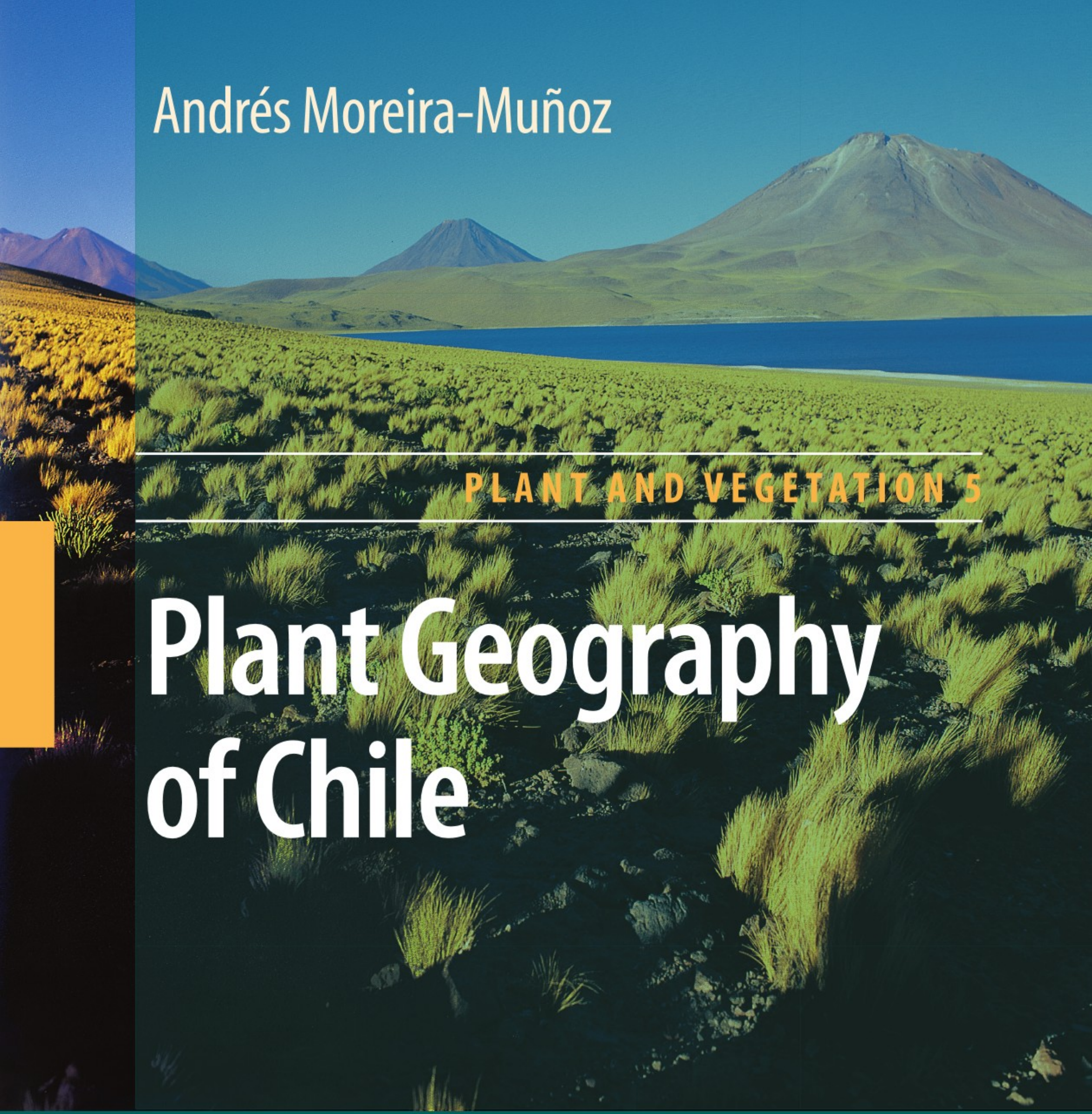

Andrés Moreira-Muñoz

PLANT AND VEGETATION 5

Plant Geography of Chile

Springer

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PLANT AND VEGETATION

Volume 5

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Plant Geography of Chile

by

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Springer

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Cover illustration: High-Andean vegetation at Laguna Miscanti (23°43′S, 67°47′W, 4350 m asl)

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Carlos Reiche (1860–1929)
In Memoriam

Foreword

It is not just the brilliant and dramatic scenery that makes Chile such an attractive part of the world. No, that country has so very much more! And certainly it has a rich and beautiful flora. Chile's plant world is strongly diversified and shows interesting geographical and evolutionary patterns. This is due to several factors: The geographical position of the country on the edge of a continental plate and stretching along an extremely long latitudinal gradient from the tropics to the cold, barren rocks of Cape Horn, opposite Antarctica; the strong differences in altitude from sea level to the icy peaks of the Andes; the inclusion of distant islands in the country's territory; the long geological and evolutionary history of the biota; and the mixture of tropical and temperate floras.

The flora and vegetation of Chile already drew the attention of the early adventurers and explorers and as from the eighteenth century attracted naturalists and collectors from Europe. In the nineteenth century famous botanists explored and studied the Chilean plant world, and gradually the flora and plant geographical patterns became subjects of scientific analyses both by European and Chilean scholars. Recently, the development of new scientific techniques have allowed to reveal the remarkable evolutionary pathways in many Chilean plant groups, and have provided clues to the origins of intriguing plant geographical patterns in the southern hemisphere floras. This shall be of interest for botanists, plant geographers, ecologists and evolutionary biologists worldwide.

I was very lucky to get into contact with Dr. Andrés Moreira-Muñoz. He is an enthusiastic and outstanding Chilean plant scientist with historical roots in this subject area. Dr. Moreira-Muñoz here presents a modern and stimulating account of the Plant Geography of Chile that analyses the floristic diversity and endemism of the country. He interprets the origins of the fascinating plant geographical patterns of Chile and explains the evolutionary background of the most important plant groups. I am very pleased to present this book as a volume in the series "Plant and Vegetation" to the international readership.

Utrecht, The Nederlands
Marinus J.A. Werger

Preface

One morning in 1897 at the Quinta Normal, Santiago: the Director of the Museo Nacional de Historia Natural, Federico Philippi welcomes the new German botanist responsible for taken the reins of the botanical section, Dr Carl Reiche. He has been committed to maintain the National Herbarium, promoting exchanges, analyzing, increasing and organizing the collections of the Herbarium. He will be also, and this is not a trivial thing, responsible for writing the new *Flora de Chile*; and he has already published the first volume. Chilean botanical knowledge showed at the end of the nineteenth century still many gaps, in spite of the great achievements of Claudio Gay and R.A. Philippi, this latter the father and mentor of the Museum's Director. It took Reiche more than 15 years to systematize, revise and add the necessary information that finally encompassed the six volumes of the *Flora de Chile* (Chap. 2). In the meantime, when Reiche was already well familiarized with the Chilean flora, he got a request for writing a synthetic book about the Chilean plant geography for the series *Die Vegetation der Erde,* edited by the great German botanists Adolf Engler and Oscar Drude. Reiche completed the assignment successfully, and 1907 published *Grundzüge der Pflanzenverbreitung in Chile*, encompassing 222 pages with two maps and several photographs (*Vegetationsbilder*). This was the first (and so far the only) *Plant Geography of Chile*. This great effort, which put the Chilean plant world in a renowned world series, only got a Spanish translation 30 years later, thanks to the engagement of G. Looser, himself a botanist and notable scientific communicator (Chap. 2).

Just as Reiche once did with the previous works of Gay and the Philippi, now it seems to be time for a renewal of Reiche's *Plant Geography*. No few things have changed in a hundred years: plants have been renamed and reclassified; taxonomy and systematics have suffered far-reaching changes; biology, geography, and biogeography have undergone paradigmatic vicissitudes. I underwent the challenge of writing a "New Plant Geography of Chile" as a doctoral student in Erlangen, Germany. In such an exponentially dynamic field, one and a half year after the publication of the thesis many things had to be revised and updated for this book.

Regarding the subject, the reader may ask why to use the old concept of "plant geography" rather than "phytogeography" or "geobotany"? As these terms are often used indistinctly, I decided to use the oldest term "plant geography", honouring the seminal works from A. von Humboldt: *Géographie des plantes*, and A.P. de Candolle's *Géographie Botanique* (Chap. 4). The present book also takes inspiration from Stanley Cain's words in his book *Foundations of Plant Geography*: "This is not a descriptive plant geography, but rather an inquiry into the foundations of the science of plant geography" (Cain 1944, p xi) (Chap. 3).

What Is This Book Not About?

This book is not a traditional geobotanical textbook. It rather attempts to enter into the discussion on the challenges that shape (post)modern biogeography in the twenty-first century. A detailed vegetation description, which is sometimes misunderstood as a main task of "plant geography", is very far from the goal of the book. The reader is redirected to recent advances in this specific field (Chap. 1). Many new concepts and methods are currently emerging in biogeography. This book doesn't offer new conceptual or methodological advances; it rather wants to be a "field guide" to the possibilities for the development of the discipline in Chile. Consequently, several conflicting approaches that have been proposed for explaining current biogeographic patterns are confronted throughout the text (e.g. vicariance versus dispersal). The result is mostly not definitive, suggesting that a dichotomy is just a too simple problem design of a much more complex problem.

What Is This Book Then About?

The present book intends to reflect the "state of the art" or a synthesis of the plant geographical discipline in Chile. The challenge is seemingly overwhelming, since in such a composite discipline like biogeography, today any intend to integrate the different views that shape it, must confront the differences inherent to the diverse approaches involved in the discipline. To what extent biogeography assumes and reflects the conflicts, assumptions and challenges inherent to (post)modern science must then be kept in mind while analysing the Chilean plant geography.

This approach leaves us the theoretical basis and practical lines of direction for the endeavour of doing plant geography in the twenty-first century, in the constantly "changing world" of biogeography (sensu Ebach and Tangney 2007) (Chap. 10). Most efforts at the regional level concentrate rather on the descriptive or on the analytical. I would like to do both and also to present the few results in a more general interpretative framework. I would like to accept the challenge posted by Morrone (2009) (Chap. 10), touching methodological as well as more theoretical aspects that will help the student build an own "road map" towards a future development of the discipline in Chile, integrating methods, data, concepts, and interpretations from different fields.

Applying one of the basic principles of geography, for a better comprehension of the subject I have often put the eye beyond the Pacific and beyond the Andes, touching aspects of the New Zealand biota, the Antarctic palaeobiomes, Argentinian Patagonia... I apologize if I have mentioned these aspects in a superficial form.

Nevertheless, I suspect that several aspects of the book are applicable or of interest for biogeographers in the other (once united) southern hemisphere territories; if so, I will be deeply satisfied.

Structure of the Book

The book is divided in five parts that organize the different chapters.

The 1st part presents an overview of the geographical and botanical scenarios that shape the Chilean vascular plant world, in the present as well as in the geologic past. In chapter one, the main physical characteristics of the Chilean territory are briefly exposed, especially the geological and tectonic origins of Chile and their effects on the palaeogeography and the evolution of the Southern Cone biomes. This contributes to a better understanding of the current climate and vegetation. The 2nd chapter makes a succinct revision of the historical development of Chilean botany, and synthesizes the current knowledge regarding the composition of the flora.

The 2nd part deals with Chilean plant geographical relationships, oriented to a synthesis of the floristic elements of the extant flora. The classification of Chilean genera into floristic elements in Chap. 3, will be the basis for the discussion of the disjunct patterns that shape the Chilean flora. This analysis will be further complemented with the task undertaken in the 4th chapter, regarding the biogeographical regionalization of the Chilean territory.

The 3rd part provides an analysis of two close related subdisciplines: island biogeography and conservation biogeography. Chapter 5 presents a synthesis of the plant world of the Chilean Pacific offshore islands, emphasizing their uniqueness and threats, while the 6th chapter analyses the fragmentation in the mainland, related to the impacts of human activities on the Chilean ecosystems. Concepts and tools developed within the field of conservation biogeography are analyzed in relation to current global changes.

The 4th part moves into the case studies, regarding specific groups that deserve special attention in biogeography. Chapter 7 gets into the biogeography of one of the most charismatic American families, the Cactaceae, of course regarding its Chilean representatives. Chapter 8 turns to another not less interesting family, the Asteraceae, the most genus/species-rich family in Chile. The last case study is presented in Chap. 9, devoted to a monogeneric family also called the "key genus in plant geography": *Nothofagus*.

The 5th and last part of the book announces several ways in which Chilean plant geography can further develop; maybe more rapidly and effectively than during the last 100 years? Chapter 10 is in this sense rather speculative, in an attempt to put Chilean plant geography in a more general context of modern biogeography. Finally, the 11th chapter only adds several digressions about the scientific endeavour and the artificial distinction between nature and culture.

Santiago, Chile Andrés Moreira-Muñoz

Acknowledgments

The book was initially developed as a doctoral study at the Geographical Institute of Erlangen-Nürnberg University, Germany. Support in form of a grant was fortunately provided by the German Academic Exchange Service (DAAD). I am much indebted to Prof. Dr. Michael Richter, who was from the first moment the main supporter of the idea. He and his family, together with all the colleagues and workers at the Geographical Institute in Erlangen made our family's stay in Germany a great life experience. From the Geography to the Botanical Garden in Erlangen there are just several blocks, and the support and friendship we found there in the person of Dr. Walter Welss and his family was also a foothold in our stay. Prof. Dr.Werner Nezadal (Erlangen) and Prof. Dr. Tod Stuessy (Vienna) gently assumed the revision of the thesis.

