foundations of Regional Reserve Networks*. Washington, DC: Island Press, 99–128.

Noss, R. F., and L. D. Harris. 1986. "Nodes, Networks, and MUM's: Preserving Diversity at All Scales." *Environmental Management* 10:299–309.

Noss, R. F., M. Korosy, D. Breininger, J. Aldredge, and R. Bjork. 2008. *An Investigation of Breeding and Non-Breeding Season Ecology, Metapopulation Dynamics, and Recovery Options for the Florida Grasshopper Sparrow (Ammodramus savannarum floridanus)*. Final Report to the US Fish and Wildlife Service, Agreement No. 401815G034. University of Central Florida, Orlando.

Noss, R. F., E. T. LaRoe, and J. M. Scott. 1995. *Endangered Ecosystems of the United States: A Preliminary Assessment of Loss and Degradation.* Biological Report 28. Washington, DC: USDI National Biological Service.

Noss, R. F., M. A. O'Connell, and D. D. Murphy. 1997. *The Science of Conservation Planning: Habitat Conservation under the Endangered Species Act.* Washington, DC: Island Press.

Noss, R. F., and R. L. Peters. 1995. *Endangered Ecosystems of the United States: A Status Report and Plan for Action.* Washington, DC: Defenders of Wildlife.

Nowak, R. M. 2002. "The Original Status of Wolves in Eastern North America." *Southeastern Naturalist* 1:95–130.

Nuttall, T. (1819) 1980. *A Journal of Travels into the Arkansas Territory during the Year 1819.* University of Oklahoma Press, reprinted by University of Arkansas Press, Little Rock.

Orme, C. D. L., R. G. Davies, M. Burgess, F. Eigenbrod, N. Pickup, V. A. Olson, A. J. Webster et al. 2005. "Global Hotspots of Species Richness Are Not Congruent with Endemism or Threat." *Nature* 436:1016–19.

Orzell, S. L., and E. L. Bridges. 2006a. "Floristic Composition and Species Richness of Subtropical Seasonally Wet *Muhlenbergia sericea* Prairies in Portions of Central and South Florida." In R. F. Noss, ed., *Land of Fire and Water: The Florida Dry Prairie Ecosystem.* Proceedings of the Florida Dry Prairie Conference, October 5–7, 2004. DeLeon Springs, FL: E. O. Painter, 136–75.

———. 2006b. "Species Composition and Environmental Characteristics of Florida Dry Prairies from the Kissimmee River Region of South-Central Florida." In R. F. Noss, ed., *Land of Fire and Water: The Florida Dry Prairie Ecosystem.* Proceedings of the Florida Dry Prairie Conference, October 5–7, 2004. DeLeon Springs, FL: E. O. Painter, 100–135.

Overpeck, J. T., R. S. Webb, and T. Webb III. 1992. "Mapping Eastern North American Vegetation Change of the Past 18 Ka: No-Analogs and the Future." *Geology* 20:1071–74.

Owen-Smith, N. 1987. "Pleistocene Extinctions: The Pivotal Role of Megaherbivores." *Paleobiology* 13:351–62.

———. 1989. "Megafaunal Extinctions: The Conservation Message from 11,000 Years B.P." *Conservation Biology* 3:405–12.

Paine, R. T. 1966. "Food Web Complexity and Species Diversity." *American Naturalist* 100:65–75.

Pan Terra, Inc. 2000. "A Correlated History of Earth, Third Millennium Edition" (poster). Pan Terra, Inc., Hill City, South Dakota.

Patten, M. A., and B. D. Smith-Patten. 2011. "'As If' Philosophy: Conservation Biology's Real Hope." *BioScience* 61:425–26.

Pauly, D. 1995. "Anecdotes and the Shifting Baseline Syndrome of Fisheries." *Trends in Ecology and Evolution* 10:430.

Peacock, E., and T. Schauwecker. 2003. "Introduction: The Nature, Culture, and Sustainability of Blackland Prairies." In E. Peacock and T. Schauwecker, eds., *Blackland Prairies of the Gulf Coastal Plain: Nature, Culture, and Sustainability.* Tuscaloosa: University of Alabama Press, 1–7.

Peet, R. K. 2006. "Ecological Classification of Longleaf Pine Woodlands." In S. Jose, E. Jokela, and D. Miller, eds., *The Longleaf Pine Ecosystem: Ecology, Silviculture, and Restoration.* New York: Springer-Verlag, 51–93.

Peet, R. K., K. A. Palmquist, and S. M. Tessel. Forthcoming. "Herbaceous Layer Species Richness of Southeastern Forests and Woodlands: Patterns and Causes." In F. S. Gilliam and M. R. Roberts, eds., *The Herbaceous Layer in Forests of Eastern North America*, 2nd ed. Oxford, UK: Oxford University Press, chap. 8.

Phillips, O. L., P. Hall, A. H. Gentry, S. A. Sawyer, and R. Vásquez. 1994. "Dynamics and Species Richness of Tropical Rain Forests." *Proceedings of the National Academy of Sciences* 91:2805–9.

Pilkey, O. H., and R. Young. 2009. *The Rising Sea.* Washington, DC: Island Press.

Pillsbury, F. C., J. R. Miller, D. M. Debinski, and D. M. Engle. 2011. "Another Tool in the Toolbox? Using Fire and Grazing to Promote Bird Diversity in Highly Fragmented Landscapes." *Ecosphere* 2(3): 1–14.

Pimm, S. L. 1984. "The Complexity and Stability of Ecosystems." *Nature* 307:321–26.

Platt, R. B. 1951. "An Ecological Study of the Mid-Appalachian Shale Barrens and of the Plants Endemic to Them." *Ecological Monographs* 21:269–300.

Platt, S. G., and C. G. Brantley. 1997. "Canebrakes: An Ecological and Historical Perspective." *Castanea* 62:8–21.

Platt, S. G., C. G. Brantley, and T. R. Rainwater. 2009. "North American Ethnobotany of Cane (*Arundinaria* spp.) in the Southeastern United States: A Review." *Castanea* 74:271–85.

Platt, W. J. 1999. "Southeastern Pine Savannas." In R. C. Anderson, J. R. Fralish, and J. M. Baskin, eds., *Savannas, Barrens, and Rock Outcrop Plant Communities of North America.* Cambridge, UK: Cambridge University Press, 23–51.

Platt, W. J., S. M. Carr, M. J. Reilly, and J. Fahr. 2006. "Pine Savanna Overstory Influences on Ground-Cover Biodiversity." *Applied Vegetation Science* 9:37–50.

Platt, W. J., G. W. Evans, and S. L. Rathbun. 1988. "The Population Dynamics of a Long-Lived Conifer (*Pinus palustris*)." *American Naturalist* 131:491–525.

Platt, W. J., J. M. Huffman, M. G. Slocum, and B. Beckage. 2006. "Fire Regimes and Trees in Florida Dry Prairie Landscapes." In R. F. Noss, ed., *Land of Fire and Water: The Florida Dry Prairie Ecosystem.* Proceedings of the Florida Dry Prairie Conference, October 5–7, 2004. DeLeon Springs, FL: E. O. Painter, 3–13.

Platt, W. J., and M. W. Schwartz. 1990. "Temperate Hardwood Forests." In R. L. Myers and J. J. Ewel, eds., *Ecosystems of Florida.* Orlando: University of Central Florida Press, 194–229.

Poiani, K. A., B. D. Richter, M. G. Anderson, and H. E. Richter. 2000. "Biodiversity Conservation at Multiple Scales: Functional Sites, Landscapes, and Networks." *BioScience* 50:133–46.

Poole, J. M., W. R. Carr, D. M. Price, and J. R. Singhurst. 2007. *Rare Plants of Texas.* College Station: Texas A&M University Press.

Porter, C. C. 1975. "A New Floridian *Polycyrtidea* with Comments on Zoogeography of Florida Mesostenini (Hymenoptera: Ichneumonidae)." *Florida Entomologist* 58:247–55.

Power, M. E., D. Tilman, J. A. Estes, B. A. Menge, W. J. Bond, L. S. Mills, G. Daily, J. C. Castilla, J. Lubchenco, and R. T. Paine. 1996. "Challenges in the Quest for Keystones." *BioScience* 46:609–20.