The thesis was improved by the attendance of several conferences thanks to grants from the Zantner-Busch Stiftung (Erlangen). At the conference "Palaeogeography and Palaeobiogeography: Biodiversity in Space and Time", NIEeS, Cambridge, UK, 10th–11th April, I attended the workshop for using the program TimeTrek for plate tectonic reconstructions. I also could attend the XVII International Botanical Congress in Vienna, 17th–23rd July 2005.

The idea of transforming the thesis into a book found absolute support in the person of Prof. Dr. Marinus Werger. He acted not just as a language editor but as a very patient reviewer guiding the editing process in all its stages. The early intention was also promoted by Dr. Leslie R. Landrum and Dr. Juan J. Morrone.

Crucial for the positive development of the book has been Springer's production and editing team: first Inga Wilde and Ria Kanters, and lately Ineke Ravesloot and Annet Shankary. Several colleagues and friends graciously read and commented on draft chapters: Federico Luebert (Berlin), Hermann Manríquez (Santiago), Patrick Griffith (Florida), Malte Ebach (Arizona), Michael Heads (Wellington), Michael Dillon (Tal Tal), Carlos Lehnebach (Wellington), and Patricio Pliscoff (Lausanne). Of course the errors and misconceptions that may still exist are exclusively my responsibility.

In Chile, the project found early support in Dr. Belisario Andrade (Pontificia Universidad Católica de Chile) and Dr. Roberto Rodríguez (Universidad de Concepción). Once back in Chile, I can only express gratitude to the colleagues

at the Pontificia Universidad Católica de Chile, which facilitated my incorporation as an assistant professor by means of a grant for young doctors. I am especially indebted to the Director of the Institute of Geography, Dr. Federico Arenas and the dean of the Faculty, Dr. José Ignacio González.

Field work in Chile during 2008–2010, especially for research on Asteraceae (Chap. 8), was supported by project Fondecyt Iniciación (2008) n° 11085016. Speaking about field work, long ago I learned from Calvin and Linda Heusser the "dirty side" of scientific field work. I will be always indebted to my old friends.

Vanezza Morales was a crucial helper in the final editing of most maps, and with computer programs like NDM/VNDM. I gratefully mention also the important advice provided by Tania Escalante (UNAM) and Claudia Szumik (U. de Tucumán). Giancarlo Scalera (Roma), and Carlos Le Quesne (Valdivia) kindly provided articles and figures. Sergio Elórtegui generously acceded to draw several original illustrations for this work and also contributed many photographs. Carlos Jaña helped finishing the most complicated figures. Sergio Moreira, Walter Welss, Hendrik Wagenseil, Jeff Marso, María Castro, Francisco Casado, and Carlo Sabaini kindly provided photos for illustrating this book.

Last but not least, I must acknowledge the life-long support of Mélica Muñoz-Schick and Sergio Moreira, who could transfer to me their passion for nature and beauty. Mélica, as ever, helped with the identification of species. Sergio also helped providing scanned images of botanical specimens, thanks to a grant to the National Herbarium provided by the Andrew W. Mellon Foundation trough the Latin American Plants Initiative (LAPI).

When the doctoral thesis was still a draft project, my way crossed the one of Paola, who soon turned to become my life companion. I would not have reached this goal without her continuous support. I could also not imagine that the relationship would be so fruitful: Sayén, Silene, Coyán, and Relmu remind me every evening that there are other important things in life than just writing books. . . there is also the possibility to read them!. . . especially when they deal not just with flowers but also with rabbits, bears, elves and fairies.

1 May 2010 Limache

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Abbreviations

AAO	Antarctic Oscillation
ACC	Antarctic circumpolar current
cfr.	Refer to
Chap.	Chapter
CONAF	Corporación Nacional Forestal
CONC	Herbario de la Universidad de Concepción
ENSO	El Niño Southern Oscillation
Fig.	Figure
GIS	Geographic information systems
ITCZ	Intertropical Convergence Zone
IUCN	International Union for Conservation of Nature
K/T boundary	Cretaceous/Cenozoic boundary
LDD	Long-distance dispersal
LGM	Last Glacial Maximum
m asl	Metres above sea level
mya	Million years ago
PAE	Parsimony Analysis of Endemicity
PDO	Pacific Decadal Oscillation
SEBA	Systematic and Evolutionary Biogeographical Association
Sect.	Section
SGO	National Herbarium Santiago, Chile
SNASPE	National public protected areas system
yr BP	Years before present

About the Author

Andrés Moreira-Muñoz was born in Los Angeles (Chile), studied at the German School in Santiago and graduated as Professional Geographer at the Pontificia Universidad Católica de Chile. Botanical interest was inherited from his grandfather and mother, both renowned botanists at the Museo Nacional de Historia Natural in Santiago. He obtained his doctoral degree in Geography from the University Erlangen-Nürnberg, Germany, under the direction of the plant geographer Prof. Michael Richter.

He currently occupies a position as assistant professor at the Instituto de Geografía, Pontificia Universidad Católica de Chile, and develops research projects about the chorology of Chilean plants, conservation biogeography and field-based education.

He is a member of several national and international associations like the Systematics and Evolutionary Biogeographical Association (SEBA), the Society for Conservation GIS (SCGIS), the IUCN Species Survival Commission, the Sociedad de Botánica de Chile, and Corporación de Investigación y Divulgación Científica Taller La Era (www.tallerlaera.cl).

Part I
Geobotanical Scenario

Chapter 1
The Extravagant Physical Geography of Chile

Abstract Current Chilean vascular flora and its biogeographical patterns are strongly related to the geographical features of the territory, past and present. Main characteristics of the physical geography of Chile are described, with emphasis on the geologic and climatic changes that affected the biome configuration since the Devonian onwards. Approaching the present time, the effects of the Pleistocene glaciations in the distribution of several communities are discussed.

Chile has been characterized as "a geographic extravaganza" (Subercaseaux 1940) due to its impressive geographical contrasts: it contains the driest desert on the planet, formidable inland ice fields, active volcanoes, fjords, geysers, a vast coastline and the major highs of the Andes.

The country stretches for 4,337 km along the south-western margin of South America from the Altiplano highs at 17°35′S to Tierra del Fuego, the Islas Diego Ramírez and Cape Horn at 56°S (Figs. 1.1 and 1.2). Chile's boundary to the west is the wide Pacific Ocean. The national territory includes several groups of Pacific oceanic islands, principally Rapa Nui (Easter Island), the Juan Fernández archipelago, and the Desventuradas Islands (Fig. 1.1) (Chap. 5). Besides this the nation has a geopolitical claim on a portion of 1,250,000 km^2 in Antarctica. Though geopolitical interests are beyond the scope of this book, and despite the modest presence of extant vascular plants in Antarctica (only *Deschampsia antartica* and *Colobanthus quitensis*), the Continent of Ice is of high interest regarding the origin of the Chilean plant world (Sect. 1.2, Box 9.1).

A. Moreira-Muñoz, *Plant Geography of Chile*, Plant and Vegetation 5,
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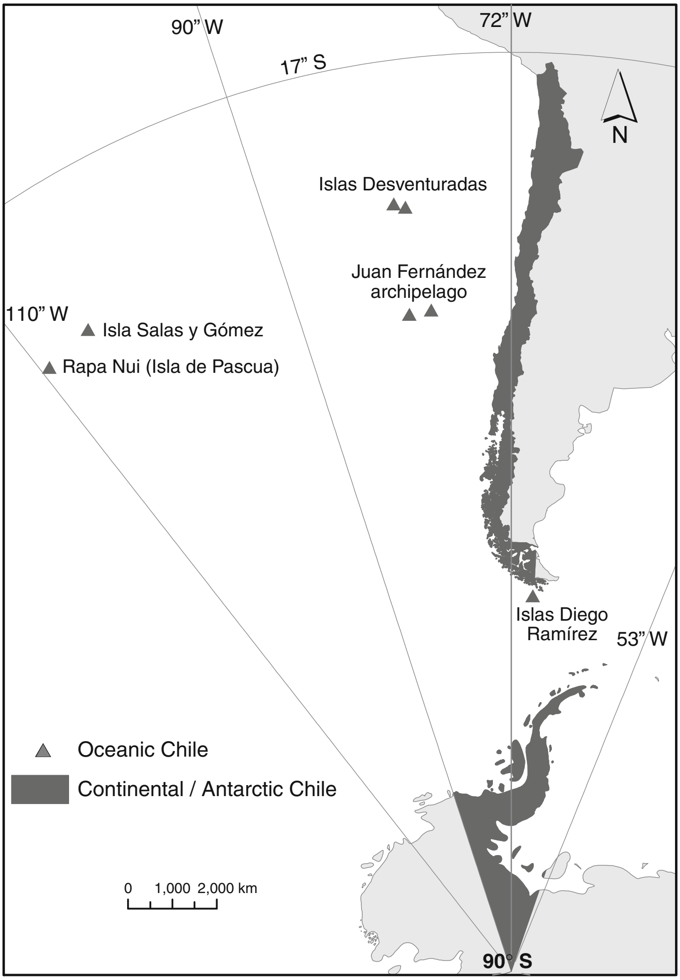

Fig. 1.1 Chile including the American continental portion, the Pacific islands, and Antarctic Peninsula. Polar stereographic projection with true scale at 71°S using ArcGIS 9. Base global map provided by ESRI Labs

The eastern margin of mainland Chile is the Andes cordillera, which reaches to a maximum of 6,962 m asl in the Monte Aconcagua at 32°39′S (Fig. 1.6). As its summit is located on the Argentinean side, the highest peak of the Chilean Andes is the Ojos del Salado volcano at 27°06′S, reaching 6,893 m asl. Contrary to the long latitudinal extent, in width Chile rarely extends more than 200 km, reaching a maximum of 360 km at Mejillones (23°S) and a minimum of 90 km at Illapel (31°37′S). The difference in altitude from the coast to the high Andes creates a series of bioclimatic variations in the altitudinal profile (Fig. 1.6). These variations, coupled with the climatic latitudinal gradient, create a variety of geographic conditions that dramatically

Fig. 1.2 Physical geography of Chile: **a** Valle de la Luna, Atacama desert, 23°S; **b** Cerro Las Vizcachas, Cordillera de la Costa, 33°S; **c** rocky coast at Concón, Valparaíso (32°50′S); **d** Laguna del Inca, Portillo, Andean pass to Argentina (32°50′S); **e** Glaciar Los Perros, Torres del Paine, Campos de Hielo Sur (51°S); **f** southern fjords and Cordillera de Darwin (55°S) (photo credits: **a**, **b**, **d**–**f** A. Moreira-Muñoz; **c** S. Elórtegui Francioli)

affect the Chilean vegetation from the arid North to the humid temperate rainforests in the South (Sect. 1.3).

1.1 Tectonics and Physiography

The main character of Chilean landscapes is driven by tectonic forcing: the geological evolution of Chile is related to the east-directed subduction of the Nazca Plate beneath the South American Plate (Pankhurst and Hervé 2007) (Fig. 1.3). The Chile Rise is an active spreading centre that marks the boundary between the Nazca Plate and the Antarctic Plate at the so called Chile Triple Junction (Fig. 1.3). The Nazca Plate is being subducted at a rate of ~65 mm/year (to the North of the Triple Junction), while the Antarctic Plate is being subducted at a slower rate of ~18 mm/year (Barrientos 2007). According to Ranero et al. (2006), the amount of sediments to the trench is variable in space and time: north of 28°S, due to aridity, there is a relatively small amount of erosion and sediment supplied to the trench; in the mid-latitude, the well developed river drainage system supplies much material to the trench; south of ~ 40°S glacial-interglacial periods might have controlled the amount of sediment supplied to the trench (Ranero et al. 2006).

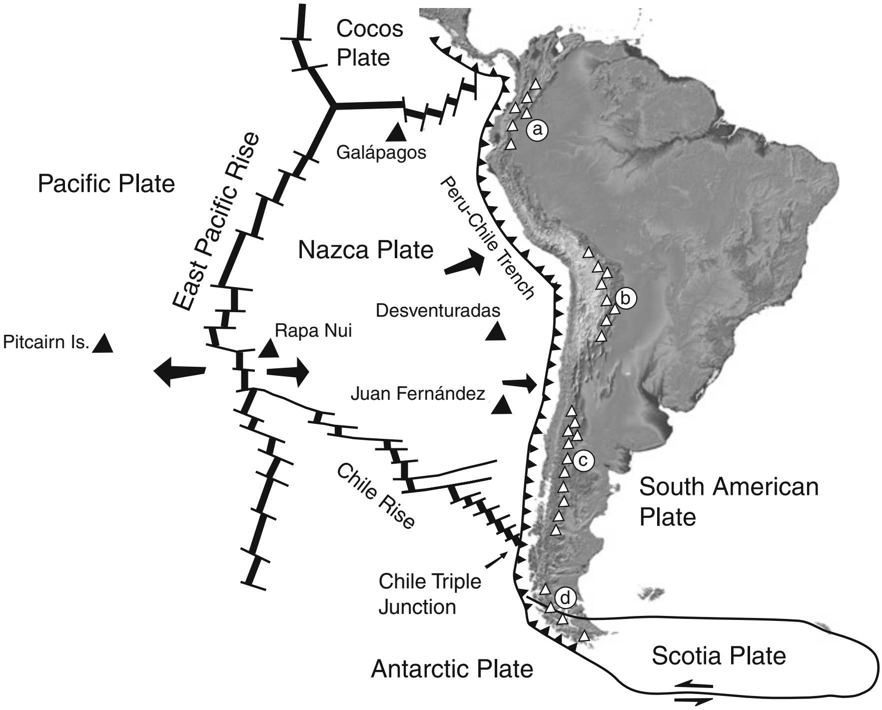

Fig. 1.3 Tectonic main features and volcanic zones of South America: **a** northern volcanic zone; **b** central volcanic zone; **c** southern volcanic zone; **d** austral volcanic zone (adapted from Orme (2007), by permission of Oxford University Press; see also Stern et al. (2007))

A prominent feature of the Nazca Plate is the Juan Ferrnández hot spot chain, a series of disconnected seamounts that disappear into the trench at 33°S (Ranero et al. 2006) (Fig. 1.3). Subduction is accompanied by intense magmatic and seismic activity (Orme 2007). Great earthquakes occur somewhere along the western South American margin every few years, and "no recorded human generation in Chile has escaped the damaging consequences of large earthquakes" (Barrientos 2007, p 263). Indeed, while writing these lines, on the 27th of February 2010, an earthquake with a magnitude of 8.8 followed by a tsunami affected Central-south Chile, resulting in hundreds of deaths and thousands homeless.

Together with earthquakes, the active volcanism along the length of the country is also a good reminder of the active tectonic processes acting below the surface (Box 1.1).

Box 1.1 Living Under the Volcano

Chilean active and inactive volcanoes comprise ca.10% of the circum-Pacific "ring of fire" (Pankhurst and Hervé 2007). These are mostly andesitic stratovolcanoes that occupy almost the entire length of the country, especially at the "South Volcanic Zone", that encompass most of the South American active volcanoes (Stern et al. 2007) (Fig. 1.3). More than 150 potentially active volcanoes have been detected, and 62 of them erupted in historical times (González-Ferrán 1994). One of the most recent is the eruption of Volcán Chaitén (43°S) on May 2008, which was responsible for the obligate abandonment of the homonymous town. The ash column reached a height of 15 km and spread wide upon the Atlantic (Figs. 1.4 and 1.5). Apart from its consequences and risks for human occupation, volcanism has been a constant source of disturbance in the Chilean ecosystems, especially in the southern temperate forests (Milleron et al. 2008).

1.1.1 Morphostructural Macrozones

Taking account of its tectonic and morphostructural features, Chile can be classified in a broad sense in five macrozones (Fig. 1.6) (Charrier et al. 2007; Stern et al. 2007):

(a) The Coastal Cordillera occupies the western part of the profile from 18°S to Chiloé Island (~ 42°S). It comprises the coastal batholith that consists predominately of Late Palaeozoic and Mesozoic igneous rocks, with paired belts of Palaeozoic metamorphic rocks cropping out south of Pichilemu (34°23′S) (Pankhurst and Hervé 2007). Very impressive is the high riffs ("acantilado") that stretches from 0 to 800 m asl at Iquique (20°S).

(b) The Central Depression is a tectonic downwarp with a Mesozoic to Quaternary sedimentary fill of volcanic, glacial and fluvial origin. This main agricultural

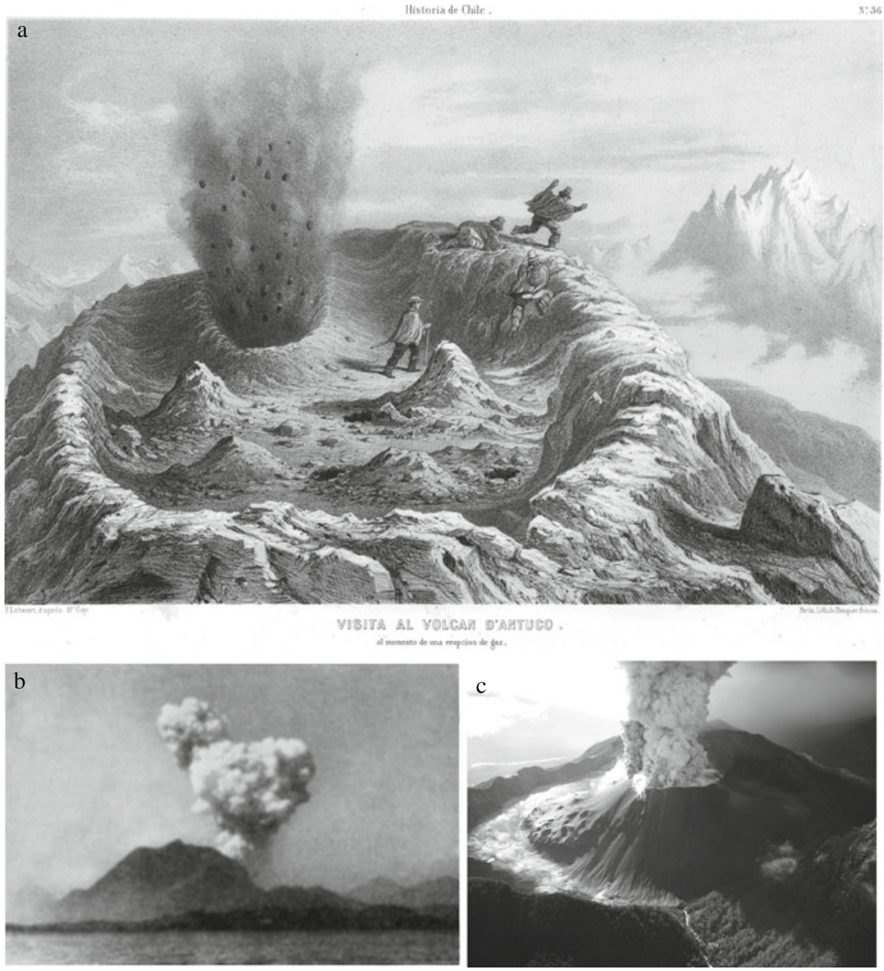

Fig. 1.4 Examples of volcanic activity in historical times: **a** ash expulsion by Volcán Antuco on the 1st March 1839, as represented in Claudio Gay's Atlas (Chap. 2); **b** eruption of Volcán Carrán in 1955 (from Illies 1959); **c** Volcán Chaitén eruption photographed on May 26, 2008 (photo by J.N. Marso, courtesy of the USGS)

and urbanized region ranges from 18°S to Copiapó (27°S), and again from Santiago (33°S) to Chiloé (42°S). It is absent between 27° and 33°S, in the so called zone of transverse river valleys or "Norte Chico" (Weischet 1970; Charrier et al. 2007). This zone corresponds also to the "flat slab" zone, a zone free of recent volcanic activity, associated to the subduction of the Juan Fernández Ridge (Fig. 1.3).

(c) The main Andean Cordillera is a chain of mountains that dates back to the Miocene, whose emergence continues today (see Box 1.5). It can be subdivided in three segments: Forearc Precordillera and Western Cordillera, between 18° and 27°S; High Andean Range, between 27° and 33°S (flat-slab subduction

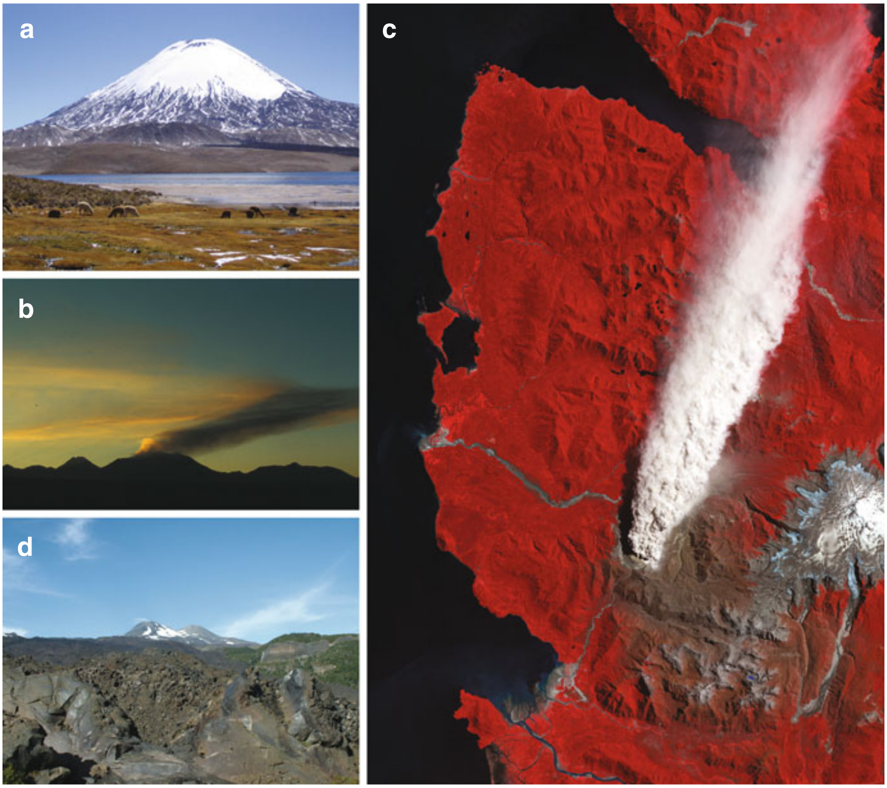

Fig. 1.5 Chilean volcanoes: **a** Parinacota volcano, 18°10′S; **b** steam expulsion of Volcán Lascar (23°20′S), on December 1996; **c** Volcán Chaitén (42°50′S), false colour Aster satellite image: plume of ash and steam advancing ca. 70 km to the north-east on January 2009; **d** lava fields around Nevados de Chillán (36°50′S) (photo credits: **a** H. Wagenseil; **b**, **d** A. Moreira-Muñoz; **c** NASA Earth Observatory (www.earthobservatory.nasa.gov))

segment); and Principal Cordillera, between 33° and ca. 42°S (Charrier et al. 2007).

(d) Patagonian Cordillera: the Andes' continuation right down into Tierra del Fuego at the southern tip of Chile, with a continuous reduction in height (Pankhurst and Hervé 2007). The origin of this low portion of the Andes has been related to an allochtonous Palaeozoic terrane (see Box 1.2). The west-southern margin of the land (42° to the South) is modeled by recent glaciations that carved the coastal areas into fjords and archipelagos comprising thousands of little islands (Pankhurst and Hervé 2007). It has been calculated that the coastal extension of Chile including these islands and southern archipelagos reaches 83,850 km! (IGM 2005).

(e) The Andean foreland of the southern Patagonian Cordillera or Magallanes basin consists of Upper Jurassic to Early Cenozoic sedimentary deposits (Charrier et al. 2007; Fosdick 2007).

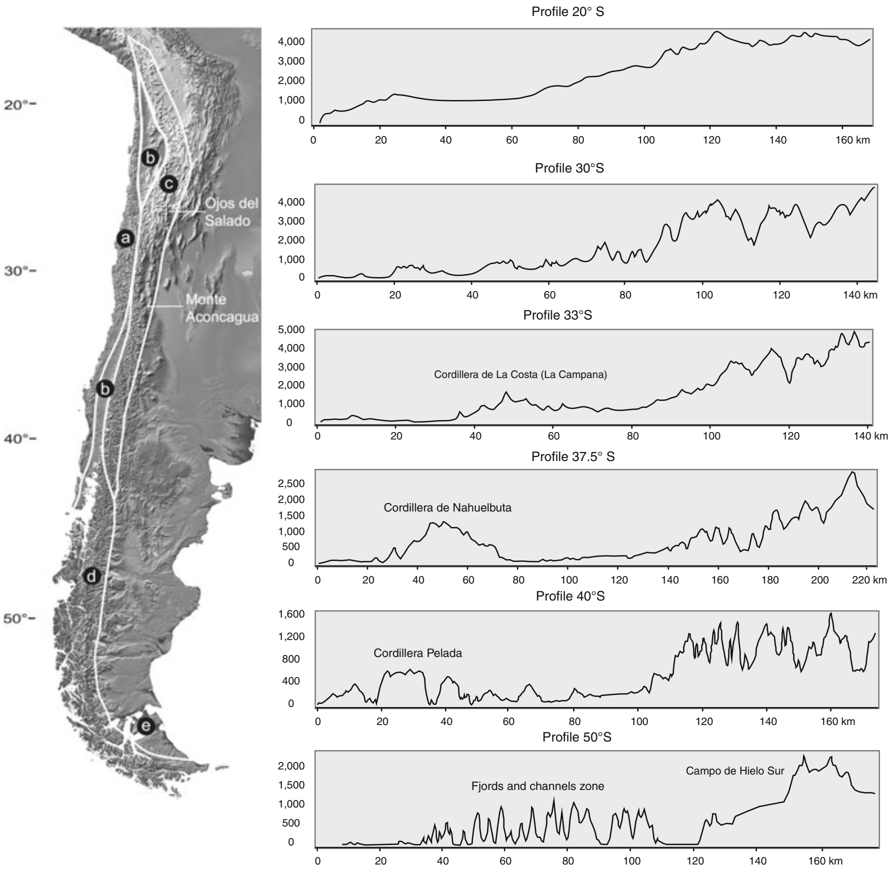

Fig. 1.6 Physiography of continental Chile, on the base of SRTM (Shuttle Radar Topography Mission) data (http://www2.jpl.nasa.gov/srtm/), five morphostructural zones (see text for explanation; for national political borders see Fig. 1.1). Altitudinal profiles have been produced with ArcGIS 9 based on Aster GDM data (http://asterweb.jpl.nasa.gov/gdem.asp). Note variations in the vertical scale, not homogeneous

Box 1.2 Patagonian Vicissitudes

The remarkable landscape and flora of Patagonia motivated early naturalists like the Perito Francisco P. Moreno to propose an independent origin of this microcontinent from the rest of South America (Moreno 1882, as quoted by Ramos 2008). The characteristic landscape and rocks led Moreno to remark strong affinities to other southern landmasses like Antarctica, Australia, and New Zealand, suggesting that Patagonia was the rest of a sunken continent.