Pranty, B., and J. W. Tucker Jr. 2006. "Ecology and Management of the Florida Grasshopper Sparrow." In R. F. Noss, ed., *Land of Fire and Water: The Florida Dry Prairie Ecosystem.* Proceedings of the Florida Dry Prairie Conference, October 5–7, 2004. DeLeon Springs, FL: E. O. Painter, 188–200.

Pressey, R. L., I. R. Johnson, and P. D. Wilson. 1994. "Shades or Irreplaceability: Towards a Measure of the Contribution of Sites to a Reservation Goal." *Biodiversity and Conservation* 3:242–62.

Pringle, J. S., and T. Witsell. 2005. "A New Species of *Sabatia* (Gentianaceae) from Saline County, Arkansas." *Sida* 21:1249–62.

Provencher, L., A. R. Litt, and D. R. Gordon. 2003. "Predictors of Species Richness in Northwest Florida Longleaf Pine Sandhills." *Conservation Biology* 17:1660–71.

Prugh, L. R., K. E. Hodges, A. R. E. Sinclair, and J. S. Brashares. 2008. "Effect of Habitat Area and Isolation on Fragmented Animal Populations." *Proceedings of the National Academy of Sciences* 105:20770–75.

Putz, F. E. 2003. "Are Rednecks the Unsung Heroes of Ecosystem Management?" *Wild Earth* 12(2/3):10–14.

Qian, H., J. D. Fridley, and M. W. Palmer. 2007. "The Latitudinal Gradient of Species–Area Relationships for Vascular Plants of North America." *American Naturalist* 170:690–701.

Quarterman, E., M. P. Burbank, and D. J. Shure. 1993. "Rock Outcrop Communities: Limestone, Sandstone, and Granite." In W. H. Martin, S. G. Boyce, and A. C. Echternacht, eds., *Biodiversity of the Southeastern United States. Upland Terrestrial Communities.* New York: Wiley, 35–86.

Quarterman, E., and C. Keever. 1962. "Southern Mixed Hardwood Forest: Climax in the Southeastern Coastal Plain, U.S.A." *Ecological Monographs* 32:167–85.

Rabinowitz, D., S. Cairns, and T. Dillon. 1986. "Seven Forms of Rarity and Their Frequency in the Flora of the British Isles." In M. E. Soulé, ed., *Conservation Biology: The Science of Scarcity and Diversity.* Sunderland, MA: Sinauer, 182–204.

Rankin, H. T., and D. E. Davis. 1971. "Woody Vegetation in the Black Belt Prairie of Montgomery County, Alabama, in 1845–46." *Ecology* 52:716–19.

Reid, C. S., P. L. Faulkner, M. H. MacRoberts, and B. R. MacRoberts. 2010. "Vascular Flora and Edaphic Characteristics of Saline Prairies in Louisiana." *Journal of the Botanical Research Institute of Texas* 4:357–79.

Reid, J. W., and J. D. Spooner. 1998. "*Stolonicyclops heggiensis*, New Genus, New Species, from Georgia, U.S.A. (Copepoda: Cyclopoida: Cyclopidae)." *Journal of Crustacean Biology* 18:405–11.

Reséndez, A. 2007. *A Land So Strange: The Epic Journey of Cabeza de Vaca.* New York: Basic Books.

Riginos, C. 2009. "Grass Competition Suppresses Savanna Tree Growth across Multiple Demographic Stages." *Ecology* 90:335–40.

Ripley, E. A. 1991. "Grassland Climate." In R. T. Coupland, ed., *Ecosystems of the World 8A. Natural Grasslands: Introduction and Western Hemisphere.* Amsterdam: Elsevier, 7–24.

Ripple, W. J., and B. Van Valkenburgh. 2010. "Linking Top-Down Forces to the Pleistocene Megafaunal Extinctions." *BioScience* 60:516–26.

Ross, M. S., J. F. Meeder, J. P. Sah, P. L. Ruiz, and G. J. Telesnicki. 2000. "The Southeast Saline Everglades Revisited: 50 Years of Coastal Vegetation Change." *Journal of Vegetation Science* 11:101–12.