This view was retained even during the time of continental drift discussion (e.g. Windhausen 1931). Current geologic and palaeomagnetic data suggests that indeed, Patagonia has seen successive periods of breaking and drifting during the whole Palaeozoic (Rapalini 2005; Ramos 2008). The TimeTrek model (see also Pankhurst et al. 2006) shows an amalgamation of Patagonia to Antarctic Peninsula during Late Carboniferous (300 mya), and a gradual separation from Antarctica into the Cretaceous (120 mya) (Fig. 1.7). Biotic exchange between South America and Antarctic Peninsula may have been favoured (and then prevented) more than just one time, following rather exchange cycles (Fig. 1.7).

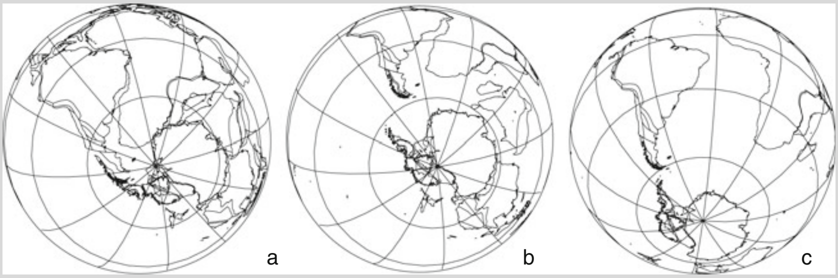

Fig. 1.7 Positions of Patagonia: **a** in the Late Carboniferous (300 mya) aggregated to the Antarctic Peninsula; **b** in the Early Cretaceous (120 mya), separated from Antarctica; **c** in the Eocene (50 mya), again close to the Antarctic Peninsula. Modeled with TimeTrek v 4.2.5, Cambridge Paleomap Services

1.2 Past Climate and Vegetation

Tectonic and geomorphologic processes, coupled with the oceanic-atmospheric system, have had enormous effects on the botanical evolution and its physiognomical expression (i.e. the vegetation). The main aspects of the palaeogeographical evolution of the territory will be resumed hereafter.

Palaeobotanical studies of Chile date back to Engelhardt (1891), Ochsenius (1891), Dusén (1907), Berry (1922a, b), Fuenzalida (1938, 1966) among others. More recent advances are centered in the Cenozoic (e.g. Cecioni 1968; Nishida 1984; Troncoso and Romero 1998; Hinojosa 2005). Constant improvement of the methods applied to the study of "climatically sensitive" sediments (e.g. coals, salt deposits, evaporites), together with studies in diversity patterns in global vegetation through time, are benefiting our understanding of the evolution of plant biomes in space and time (Willis and McElwain 2002).

The floristic and vegetational history of southern South America is strong related to the tectonic and climatic history of the *Gondwana* continent (McLoughlin 2001)

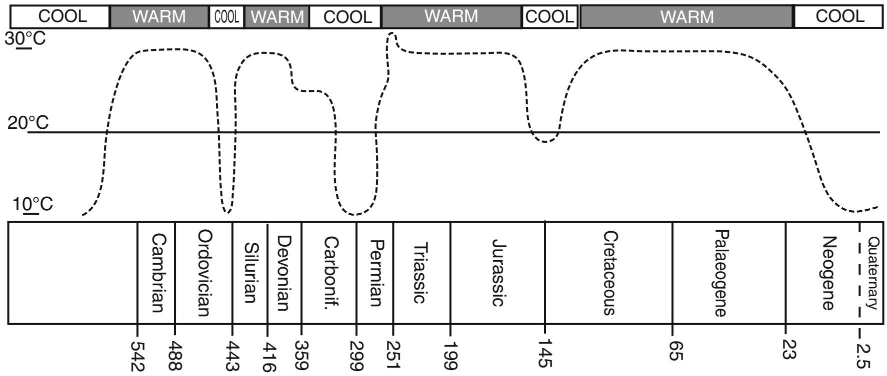

Fig. 1.8 Global climate change since the Cambrian onwards. Adapted from Frakes et al. (1992) and Scotese et al. (1999). Dates have been updated with the 2004 Geologic Time Scale (Gradstein et al. 2004)

(Box 1.3, Table 1.1). "During the 500 million years that Gondwana and its fragments existed, the Earth's global climate system has shifted from 'Ice House' conditions to 'Hot House' conditions four times" (Scotese et al. 1999) (Fig. 1.8). These global climatic fluctuations have constantly affected the biotic evolution and biogeography: floristic regions can be tracked back even to the mid-late Silurian, the time when according to most palaeobotanical evidence, the vascular plants have conquered the land surface (Willis and McElwain 2002; Raymond et al. 2006) (Box 2.3).

1.2.1 The Palaeozoic (542–251 mya)

Several orogenic events affected the western margin of Gondwana from the Late Proterozoic to the Palaeozoic (Ramos and Aleman 2000; Pankhurst et al. 2006). The Famatinian orogeny in the Ordovician (~490–450 mya) is characterized by the amalgamation of several allochtonous terranes, like Cuyania and Chilenia, implying that North America had collided with West Gondwana by that time (Astini et al. 1995). Mejillonia and Patagonia terranes amalgamated in the Early Permian, as the last convergence episodes (Ramos 2009) (Box 1.2). The development of preAndean foreland basins during the Palaeozoic, set the stage for the initiation of the Andes long before the event that culminated in massive Cenozoic uplift (Orme 2007). During the Late Palaeozoic, Gondwana became amalgamated to the supercontinent of Laurussia to form the vast single landmass called Pangaea.

From the Early **Devonian** to the Late Carboniferous (400–300 mya), global vegetation evolved from one dominated by small, weedy plants, only several decimetres in height, to fully forested ecosystems with trees reaching sizes of 35 m (Willis and McElwain 2002). During the Middle to Late Devonian (390–360 mya) warm, humid climates with high levels of atmospheric CO_2 prevailed worldwide, favouring the appearance of earliest arborescent forms of plants (see Box 2.3).

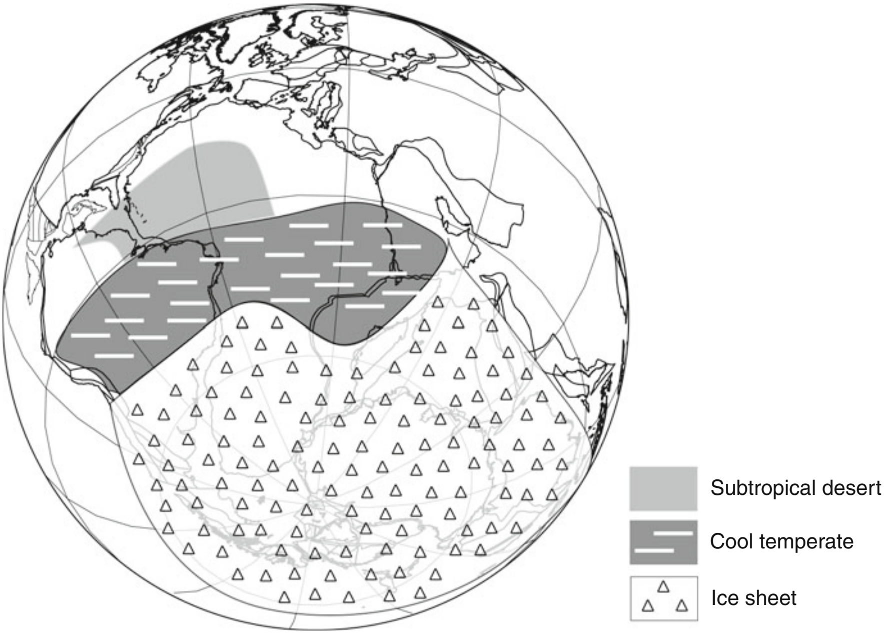

Fig. 1.9 Late Carboniferous biomes (adapted from Willis and McElwain (2002) on a TimeTrek 4.2.5 model, Cambridge Paleomap Services)

By the Late **Carboniferous** (330–299 mya) the southern flora consisted mainly of likely pteridosperms, lycopsids, Cordaites and Ginkgophytes (Vega and Archangelsky 1997). Diversity was rather low, and the southern flora was uniformly developed across Gondwana between 30°S and 60°S (Anderson et al. 1999; DiMichele et al. 2001). However, Cúneo (1989) suggests that floristic differentiation was also apparent on the west coast of South America. The presence of *Lepidodendron* and *Sigillaria* (lycopod trees) has been reported from the Carboniferous deposits of Chile (Charrier 1988). Late Carbonifeous ended in a widespread glaciation, one of the most severe in Earth's history. The Permo-Carboniferous glaciation (310–290 mya) lasted for around 30 million years (Beerling 2002); Gondwanan continents were locked in deep glaciation (Fig. 1.9).

The **Permian** (299–251 mya) was characterized by major global climate changes, from glaciated (icehouse) to completely ice-free (hothouse) stages (Fig. 1.8). "With the onset of glaciation in the Permian, the flora changed dramatically with the appearance of *Glossopteris* and the disappearance of most of the Late Carboniferous elements" (DiMichele et al. 2001, p 467). By the Middle Permian, one of the most striking vegetation changes was the relatively increased proportion of seed plants together with a reduction of the swamp-dwelling lycopsids and sphenopsids (Wnuk 1996, McAllister Rees et al. 2002). *Glossopteris,* a gymnosperm genus with many species, turned to be the characteristic plant of Gondwana (DiMichele et al. 2001). Indeed, *Glossopteris* dominant presence across Gondwana

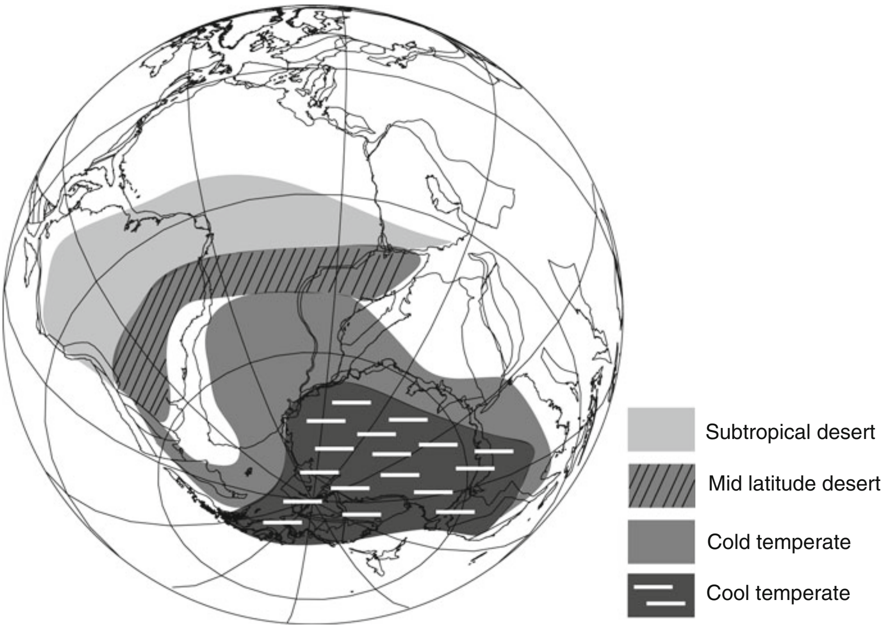

Fig. 1.10 Middle Permian biomes (adapted from Willis and McElwain (2002) on a TimeTrek 4.2.5 model, Cambridge Paleomap Services)

is one of the keys that supported the continental drift theory of Alfred Wegener. *Botrychiopsis*, another typical species from west Gondwana, went extinct when the environmental conditions typical of a greenhouse stage were created by the end of the Permian (Jasper et al. 2003).

The Permian flora of Gondwana was significantly more diversified than the one of the Late Carboniferous (Cúneo 1989), and the floristic provinciality changed during the course of the Permian. The belt located between 60° and 45°S in western Gondwana was called the "Southern temperate semiarid belt of middle latitudes", characterized by *Glossopteris* and moderately thermophilic vegetation with abundant tree-ferns and lycopods (McLoughlin 2001; Chumakov and Zharkov 2003) (Fig. 1.10).

1.2.2 The Mesozoic (251–65.5 mya)

The transition from the Palaeozoic to the Mesozoic is characterized by a dramatic event: the Permian-Triassic extinction event, which apparently saw the destruction of 90% of marine life on Earth due to extensive volcanism, under other causes (Benton and Twitchett 2003). The impacts on the terrestrial ecosystem were not so drastic, or paradoxically even favorable for some plants (Looy et al. 2001).

The **Triassic** (251–199.6 mya) climate was relatively warm compared to today, and continentality and aridity were more extended due to the permanence of the single continent Pangaea. The Triassic flora remained broadly similar to that of the Permian, dominated by gymnosperms (seed ferns, cycads, and ginkgos). During the Triassic, *Glossopteris*-dominated communities were replaced by *Dicroidium* (a seed fern) dominated floras across the Southern Hemisphere (McLoughlin 2001). Also, the major radiation of conifers, e.g. the Araucariaceae began in the Triassic (see Sect. 2.2). Other important components of the southern flora were ginkgophytes, putative gnetales, bennettitales, and cycadales, plus many lycophytes and osmundacean, gleicheniacean, dicksoniacean, dipteridacean and marattiacean ferns (McLoughlin 2001, p 286; Artabe et al. 2003) (see Sect. 2.2).

The **Jurassic** (199.6–145.5 mya), better known for the diversification of charismatic faunal groups like the dinosaurs, is also considered one of the most important periods in plant evolution. By the Early Jurassic, both composition and distribution of southern hemisphere vegetation had changed dramatically. *Glossopteris* and *Dicroidium* no longer dominated the southern flora. Instead they were replaced by cycads, bennettites, ginkgos, and conifers, and for the first time global floras contained a significant portion of forms that are recognizable in our present floras. The floral assemblage for Cerro La Brea, Mendoza, Argentina (Early Jurassic) shows the presence of 14 taxa belonging to the Equisetaceae, Asterothecaceae, Marattiaceae, Osmundaceae, Dipteridaceae, and several conifers (Artabe et al. 2005).

While Gondwana drafted towards the equator, five distinct biomes settled during the Early Jurassic (McAllister Rees et al. 2000) (Fig. 1.11). Southern South America must have been occupied by a "winterwet biome" with a climate similar

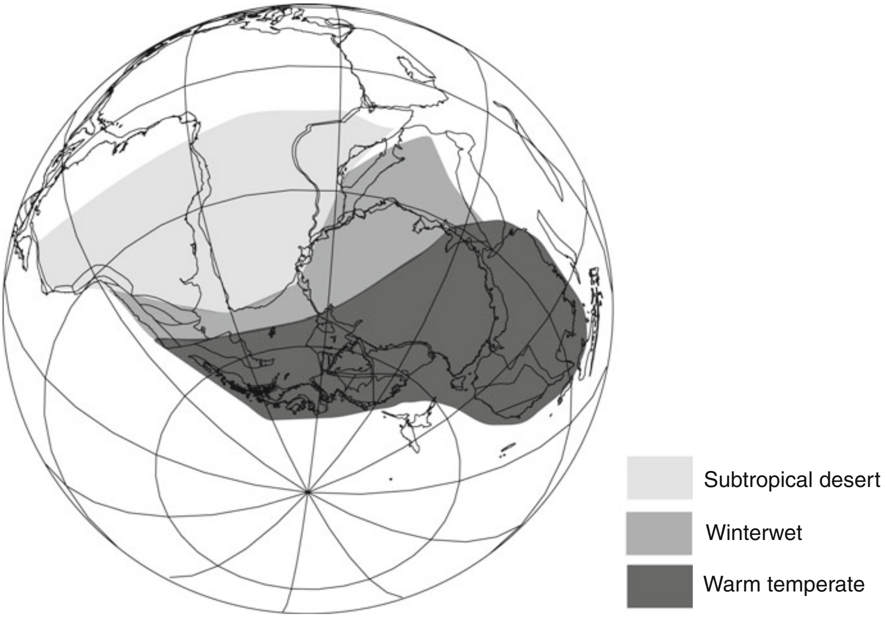

Fig. 1.11 Early Jurassic biomes (adapted from Willis and McElwain (2002) on a TimeTrek 4.2.5 model, Cambridge Paleomap Services)

to that of today's Mediterranean-type one. The relatively increased proportion of plants with small leaves and other xerophytic features clearly indicates seasonal water deficits (Willis and McElwain 2002). In the Middle Jurassic, main components of this biome, like Cycadales, Bennettitales, conifers, ferns, and Sphenopsids, reached northernmost Chile, i.e. current arid Atacama (Fuenzalida 1966; Herbst and Troncoso 1996).

Quattrocchio et al. (2007) listed more than a hundred species from the Jurassic of the Neuquén basin, Argentina. Clearly dominant groups were the Cheirolepidiaceae, Araucariaceae and Podocarpaceae, together with Cyatheaceae, Osmundaceae, Marattiaceae, Dipteridaceae, Lycopodiaceae, Schizaeaceae, Anthocerotaceae, Ricciaceae, Cycadales/Bennettitales, Caytoniaceae and Gnetales. The authors further propose an environmental model in which the Araucariaceae and Podocarpaceae occupied mostly high-altitude places, while ferns, cycads and Cheirolepidiaceae may have been restricted to more low-lying and humid places (Fig. 1.12). Let us keep in mind that there was still not such thing like an elevated Andes (Box 1.5)

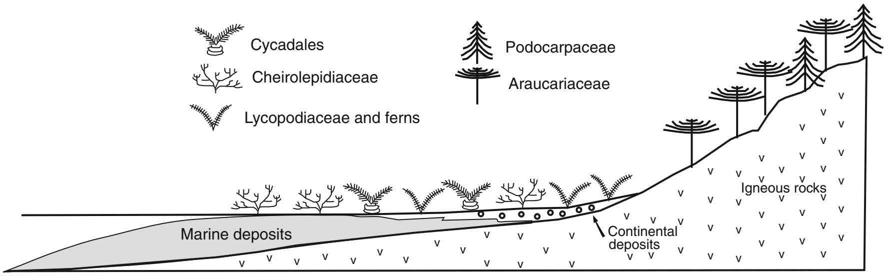

Fig. 1.12 Palaeoenvironmental reconstruction of middle Jurassic flora from southern South America (adapted from Quattrocchio et al. 2007, with permission of the authors)

Box 1.3 Gondwana Breaks-Up

Most authors recognize three major separation events of Gondwana that affected the evolution of the South American flora: the separation between W and E Gondwana during the Jurassic (180–150 mya); the separation America/Africa between 119 and 105 mya, and the split between Antarctica and southern South America (32–28 mya) (Table 1.1). These ages serve as reference; but there is no real consensus on the time of fragmentation of the different components. The crucial separation of Australia from Antarctica and South America from Antarctica and the development of the Drake Passage is still a controversial issue: "South America may have separated from Antarctica as early as the Late Jurassic, or as late as the Palaeocene or Eocene" (Orme 2007, p 10) (see Box 9.1). The TimeTrek model shows indeed an early separation of South America and Antarctica at around 120 mya (Early Cretaceous) (Fig. 1.7).

Table 1.1 Three stages in the break-up of Gondwana (as resumed by McLoughlin 2001)

Major separation events	Period and causes	Palaeoreconstructions on a TimeTrek v. 4.5.2 model
(W Gondwana / E Gondwana)	During Middle to Late Jurassic (180–150 mya): breakup associated with development of a series of deep seated mantle plumes beneath the extensive Gondwanan continental crust in S Africa (c 182 mya) and the Transantarctic mountains (c 176 mya) (Storey 1995)	
Africa–S America separation	Early Cretaceous (119–105 mya): opening of the South Atlantic Ocean, due to the emplacement of Plume-related Parana-Etendecka continental flood basalts in Brazil and Namibia (137–127 mya). Final break-up of Africa and S America was completed only at 80 mya	
West Antarctica-S America	Early Oligocene (ca 30 mya): beginning at ~35–30.5 mya as a subsidence in the Powell Basin followed by seafloor spreading. Opening of the Drake Passage between the southern tip of South America and the northern end of Antarctic Peninsula allowed deep water circulation and the installation of the Antarctic Circumpolar Current (ACC) between 41 and 24 mya (see Box 9.1)	

Southern Floras during Early **Cretaceous** did not differ much from the Late Jurassic ones (Fig. 1.13). Most famous is the middle Cretaceous, known as the period of expansion and radiation of the angiosperms (see also Box 2.4). Angiosperms evolving during this time include a number of

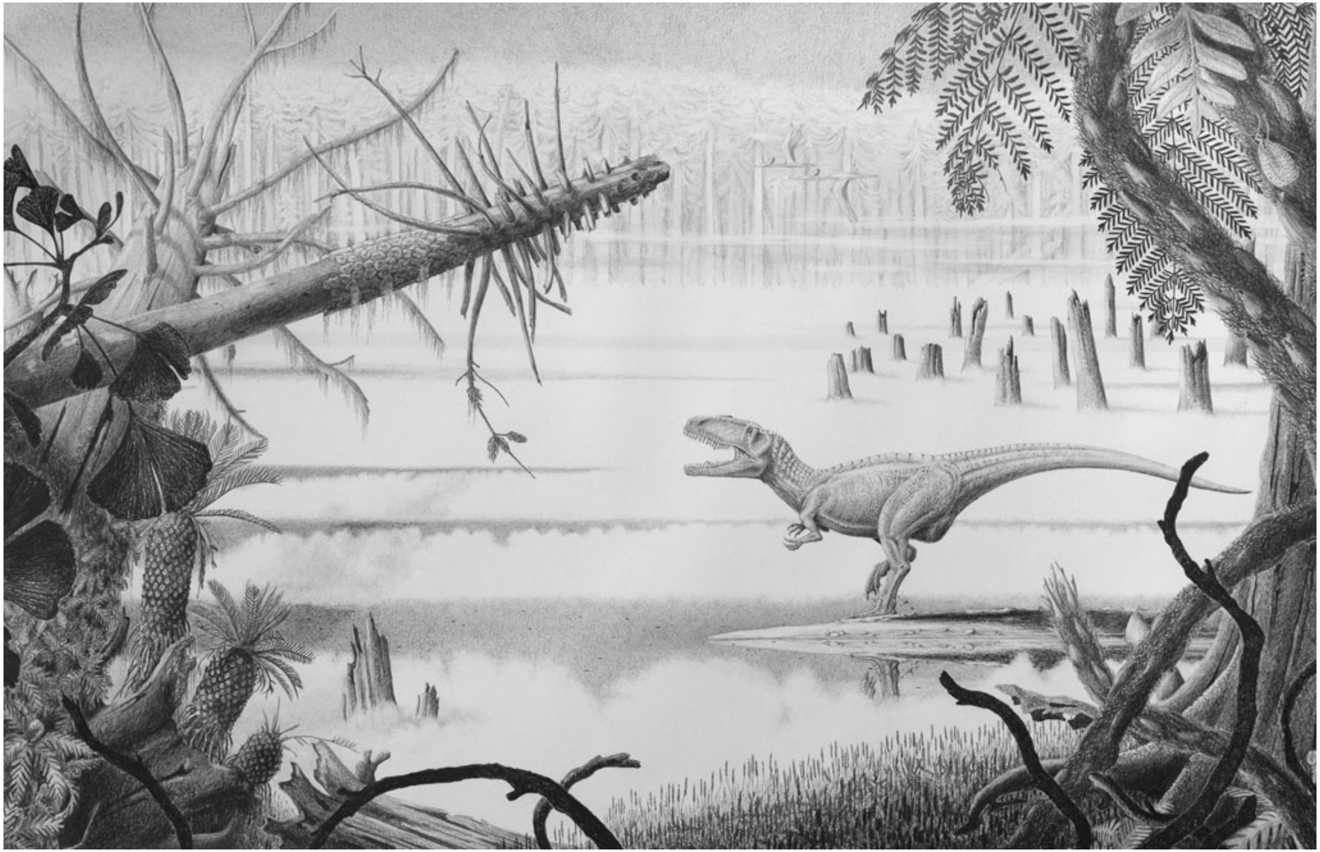

Fig. 1.13 Illustration of the biotic assemblage from the limit Jurassic/Cretaceous (145.5 mya) of the Southern Cone. Theropod dinosaur on a swamp surrounded by ginkgos, araucarias, and arborescent ferns (original illustration by Sergio Elórtegui Francioli)

families that constitute a significant part of the present-day global flora (e.g. Betulaceae, Gunneraceae, Fagaceae/Nothofagaceae). For the early Late Cretaceous (Cenomanian to Coniacian), Troncoso and Romero (1998) reported a Neotropical flora showing a notable change compared to the previous ones. They reported the definitive replacement of the dominance of gymnosperms by angiosperms, including representatives of extant families, such as the Lauraceae, Sterculiaceae, Bignoniaceae, and Monimiaceae; and from extant genera like *Laurelia, Peumus,* and *Schinopsis* (this last genus is currently not present in Chile).

By the Late Cretaceous, (Campanian-Maastrichtian) Troncoso and Romero (1998) reported a Neotropical flora with marginal presence of *Nothofagus* (Campanian first appearance of *Nothofagus* in Antarctica; Maastrichtian first appearance of *Nothofagus* in the fossil record from Central Chile and Tierra del Fuego) (see also Chap. 9). In spite of its marginal presence, it is the peak of northern expansion of *Nothofagus* in South America, reaching 30°S (Torres and Rallo 1981) (Fig. 1.14). This expansion of *Nothofagus* is challenging since the Late Cretaceous is considered a rather greenhouse world (Box 1.4). It is but possible that transient small icecaps existed during this mostly warm period. It has been proposed that relatively large and short-term global sea level variations may have been connected with small and ephemeral ice sheets in Antarctica, probably related to short intervals of peak Milankovitch forcing (Gallagher et al. 2008).