Ross, M. S., J. J. O'Brien, R. G. Ford, K. Zhang, and A. Morkill. 2009. "Disturbance and the Rising Tide: The Challenge of Biodiversity Management on Low-Island Ecosystems." *Frontiers in Ecology and the Environment* 7:471–78.

Rostlund, E. 1957. "The Myth of a Natural Prairie Belt in Alabama: An Interpretation of Historical Records." *Annals of the Association of American Geographers* 47:392–411.

———. 1960. "The Geographic Range of the Historic Bison in the Southeast." *Annals of the Association of American Geographers* 50:395–407.

Saha, S., K. Bradley, M. S. Ross, P. Hughes, T. Wilmers, P. L. Ruiz, and C. Bergh. 2011. "Hurricane Effects on Subtropical Pine Rocklands of the Florida Keys." *Climatic Change* 107:169–84.

Samson, F. B., and F. L. Knopf, eds. 1996. *Prairie Conservation: Preserving North America's Most Endangered Ecosystem.* Washington, DC: Island Press.

Sandel, B., L. Arge, B. Dalsgaard, R. G. Davies, K. J. Gaston, W. J. Sutherland, and J.-C. Svenning. 2011. "The Influence of Late Quaternary Climate-Change Velocity on Species Endemism." *Science* 334:660–64.

Sauer, C. 0. 1950. "Grassland, Climax, Fire and Man." *Journal of Range Management* 3:16–22.

Schafale, M. P., and A. S. Weakley. 1990. "Classification of the Natural Communities of North Carolina: Third Approximation." Raleigh, NC: North Carolina Natural Heritage Program.

Schauwecker, T., and J. MacDonald. 2003. "Plant Assemblage Response to Disturbance at a Blackland Prairie Restoration Site in Northeastern Mississippi." In E. Peacock and T. Schauwecker, eds., *Blackland Prairies of the Gulf Coastal Plain: Nature, Culture, and Sustainability.* Tuscaloosa: University of Alabama Press, 246–53.

Schmidtling, R. C., and V. Hipkins. 1998. "Genetic Diversity in Longleaf Pine (*Pinus palustris*): Influence of Historical and Prehistorical Events." *Canadian Journal of Forest Research* 28:1135–45.

Schmitz, M., W. Platt, and J. DeCoster. 2002. "Substrate Heterogeneity and Number of Plant Species in Everglades Savannas (Florida, USA)." *Plant Ecology* 160:137–48.

Shmida, A., and M. V. Wilson. 1985. "Biological Determinants of Species Diversity." *Journal of Biogeography* 12:1–20.

Shure, D. J. 1999. "Granite Outcrops of the Southeastern United States." In R. C. Anderson, J. R. Fralish, and J. M. Baskin, eds., *Savannas, Barrens, and Rock Outcrop Plant Communities of North America.* Cambridge, UK: Cambridge University Press, 99–118.

Sims, P. L., and P. G. Risser. 2000. "Grasslands." In M. G. Barbour and W. D. Billings, eds., *North American Terrestrial Vegetation*, 2nd ed. Cambridge, UK: Cambridge University Press, 323–56.

Slapcinsky, J. L., D. R. Gordon, and E. S. Menges. 2010. "Response of Rare Plant Species to Fire in Florida's Pyrogenic Communities." *Natural Areas Journal* 30:4–19.

Small, J. K. 1927. "Among Floral Aborigines." *Journal of the New York Botanical Garden* 28:1–20, 25–40.

Soltis, D. E., A. B. Morris, J. S. McLachlan, P. S. Manos, and P. S. Soltis. 2006. "Comparative Phylogeography of Unglaciated Eastern North America." *Molecular Ecology* 15:4261–93.

Sorrie, B. A. 2011. *A Field Guide to the Wildflowers of the Sandhills Region.* Chapel Hill: University of North Carolina Press.

Sorrie, B. A., and A. S. Weakley. 2001. "Coastal Plain Plant Endemics: Phytogeographic Patterns." *Castanea* 66:50–82.