Southern South America, already isolated from the rest of western Gondwana, was occupied mainly by a "subtropical desert" and a "warm temperate" biome

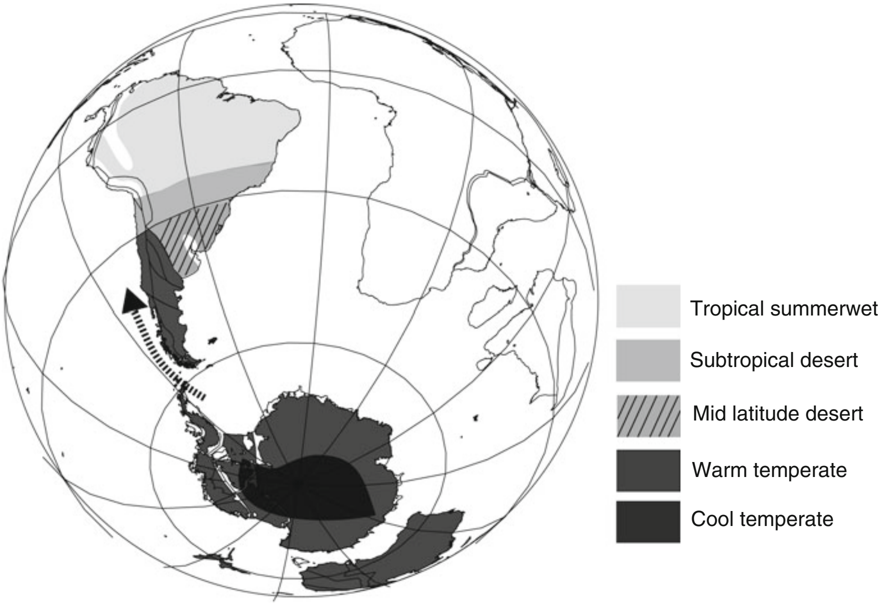

Fig. 1.14 Late Cretaceous biomes; *arrow* shows northernmost expansion of *Nothofagus* (see text) (adapted from Willis and McElwain (2002) on a TimeTrek 4.2.5 model, Cambridge Paleomap Services)

(Fig. 1.14), the latter being characterized by Araucariaceae, Nothofagaceae, Proteaceae, and Winteraceae (Willis and McElwain 2002). “The presence of tropical elements in the austral margin of South America gives support to the expansion of a warm climate towards high latitudes during the mid Cretaceous” (Barreda and Archangelsky 2006). Troncoso and Romero (1998) also reported the presence of Neotropical palaeofloras in the mid- and Late Cretaceous from Magallanes and Tierra del Fuego. Microfossils assigned to the Arecaceae (Palmae) have been reported since the Maastrichtian (Hesse and Zetter 2005).

Box 1.4 Floral Extinction at the K/T Boundary ?

A permanent question is whether massive extinction events that mostly affected the terrestrial fauna affected as well the global flora (McElwain and Punyasena 2007). It seems that at the K/T boundary, at least several groups suffered similar luck than dinosaurs, plesiosaurs, and ammonoids. For example, the seed-ferns, a group that dominated the vegetation formations in many parts of the world from the Triassic to the Cretaceous, are considered to have disappeared at the end of the Cretaceous. Neverthless, exceptions are the rule, and there is a seed-fern fossil recent discovered in Tasmania that has been dated from the Early Eocene (McLoughlin et al. 2008).

Recent findings on the Lefipán Formation in NW Chubut province dated as Maastrichtian, supports the catastrophic character of the K/T boundary (Cúneo et al. 2007). The discovery of a highly diversified assemblage of dicot leaves with probably more than 70 species, as well as several monocots, podocarp conifers, and ferns, suggests that the latest Cretaceous floras were probably more diverse than those known from Patagonia during the Palaeocene. This means that the K/T event indeed affected the terrestrial ecosystems of southern latitudes. The recovery of floral diversity must have taken most of the Palaeocene until the recovering of plant richness by the early Eocene (Cúneo et al. 2007).

1.2.3 The Cenozoic (65.5 mya Onwards)

The deep-sea oxygen isotope record permits a detailed reconstruction of the Cenozoic global climate, that has suffered a number of episodes of global warming and cooling, and ice-sheet growth and decay (Zachos et al. 2001) (Fig. 1.15). The most pronounced warming occurred from the Mid-Palaeocene (59 mya) to the Early Eocene (52 mya), showing a peak in the so called Early Eocene Climatic Optimum (52–50 mya) (Fig. 1.15). This period was one of the warmest periods in the Earth’s history: temperature estimates of between 9 and 12°C higher than present have been proposed (Zachos et al. 2001). This optimum was followed by a trend toward cooler conditions in the Late Eocene. According to Zachos et al. (2001), ice-sheets appeared in the Early Oligocene, and persisted until a warming phase that reduced the extent of Antarctic ice in the Late Oligocene Warming (Fig. 1.15). From this point (26–27 mya) until the middle Miocene (15 mya), the global ice volume remained low with the exception of several brief periods of glaciation. This warm phase peaked in the Middle Miocene Climatic Optimum (17–15 mya), and was followed by a gradual cooling and reestablishment of a major ice-sheet on Antarctica towards the Plio/Pleistocene (Zachos et al. 2001) (Fig. 1.15).

In the Early **Palaeocene** (~65–55 mya) the global position of South America had moved close to the present-day position (Fig. 1.14). Nevertheless, the cold circumpolar ocean current had not yet developed, and Pacific Ocean currents carried heated tropical waters to high latitudes. As a consequence, a permanent ice cover at the poles was absent, and the prevailing low relief of the continents, coupled with high seas, resulted in rain-bearing winds penetrating far into the interior of all the main landmasses (Willis and McElwain 2002).

South America was mainly occupied by "tropical everwet", "subtropical desert" and "warm temperate" biomes. The warm temperate biome was composed of evergreen and deciduous dicots (e.g. *Nothofagus*), and podocarps. South of 70°S, and widespread in Antarctica, a "warm cool temperate biome" was established, composed mainly by *Araucaria, Podocarpus, Dacrydium*, evergreen *Nothofagus*, and to a minor extent members of the Loranthaceae, Myrtaceae, Casuarinaceae, Ericaceae, Liliaceae, and Cunoniaceae (Truswell 1990).

Troncoso and Romero (1998) emphasized the neotropical character of the Palaeocene palaeofloras of Central and Southern Chile. Zonal vegetation was composed mainly of rainforests with palms, mangroves, and in the higher parts, azonal vegetation composed of Gymnosperms (Cheirolepidaceae, Araucariaceae, Podocarpaceae, Zamiaceae) and *Nothofagus*, accompanied by Myrtaceae, Proteaceae and Lauraceae. Fossil Boraginaceae related to extant *Cordia*

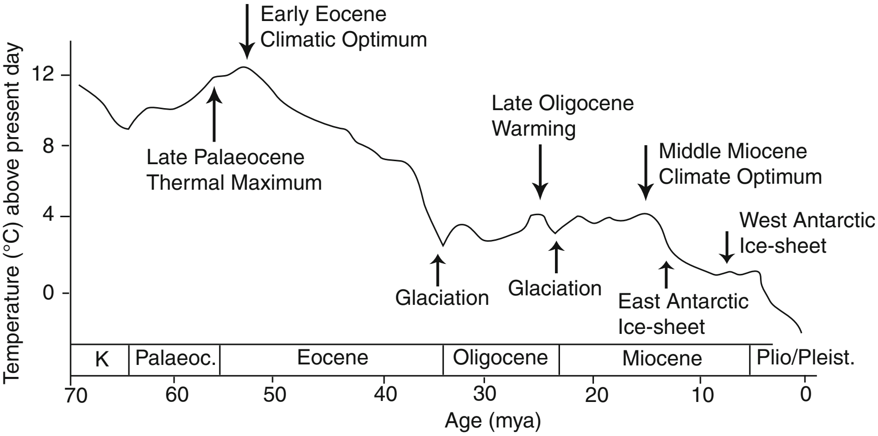

Fig. 1.15 Global climatic fluctuations during the Cenozoic, based on global deep-sea oxygen and carbon isotope records (adapted from Zachos et al. 2001)

have been described by Brea and Zucol (2006) from the Late Palaeocene of Chubut, Argentina. A rich assemblage of micro- and megafossils has been described by Troncoso et al. (2002) from the Ligorio Márquez Formation in Aisén (47°S). Of the twenty leaf species reported, fourteen are from the Lauraceae; the rest corresponding to the Melastomataceae, Myrtaceae, Sapindaceae, and others. Furthermore, seven Pteridophyta, two conifers, and four angiosperms are represented by palynological species. In spite of this predominantly tropical character, the presence of temperate taxa like *Nothofagus* and Podocarpaceae confirms the warm temperate tendency at 47°S (Okuda et al. 2006).

Recently Iglesias et al. (2007) reported a greater species richness than was previously known from Palaeocene Patagonia, including more than 43 species of angiosperm leaves. At the end of the Palaeogene, representatives of most of the angiosperm modern classes and many orders were already present in southern South America (Gandolfo and Zamaloa 2003; Prámparo et al. 2007).

Eocene (55.8–33.9 mya) floras of Southern South America show subtropical to fully tropical forests, with zones of seasonal dryness in Chile (Romero 1986). The three extant South American tribes of the Proteaceae were already present in the early Eocene, forming the Australia-Antarctica-South America connection (González et al. 2007). Late Eocene fossil leaves, flowers and fruits assigned to the Escalloniaceae have also been reported as being involved in this austral connection (Troncoso and San Martín 1999).

Remarkable is the presence of *Eucalyptus* macrofossils in the Patagonian Early Eocene (Gandolfo et al. 2007), since the genus shows an extant distribution in Australasia, mainly Australia and Tasmania (not New Zealand). The South American macrofossils reported by Gandolfo et al. (2007) are to date the most ancient register for the genus.

The Laguna del Hunco palaeoflora in NW Chubut, Argentina, shows the most complete example of Early Eocene vegetation in South America. This palaeoflora is one of the world's most diverse Cenozoic assemblages of angiosperms (Wilf et al. 2005, 2007). This assemblage comprises tropical elements restricted today to temperate and tropical Australasia (e.g. *Dacrycarpus, Papuacereus, Eucalyptus*); tropical elements (e.g. *Roupala, Bixa, Escallonia*), and the disjunct element South America/Australasia (e.g. *Eucryphia, Orites, Lomatia*) (see Fig. 3.5). Fossil plants at Laguna del Hunco are extremely abundant, diverse (>150 leaf species), and well-preserved. During the early Eocene the area was a subtropical rainforest with land connections both to Australasia via Antarctica and to the Neotropics (Fig. 1.16).

Wilf et al. (2007) suggest that the Laguna del Hunco plant lineages retreated to geographically disparate rainforest refugia following post-Eocene cooling and drying in Patagonia. Only few lineages adapted and persisted in temperate South America.

The continuous decrease in temperature during the Eocene allowed a new displacement of *Nothofagus* towards South-Central Chile. Therefore this time-span is characterized by a mixed tropical-subantarctic palaeoflora (Troncoso and Romero 1998). In spite of the prevalence of mixed palaeofloras during the Eocene, results obtained by Gayó et al. (2005) at Bahía Cocholgüe (36,5°S) suggest that tropical floras persisted in central Chile during the Early Eocene and formed a belt between

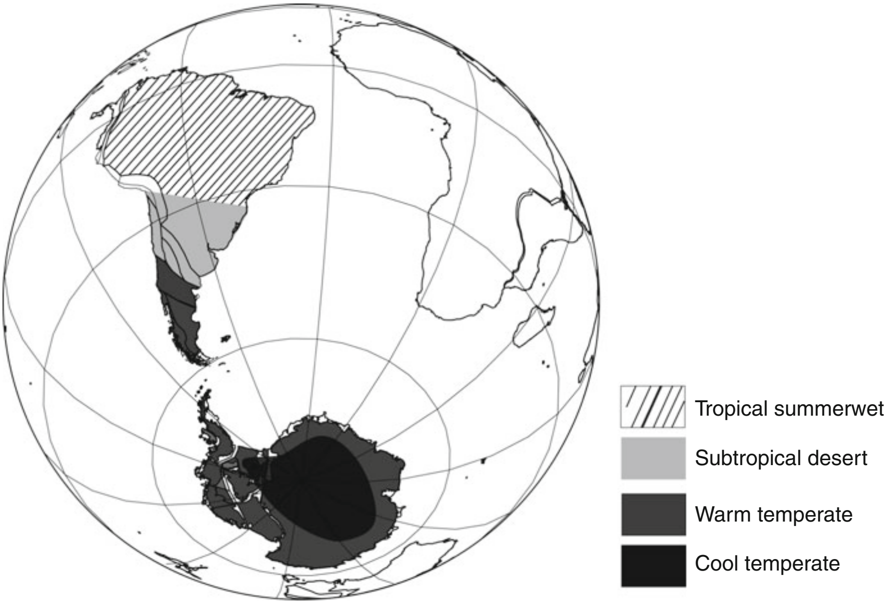

Fig. 1.16 Early Eocene biomes (adapted from Willis and McElwain (2002) on a TimeTrek 4.2.5 model, Cambridge Paleomap Services)

25°S and 37°S. This persistence of tropical floras (composed mainly by Lauraceae and Myrtaceae) might be related to the influence of the Early Eocene Climatic Optimum (Fig. 1.15) and to a shrinking tropical belt (Gayó et al. 2005).

The transition from the Eocene to the **Oligocene** (33.9–23.03 mya) was a period of significant global climatic cooling and increased aridity, major changes in oceanic circulation, and the initiation of ice on Antarctica (Zachos et al. 2001; Convey et al. 2008) (Fig. 1.15). Major reorganization and redistribution of global vegetation followed these climatic trends, with a reduction of tropical forests and the expansion of temperate vegetation toward the equator (Willis and McElwain 2002). A Subantarctic palaeoflora expanded its distribution range across southern South America, occupying an area that became to extend from the island of Tierra del Fuego to the south of Central Chile (Romero 1993) (Fig. 1.17).

This implicates the massive retreat of tropical and subtropical components from the Sapindaceae and Lauraceae, the generic replacement of genera in the Rhamnaceae, Myrtaceae, Bignoniaceae, Flacourtiaceae/Salicaceae; and the regional extinction of several families like Moraceae, Annonaceae, Dilleniaceae, Malpighiaceae, Vochysiaceae, Tiliaceae, Sterculiaceae, Sapotaceae, and Styracaceae (Troncoso and Romero 1998). Permanent ice sheets persisted on Antarctica until the Late Oligocene (26–27 mya), when a warming trend reduced the extent of Antarctic ice (Zachos et al. 2001).

From the "Late Oligocene Warming" (26–27 mya) (Fig. 1.15) until the Middle Miocene (~15 mya), the global ice volume remained low and water showed slightly higher temperatures, intermingled with brief periods of glaciation (Zachos

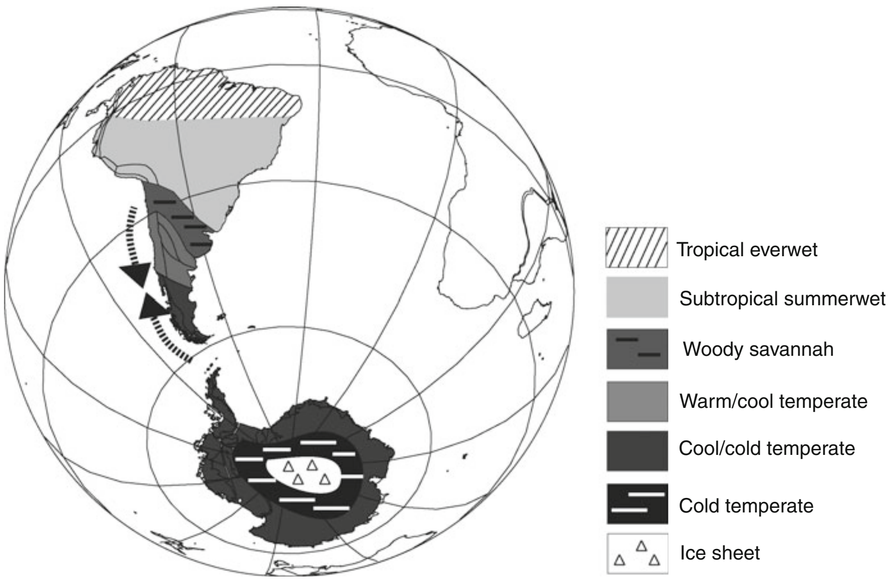

Fig. 1.17 Early Oligocene biomes; arrows show mixture of tropical and austral floras (adapted from Willis and McElwain (2002) on a TimeTrek 4.2.5 model, Cambridge Paleomap Services)

et al. 2001). This was followed by a gradual cooling and reestablishment of a major ice-sheet on Antarctica by 10 mya (Fig. 1.18). The continental interior became increasingly arid/cold and large areas of shorelines were exposed due to a falling sea level. Outside the core a depauperate "cold temperate" biome survived, having lost its main forests components and with some herbs and C_3 grasses remaining. During the Late Miocene most of Western South America was occupied by a "cool temperate" biome. The "winterwet" and "subtropical summerwet" biomes were restricted to a reduced proportion of today's Atacama Desert (Fig. 1.18).

The **Miocene** (23.03–5.33 mya) is characterized by a development of modern angiosperm families like Asteraceae, Poaceae, Malvaceae, Fabaceae and Cyperaceae, related to more open communities replacing tropical forests in southern South America (Barreda et al. 2007; Palazzesi and Barreda 2007). Tropical forests were still abundant during the Early Miocene of Patagonia; the vegetation increasingly acquired a more complex aspect, due to the wider distribution of grasses and shrubs. Barreda et al. (2007) list 60 angiosperm families present in the fossil record during the Miocene in Argentina. More diversified families are the Malvaceae (33 taxa), Fabaceae (32), and Asteraceae (25).

During the Early and Middle Miocene, the subantarctic flora reached the southern part of Central Chile (Troncoso and Romero 1998). In the middle Miocene of Central Chile a change from the previous subantarctic palaeoflora into a mixed palaeoflora with a predominance of neotropical taxa and the retreat of subantarctic taxa occurred (Hinojosa 2005). The subsequent subtropical palaeoflora that

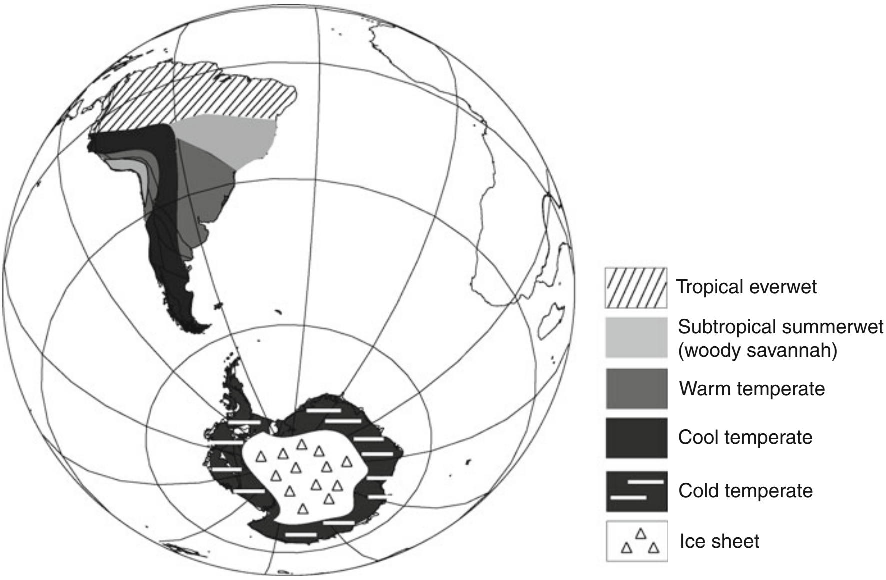

Fig. 1.18 Miocene biomes (adapted from Willis and McElwain (2002) on a TimeTrek 4.2.5 model, Cambridge Paleomap Services)

occupied central Chile during the lower to mid Miocene, 20–15 mya, developed under a warmer and more humid palaeoclimate, with an incipient Andean rain shadow effect, is the nearest ancestor of the sclerophyllous modern vegetation of central Chile (Hinojosa et al. 2006).

In northern Chile, the hyperarid climate became established at the Oligocene/Miocene boundary (ca. 25 mya) (Dunai et al. 2005; Nalpas et al. 2008), and was followed by more humid (semiarid periods interrupted by short arid events up to the earliest Late Pliocene (Hartley and Chong 2002, Box 3.1)).

Global deep-sea oxygen and carbon isotope records indicate additional cooling and small-scale icesheet expansion on west-Antarctica during the Late Miocene until the Early Pliocene (6 mya). The early Pliocene is marked by a subtle warming trend between 3.3 and 3 mya. Afterwards cooling again increased (Zachos et al. 2001).

Box 1.5 Slow or Rapid Andean Uplift?

The Late Miocene has been proposed as the initial phase of the Andes uplift. Gregory-Wodzicki (2000), on the base of palaeobotanical data, proposed a surface uplift in the order of 2,300–3,400 m asl since the late Miocene at uplift rates of 0.2–0.3 mm/year. More recently Ghosh et al. (2006) obtained results that indicate a surprisingly rapid uplift of the Bolivian Altiplano at an average rate of 1.03 ±0.12 mm per year between ~10.3 and ~6.7 mya (i.e. from 0 to 4,000 m asl since the Middle/Late Miocene). These results challenge the known forces responsible for the uplift and are in conflict with geological evidence (e.g. Hartley 2003, proposed a proto-Central Andean mountain range placed between 15 and 9 mya). Geomorphological evidence, i.e. lahar deposits in the Coastal Cordillera of central Chile (33°40′–34°15′S) still supports an Oligocene–Miocene uplift of the Andes (Encinas et al. 2006). New findings by Garzione et al. (2008) and Hoke and Garzione (2008) based on isotope data, suggest that the Andes elevation remained relatively stable for long periods (tens of millions of years), separated by rapid (1 to 4 million years) changes of 1.5 km or more.

Most families already present in the mid to late Miocene continue to be present during the **Pliocene** (5.33–1.81 mya) (e.g. Arecaceae, Lauraceae, Myrtaceae, Anacardiaceae, Asteraceae, Chenopodiaceae/Amaranthaceae). Several families like the Fabaceae increasingly diversified (Barreda et al. 2007).

Southern South America was dominated by grasslands, steppes, and shrublands, with rainforests restricted to the moist temperate forests of south-western Patagonia (Dowsett et al. 1999; Haywood et al. 2002) (Fig. 1.19). Barreda et al. (2007)

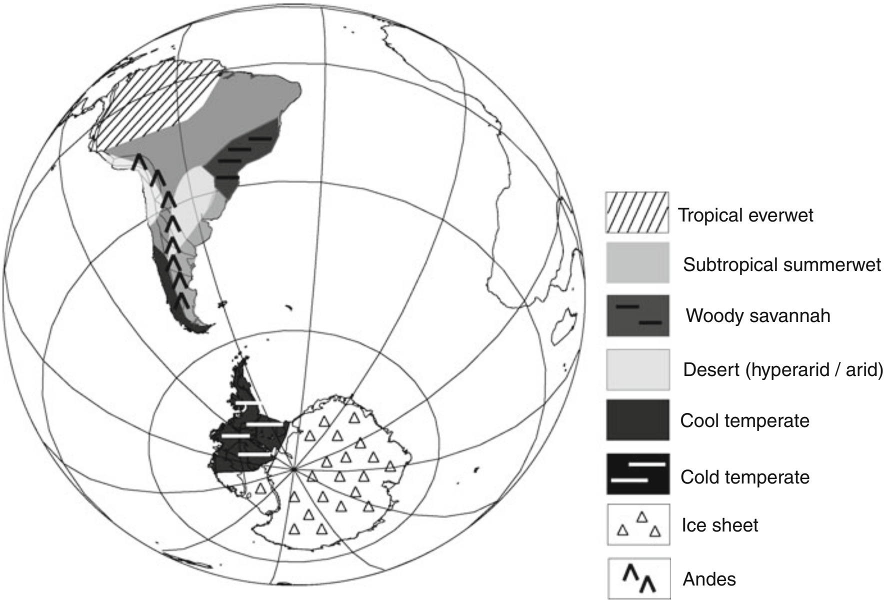

Fig. 1.19 Pliocene biomes (adapted from Dowsett et al. (1999) and Haywood et al. (2002), on a TimeTrek 4.2.5 model, Cambridge Paleomap Services)

recognize a neotropical palaeo-floristic province from 32°S to the north and a proto-espinal/steppe province to the south, together with a Nothofagacean province at the southwest.

The Cerro Centinela palaeoflora in Central Chile contains representatives of more than 20 modern families of different affinities: tropical genera not found in Chile any longer (e.g. *Nectandra Ocotea, Miconia*), subtropical genera (*Schinus*, *Schinopsis*, *Acacia*) and temperate or austral genera (*Araucaria* sección *Eutacta, Nothofagus*) (Troncoso and Encinas 2006). Appealing is the presence of the fern genus *Dicksonia*, found today mainly in Australasia (Malesia, New Guinea, Australia, New Caledonia) and in Juan Fernández (Chap. 5).

The end of the Cenozoic, traditionally treated as the "Quaternary", has been divided into two epochs: the Pleistocene (1.8 mya to 11,500 year BP) and the Holocene (11,500 year BP to the present). The Pleistocene is vastly known as the most recent epoch of glaciations. The last Pleistocene glaciation cycle is known from southern Chile as the Llanquihue glaciation, which is correlated with the Wisconsin/Weichselian glaciations in the northern hemisphere, according to global cooling data (Andersen et al. 1995; Lowell et al. 1995; Moreno et al. 2001).

In Chile glaciations affected to some extent all the ecosystems ranging from the arid north to the humid south. Several proxy-data used for Quaternaty palaeoreconstructions are specific for each environment: rodent middens in the north (Betancourt and Saavedra 2002; Maldonado et al. 2005), tree rings in central Chile (Barichivich et al. 2009), and sediment cores containing fossil pollen in the formerly glaciated south (Heusser 2003; Moreno 2004) (Box 1.6). The pollen analysis is complemented with the study of macrofossils (leaves), beetles (e.g. Ashworth et al. 1991), and more recently, chironomid stratigraphies (Massaferro et al. 2009).

Box 1.6 Six Steps for Palaeoenvironmental Reconstruction

Hereafter the main steps for getting pollen sample cores are briefly exposed (arbitrary extracted from Heusser 2003, Chap. 10):

1. Select a suitable site for sampling, on the base of aerial photographs and topographic maps, referring to the glacial borders and little sedimentary bogs or mires. Take account of accessibility for heavy coring equipment.
2. Get a piston sampler equipped with core tubes 5 cm in diameter and 1 m in length, with 1.5 m long extension rods.
3. With the piston sampler managed by three to four people, get the samples. You may need to build a wooden platform on the bog and a chain host to lift the sampler to the surface.
4. Extrude increments onto clear plastic, examine and describe them (color, texture, layers) and wrap them in aluminum foil. Take multiple cores at each coring location to ensure overlap at core breaks.

5. Once in the laboratory, identify the pollen grains under a microscope, at every < 5 cm interval in every sample core.
6. Voilá! You are ready to begin your own palaeoenvironmental reconstruction.

Note: Calvin and Linda Heusser, together with an international research team, worked for more than 40 years in southern Chile. They could get thousands of samples from 50 coring sites to reconstruct the glacial history and discern the palaeoecological factors responsible for vegetation changes over 50,000 years.

Calvin Heusser and coring team at Taiquemó site (Chiloé) in the late nineties. From left to right: Tom Lowell, Patricio Moreno, Linda Heusser, Calvin Heusser, David Marchant (Photo A. Moreira-Muñoz)

Glaciation effects were especially drastic from 42° (Chiloé) southward, were glaciers and ice lobes virtually devastated the temperate forests at the Last Glacial Maximum (LGM) between 29,400 and 14,450 year BP (Fig. 1.20). Vivid remnants of this widespread glaciation are the *Campo de Hielo Patagónico Norte* and *Campo de Hielo Patagónico Sur*, together with *Cordillera de Darwin* in southernmost Patagonia (Fig. 1.20).