———. 2006. "Conservation of the Endangered *Pinus palustris* Ecosystem Based on Coastal Plain Centres of Plant Endemism." *Applied Vegetation Science* 9:59–66.

Soulé, M. E. 2010. "Conservation Relevance of Trophic Cascades." In J. Terborgh and J. A. Estes, eds., *Trophic Cascades: Predators, Prey, and the Changing Dynamics of Nature.* Washington, DC: Island Press, 337–51.

Soulé, M. E., D. T. Bolger, A. C. Alberts, J. Wright, M. Sorice, and S. Hill. 1988. "Reconstructed Dynamics of Rapid Extinctions of Chaparral-Requiring Birds in Urban Habitat Islands." *Conservation Biology* 2:75–92.

Soulé, M. E., J. A. Estes, J. Berger, and C. Martinez del Rio. 2003. "Ecological Effectiveness: Conservation Goals for Interactive Species." *Conservation Biology* 17:1238–50.

Soulé, M. E., J. A. Estes, B. Miller, and D. L. Honnold. 2005. "Strongly Interacting Species: Conservation Policy, Management, and Ethics." *BioScience* 55:168–76.

Soulé, M., and R. Noss. 1998. "Rewilding and Biodiversity: Complementary Goals for Continental Conservation." *Wild Earth* 8(3):18–28.

Soulé, M., and J. Terborgh, eds. 1999. *Continental Conservation: Scientific Foundations of Regional Reserve Networks.* Washington, DC: Island Press.

Staver, A. C., S. Archibald, and S. Levin. 2011a. "The Global Extent and Determinants of Savanna and Forest as Alternative Biome States." *Science* 334:230–32.

———. 2011b. "Tree Cover in Sub-Saharan Africa: Rainfall and Fire Constrain Forest and Savanna as Alternative Stable States." *Ecology* 92:1063–72.

Staver, A. C., W. J. Bond, W. D. Stock, S. J. van Rensburg, and M. S. Waldram. 2009. "Browsing and Fire Interact to Suppress Tree Density in an African Savanna." *Ecological Applications* 19:1909–19.

Steele, E. S. 1911. "New or Noteworthy Plants from the Eastern United States." *Contributions from the United States National Herbarium* 13:359–74.

Stein, B. A., L. S. Kutner, and J. S. Adams, eds., 2000. *Precious Heritage: The Status of Biodiversity in the United States.* Oxford, UK: Oxford University Press.

Stephenson, K. E. 2011. "Distribution of Grasslands in 19th Century Florida." *American Midland Naturalist* 165:50–59.

Stoddard, H. L. 1969. *Memoirs of a Naturalist.* Norman: University of Oklahoma Press.

Stout, I. J., and W. R. Marion. 1993. "Pine Flatwoods and Xeric Pine Forests of the Southern (Lower) Coastal Plain." In W. H. Martin, S. G. Boyce, and A. C. Echternacht, eds., *Biodiversity of the Southeastern United States. Lowland Terrestrial Communities.* New York: Wiley, 373–446.

Stowe, J. P., J. M. Varner III, and J. P. McGuire. 2002. "Montane Longleaf Pinelands…Little-Known and Disappearing Treasures." *Tipularia* 17:8–15.

Strauss, B. H., R. Ziemlinski, J. L. Weiss, and J. T. Overpeck. 2012. "Tidally Adjusted Estimates of Topographic Vulnerability to Sea Level Rise and Flooding in the United States." *Environmental Research Letters* 7 stacks.iop.org/ERL/7/014033.

Streng, D. R., J. S. Glitzenstein, and W. J. Platt. 1993. "Evaluating Season of Burn in Longleaf Pine Forests: A Critical Literature Review and Some Results from an Ongoing Long-term Study." In S.M. Hermann, ed., *The Longleaf Pine Ecosystem: Ecology, Restoration, and Management. Proceedings of the 18th Tall Timbers Fire Ecology Conference*, 227-63.

Tanner, J. T. 1942. *The Ivory-Billed Woodpecker*. Research Report No. 1, National Audubon Society.

Terborgh, J., and J. A. Estes, eds. 2010. *Trophic Cascades: Predators, Prey, and the Changing Dynamics of Nature*. Washington, DC: Island Press.

Thatcher, C. A., F.T. van Manen, and J. D. Clark. 2006. "Identifying Suitable Sites for Florida Panther Reintroduction." *Journal of Wildlife Management* 70:752–63.

Thornton, D. H., M. E. Sunquist, and M. B. Main. 2004. "Ecological Separation within Newly Sympatric Populations of Coyotes and Bobcats in South-Central Florida." *Journal of Mammalogy* 85:973–82.

Tilman, D., P. B. Reich, and J. M. H. Knops. 2006. "Biodiversity and Ecosystem Stability in a Decade-Long Grassland Experiment." *Nature* 441:629–32.

Tompkins, R. D., C. M. Luckenbaugh, W. C. Stringer, K. H. Richardson, E. A. Mikhailova, and W. C. Bridges Jr. 2010. "Suther Prairie: Vascular Flora, Species Richness, and Edaphic Factors." *Castanea* 75:232–44.

Transeau, E. N. 1935. "The Prairie Peninsula." *Ecology* 16:423–37.

Triplett, J.K., A.S. Weakley, and L.G. Clark. 2006. "Hill Cane (*Arundinaria appalachiana*), a New Species of Bamboo (Poaceae: Bambusoideae) from the Southern Appalachian Mountains." *Sida* 22:79–95.

Truett, J. C. 2010. *Grass: In Search of Human Habitat*. Berkeley: University of California Press.

Tschinkel, W. R. 2002. "The Natural History of the Arboreal Ant, *Crematogaster ashmeadi*." *Journal of Insect Science* 2(12):1–15.

Tucker, J. W., G. R. Schrott, and R. Bowman. 2010. "Fire Ants, Cattle Grazing, and the Endangered Florida Grasshopper Sparrow." *Southeastern Naturalist* 9:237–50.

Tyndall, R. W. 1992. "Historical Considerations of Conifer Expansion in Maryland Serpentine 'Barrens.'" *Castanea* 57:123–31.

Tyndall, R. W., and J. C. Hull. 1999. "Vegetation, Flora, and Plant Physiological Ecology of Serpentine Barrens of Eastern North America." In R. C. Anderson, J. R. Fralish, and J. M. Baskin, eds., *Savannas, Barrens, and Rock Outcrop Plant Communities of North America*. Cambridge, UK: Cambridge University Press, 67–82.

Vale, T. R. 1998. "The Myth of the Humanized Landscape: An Example from Yosemite National Park." *Natural Areas Journal* 18:231–36.

Varner, J. M., III, J. S. Kush, and R. S. Meldahl. 2003. "Vegetation of Frequently Burned Old-Growth Longleaf Pine (*Pinus palustris* Mill.) Savannas on Choccolocco Mountain, Alabama, USA." *Natural Areas Journal* 23:43–52.

Wahlenberg, W. G. 1946. *Longleaf Pine: Its Use, Ecology, Regeneration, Protection, Growth and Management*. Washington, DC: C. L. Pack Forestry Foundation and USDA Forest Service.

Waldron, J. L., S. M. Welch, and S. H. Bennett. 2008. "Vegetation Structure and the Habitat Specificity of a Declining North American Reptile: A Remnant of Former Landscapes." *Biological Conservation* 141:2477–82.

Walker, J., and R. K. Peet. 1984. "Composition and Species Diversity of Pine-Wiregrass Savannas of the Green Swamp, North Carolina." *Vegetatio* 55:163–79.

Wallace, S. C., and X. Wang. 2004. "Two New Carnivores from an Unusual Late Tertiary Forest Biota in Eastern North America." *Nature* 431:556–59.

Ware, S., C. Frost, and P. D. Doerr. 1993. "Southern Mixed Hardwood Forest: The Former Longleaf Pine Forest." In W. H. Martin, S. G. Boyce, and A. C. Echternacht, eds., *Biodiversity of the Southeastern United States. Lowland Terrestrial Communities*. New York: Wiley, 447–93.

Watts, W. A. 1983. "Vegetational History of the Eastern United States 25,000 to 10,000 Years Ago." In S. C. Porter, ed., *Late-Quaternary Environments of the United States*. Vol. 1. *The Late Pleistocene*. Minneapolis: University of Minnesota Press, 294–310.

Watts, W. A., and B. C. S. Hansen. 1994. "Pre-Holocene and Holocene Pollen Records of Vegetation History from the Florida Peninsula and Their Climatic Implications." *Palaeogeography, Palaeoclimatology, Palaeoecology* 109:163–76.

Watts, W. A., B. C. S. Hansen, and E. C. Grimm. 1992. "Camel Lake: A 40,000-Yr Record of Vegetational and Forest History from Northwest Florida." *Ecology* 73:1056–66.

Way, A. G. 2008. "Burned to be Wild: Science, Society, and Ecological Education in the Southern Longleaf Pine." PhD diss. University of Georgia, Athens.

Weakley, A. S. 2008. "Flora of the Carolinas, Virginia, Georgia, Northern Florida, and Surrounding Areas." University of North Carolina, Chapel Hill. Working draft of April 7, 2008.

Webb, S. D. 1977. "A History of Savanna Vertebrates in the New World." Part I: "North America." *Annual Review of Ecology and Systematics* 8:355–80.

———. 1990. "Historical Biogeography." In R. L. Myers and J. J. Ewel, eds., *Ecosystems of Florida*. Orlando: University of Central Florida Press, 70–100.

Weigl, P., M. A. Steele, L. J. Sherman, J. C. Ha, and T. L. Sharpe. 1989. "The Ecology of the Fox Squirrel (*Sciurus niger*) in North Carolina: Implications for Survival in the Southeast." *Bulletin of the Tall Timbers Research Station* 24:1-93.

Weigl, P. D., and T. W. Knowles. 1995. "Megaherbivores and Southern Appalachian Grass Balds." *Growth and Change* 26:365–82.

White, R. E. 1983. *A Field Guide to the Beetles of North America*. Boston: Houghton Mifflin.

White, R., A. Murray, and M. Rohweder. 2000. *Pilot Analysis of Global Ecosystems: Grassland Ecosystems*. Washington, DC: World Resources Institute.

Whitman, W. 1882. *Leaves of Grass*. Philadelphia: Rees Welsh and Company.

Whittaker, R. H. 1962. "Classification of Natural Communities." *Botanical Review* 28:1–239.

———. 1975. *Communities and Ecosystems*. 2nd ed. New York: Macmillan.

Willard, D. A., and C. E. Bernhardt. 2011. "Impacts of Past Climate and Sea Level Change on Everglades Wetlands: Placing a Century of Anthropogenic Change into a Late-Holocene Context." *Climatic Change* 107:59–80.

Willcox, E. V., and W. M. Giuliano. 2010. "Seasonal Effects of Prescribed Burning and Roller Chopping on Saw Palmetto in Flatwoods." *Forest Ecology and Management* 259:1580–85.

Willcox, E. V., G. W. Tanner, W. M. Giuliano, and R. McSorley. 2010. "Avian Community Response to Grazing Intensity on Monoculture and Mixed Florida Pastures." *Rangeland Ecology and Management* 63:203–22.

Williams, J. W., B. N. Shuman, T. Webb III, P. J. Bartlein, and P. L. Leduc. 2004. "Late-Quaternary Vegetation Dynamics in North America: Scaling from Taxa to Biomes." *Ecological Monographs* 74:309–34.

Williams, J. W., T. Webb III, P. H. Richard, and P. Newby. 2000. "Late Quaternary Biomes of Canada and the Eastern United States." *Journal of Biogeography* 27:585–607.

Wilson, E. O. 1984. *Biophilia.* Cambridge, MA: Harvard University Press.

Wilson, J. B., M. T. Sykes, and R. K. Peet. 1995. "Time and Space in the Community Structure of a Species-Rich Grassland." *Journal of Vegetation Science* 6:729–40.

Wiser, S. K., and P. S. White. 1999. "High-Elevation Outcrops and Barrens of the Southern Appalachian Mountains." In R. C. Anderson, J. R. Fralish, and J. M. Baskin, eds., *Savannas, Barrens, and Rock Outcrop Plant Communities of North America.* Cambridge, UK: Cambridge University Press, 119–32.

Witsell, C. T. 2007. "The Vascular Flora of Saline County, Arkansas." MS thesis. University of Arkansas, Little Rock.

Wunderlin, R. P., and B. F. Hansen. 2011. *Guide to the Vascular Plants of Florida*. 3rd ed. Gainesville: University Press of Florida.

Zhang, K., J. Dittmar, M. Ross, and C. Bergh. 2011. "Assessment of Sea Level Rise Impacts on Human Population and Real Property in the Florida Keys." *Climatic Change* 107:129–46.

Zobel, M., M. Otsus, J. Liira, M. Moora, and T. Möls. 2000. "Is Small-Scale Species Richness Limited by Seed Availability or Microsite Availability?" *Ecology* 81:3274–82.

Zollner, D., S. Simon, and T. L. Foti. 2003. "A Plant Community Classification for Arkansas's Blackland Prairie Ecosystem." In E. Peacock and T. Schauwecker, eds., *Blackland Prairies of the Gulf Coastal Plain: Nature, Culture, and Sustainability*. Tuscaloosa: University of Alabama Press, 111–45.

About the Author

REED NOSS is professor of biology at the University of Central Florida and president of the Florida Institute for Conservation Science. He has served as editor-in-chief of *Conservation Biology* and president of the Society for Conservation Biology. He currently conducts research on vulnerability of species and ecosystems to sea-level rise, climate adaptation strategies, road ecology, and changes in ecological processes and species assemblages along urban–rural–wildland gradients.

Index

Page numbers with "f" refer to figures and photos, those with "t" refer to tables.

A

Adaptations: to dolomite substrate, 75; to dry conditions, 55, 139, 150, 153, 262; to fire, 47, 62, 91, 98, 198–202, 200t; to grazing , 39, 99; to saline conditions, 160; to sea-level rise, 43

Adaptive management, 256–57

Agriculture: crops that evolved from wild grasses, 112; early, 62, 63f, 66f, 67; monoculture pasture, 225–26, 252; mowing/haying, 39, 100f, 163, 178, 211; oldfields, 139, 141, 235; soil erosion due to, 128

Alabama: calcareous grassland, 132–34, 135f; endemism, 85; geology, 150, 157; Ketona Glades, 73–76; longleaf pine ecosystem, 179; post-tornado salvage logging, 179; sandstone glade, 147; See also Black Belt Prairie

Alpine tundra, 2f, 155, 215

Altamaha Formation (Grit), 147, 148, 149, 160, 165

Alternative stable states, 2, 11, 194, 196f, 197, 236

Amphibians. See Animals, herpetofauna

Animals: adaptations to fire, 198, 201–2; alligators, 123, 186, 188; ants, 58t, 104, 148, 201, 202, 209, 224, 248; ; aquatic, 76, 85, 151, 235; balsam fir-moose-gray wolf system, 183; birds (See Birds); bison, 39, 67, 161–62, 217, 217f, 218–23, 235; blackland prairie, 123, 125, 126, 129; calcareous grassland, 132, 138, 141, 143, 144; canebrake, 235; charismatic species, 109; coyote, 186–88; ecologically pivotal species, 183, 184–91 (See also Herbivores); effects of sea-level rise on, 43, 189; feral, 27, 187, 188, 224–25; foundation species, 190–91, 192; gopher tortoise, 56t, 70, 79, 105, 148, 187, 190; grasshoppers, 88, 106, 129, 141, 202; grassy bald, 215, 216–17, 217f; herpetofauna (amphibians and reptiles), 27, 55, 57t, 68, 70, 90-91, 104-5, 123, 148, 166, 168, 173, 190, 212; igneous/ metamorphic outcrop, 151; Joshua Creek, 27, 28–29, 189; keystone species, 67, 80, 108–9, 185–91, 212–13, 221; Mills Creek, 69–70; moths, 104, 126, 138, 190, 201, 202; panther (puma) (See Florida panther); pasture, 226; Piedmont prairie, 161–62; pine savanna/woodland/ rockland, 166, 168; saline barren, 161; salt lick and buffalo trace, 218–23; sandstone glade, 148; serpentine barren,