At the LGM, periglacial effects like solifluction and glaciofluvial activity also should have affected the Andes, the longitudinal depression, and the coastal Cordillera between 39 and 43°, affecting principally the Valdivian and evergreen northpatagonian forests (Heusser 2003).

Glacial conditions forced forest formations to migrate equatorward and tree-lines to lower in altitude (Villagrán et al. 1998; Heusser 2003). Vegetation close

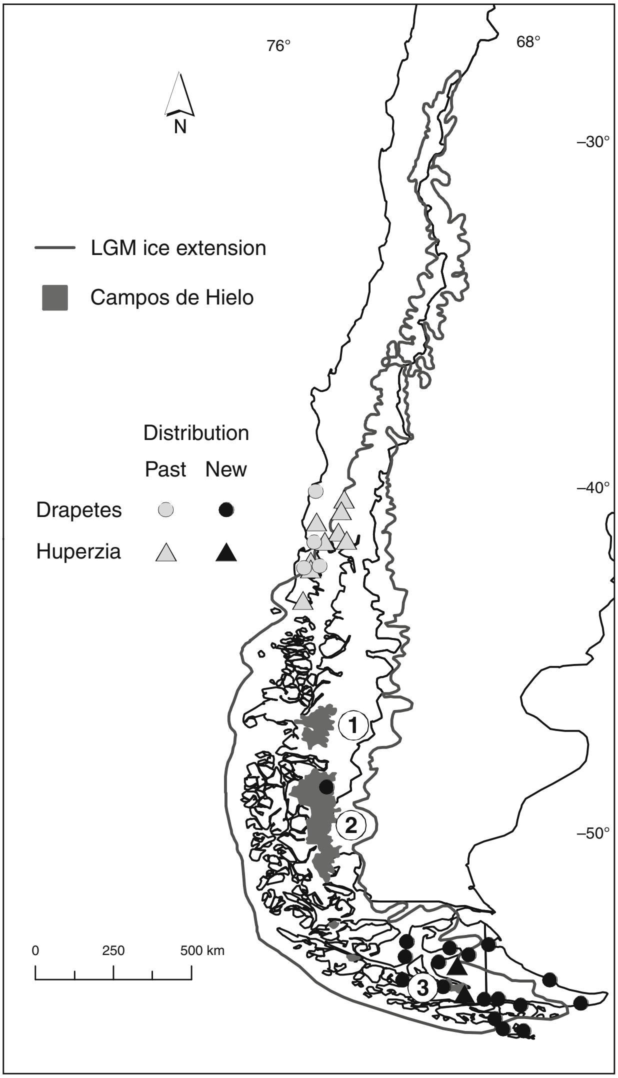

Fig. 1.20 Maximal extension of the last cycle of the Llanquihue glaciation (after Denton et al. 1999; Heusser 2003). Remnants of the Pleistocene glaciations: (1) Campo de Hielo Patagónico Norte, (2) Campo de Hielo Patagónico Sur, (3) Cordillera de Darwin. Also shown is the past and current distribution of *Huperzia fuegiana* and *Drapetes muscosus* (adapted from Heusser (2003) and Moore (1983), and collections of the National Herbarium SGO)

to the glaciated areas was structurally open, forming a steppe-tundra and turning to parkland and open woodland towards north-central Chile. In the northern part of the Central Depression (Tagua Tagua, 34.5°S), at ~14,500 year BP, Lateglacial warmth and dryness induced the retreat of *Nothofagus-Prumnopitys* woodland first by a spread of grassland and ultimately by herb-shrub communities composed by xeric Amaranthaceae and Asteraceae (Heusser 1997). The presence of *Nothofagus dombeyi* type pollen until ~10,000 year BP in the Central Depression exemplifies the downward altitudinal migration of taxa: this species is today restricted to the Andes at this latitude, which is also its northern distribution limit (see Sect. 9.1, Fig. 9.5). Similar situation was suffered by conifers in the south: the current disjunct range of several species in both cordilleras is a relict of a formerly wider distribution (before the colder period at 30,000–14,000 year BP), as shown by the (fossil) presence of *Fitzroya* and *Pilgerodendron* in the Central Depression (Villagrán et al. 2004).

Termination of the last glaciation was (differentiated locally) more or less at 15,000 year BP. Subantarctic species at low altitude in Los Lagos-Chiloé region, Like *Lepidothamnus fonkii* (Podocarpaceae), *Astelia pulima* (Asteliaceae) and *Donatia fascicularis* (Stylidiaceae), migrated to higher altitudes. Other species like *Huperzia fuegiana* (Lycopodiaceae) and *Drapetes muscosus* (Thymelaeaceae) were pushed to the south and are today restricted to southernmost Patagonia or Fuegia (Fig. 1.20).

The impacts of the Quaternary glaciations were not restricted to the southern Andes at all, and affected also the vegetation in the Central Chilean Andes (Villagrán et al. 1998). The changes on vegetation associated to the last glaciations cycle, as emphasized by these authors are:

(1) Existence of disjuct populations of conifers (*Fitzroya, Araucaria, Prumnopitys, Austrocedrus*) on the Costal cordillera between 37 and 42° S, dissociated from the main distribution on the Andes (Fig. 2.18). These are remnants of a widespread distribution of these species in the central depression when the climate was cooler. Same for the Magellanic moorlands located on the summits of the Cordillera de la Costa.
(2) Current concentration of endemic and monotypic species between 36 and 40°S has been interpreted as the function of refugia for laurifolious forests during the Pleistocene.
(3) High level of endemism at species level showed by the extant high Andean flora of central Chile is the consequence of repeated cycles of isolation associated to the adavance of Andean glaciers during the Pleistocene.
(4) The current presence of Andean scrub communities in the Coastal cordillera between 32 and 34°, could be the expression of a range expansion of these communities experimented during the last glaciaton.

The Andes of Central Chile were locally glaciated on the tops of the mountains, and it is presumed that the Andean flora descended altitudinally and also migrated northwards during the Pleistocene (Simpson 1971; Villagrán et al. 1998).

Especially the altitudinal migrations are hypothesised to have affected communities as a whole, but there is also possible that there was a recombination and redistribution of the taxa forming today these communities (Patricio Moreno pers. comm.). Whether the Quaternary glaciations affected only the distribution ranges or had deeper evolutionary implications is still a matter of discussion (Box 1.7). As example, as the glacial tongues advanced down from the Andes into the central depression, valleys like the Río Maule (36°S) and Río Biobío (37° to 38°S) could have acted as barriers, interrupting gene flow between plant populations and communities, as resulting from the study of *Hypochaeris acaulis* populations (Tremetsberger et al. 2003).

Box 1.7 How to Survive a Glaciation? The Refugial Debate

The Campos de Hielo Norte and Sur are considered the biggest inland icecaps after Greenland, current reminders of the maximal extension of the Pleistocene glaciations. Figure 1.20 suggests almost complete depletion of the southern biota at the LGM. But the relative rapid reoccupation of deglaciated areas under warmer conditions by the rainforest taxa suggests the continued permanence of exemplars somewhere not so far from the glacial lobes.

Debate continues on possible impacts from the ice ages and possible locations of refugial sites in the Southern Andes (Knapp and Mallet 2003). As 2/3 of the actual area of the southern forests was depleted, the traditional view proposes that taxa mostly survived the glaciations in the foreland of the glaciers and on several nunataks. This view has been recently challenged by Fickert et al. (2007), who suggest, based on research on six active glaciers (e.g. Monte Tronador in southern Chile), that the size of possible refugia would be considerably enlarged if debris-covered glaciers are considered. The nunatak theory just offers a too small area for a survival of viable plant populations (Fickert et al. 2007). Debris-covered glaciers should be added to the recent systematization of three main types of glacial refugia proposed by Holderegger and Thiel-Egenter (2009): i.e. nunatak, peripheral and lowland refugia. Concrete results provided by Premoli et al. (2000) suggest that the populations of *Fitzroya cupressoides* survived the Last Glacial Maximum in multiple refugia rather than in only one refugium, such as an ice-free area of coastal Chile (Single Refugium hypothesis). Multiple refugia in the eastern side of the Cordillera are also hypothesized for the survival of *Austrocedrus chilensis* (Pastorino and Gallo 2002).

Pleistocene and Holocene changes have disrupted species ranges, extirpated local populations, and changed selective pressures (Premoli et al. 2000), but it is doubtful that they affected speciation processes. Some authors have emphasized the role of the last glaciations in speciation, but others call this a “failed paradigm” (Klicka and Zink 1997). It is possible that molecular studies of populations of Quaternary species help define the relict characteristic of these species (Willis and Niklas 2004) (see Sect. 9.6).

1.3 Current Climate and Vegetation

A few crucial features of the present climate and vegetation will be outlined here, as a detailed description of these aspects is beyond the scope of this book. The reader is redirected to the most updated references on these topics, especially Luebert and Pliscoff (2006), Veblen et al. (2007), Garreaud et al. (2009). A fine synthesis of the southern Andean vegetation is also provided by Heusser (2003).

South America is situated within the influence of the Intertropical Convergence Zone (ITCZ) and related circulation systems (Orme 2007). This band is a major feature of the global circulation and the Chilean climate certainly depends upon this regional situation. The yearly N-S displacement of the Subtropical Anticyclone (South Pacific High) is one of the principal factors affecting the climatic latitudinal gradient in Chile (Garreaud and Muñoz 2004; Emck et al. 2006) (Fig. 1.21).

The displacement of the South Pacific High towards the south during the austral summer promotes Mediterranean-type climatic conditions in Central Chile (Luebert and Pliscoff 2006). During this displacement, tropical rainfall can reach the northern Altiplano, but this influence decreases at around 23°S (Vuille and Baumgartner 1998) due to the influence of the Andes as a “climatic wall” (Garreaud and Aceituno 2007). The displacement of the Anticyclone towards the North in the austral winter allows the entrance of the westerlies from the SW, promoting an intense and regular rainfall period with a maximal influence at around 47°S (Luebert and Pliscoff 2006). South of this latitude, the influence of the high pressures located around Antarctica generates a decrease in precipitation (Endlicher and Santana 1988). From Antarctica comes another important feature of the Chilean climate, i.e. the cool Humboldt Current derived from the Antarctic Circumpolar Current (Orme 2007).

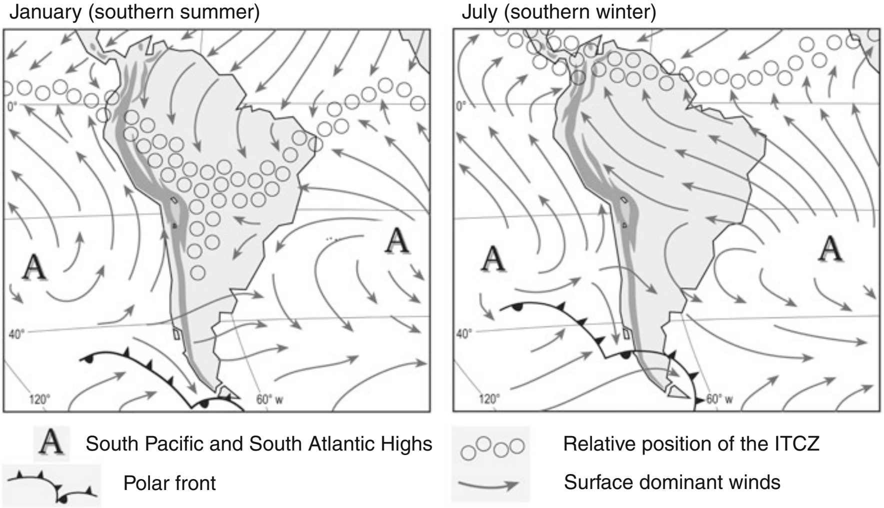

Fig. 1.21 Atmospheric circulation over South America. Note the yearly N–S displacement of the Intertropical Convergence Zone (ITCZ) (adapted from Emck et al. 2006)

The Humboldt Current is characterised by a predominant northward flow of surface waters of subantarctic origin and by strong upwelling of cool nutrient-rich subsurface waters of equatorial origin (Thiel et al. 2007). The current produces a decrease in the coastal zone temperatures in North- and Central Chile, and aided by tropospheric subsidence creates a temperature inversion that increases the conditions of aridity in western South America from near the equator to beyond the Tropic of Capricorn (Trewartha 1961; Orme 2007). Regarding precipitation, these factors generate a gradient of decreasing rainfall from the SW towards the NE, from ca. 5,000 mm in the SW to 0 mm in the Atacama (Fig. 1.22a). Only at the northern Altiplano this tendency is reverted by the tropical rains reaching northern Chile from the Amazonas basin.

1.3.1 Bioclimatic Zones

On the base of the early climatic classification done by W. Köppen (1930), Chilean bioclimatic classifications were progressively developed by Di Castri (1968), Quintanilla (1974), Di Castri and Hajek (1976), and Amigo and Ramírez (1998). Coupling the pioneer plant geographical works of Reiche (1907) and Pisano (1954), with the bioclimatic classifications and phytosociological information (e.g. Oberdorfer 1960), several attempts have been made for a vegetation classification of the country, like the ones from Schmithüsen (1956), Quintanilla (1983), and Gajardo (1994).

A systematic revision of previous classification schemes integrated to the analysis of global climatic surfaces on a GIS-based platform allowed Luebert and Pliscoff (2006) to generate the most accurate bioclimatic and vegetation synthesis to date. The classification considers bioclimatic and floristic data on the base of the conceptual framework promoted by Rivas-Martínez and Rivas-Sáenz (1996–2009). The application of the method for Chile resulted in the identification of 17 vegetation formations and 127 vegetational belts (Luebert and Pliscoff 2006). The highest rank of the bioclimatic classification is the "macrobioclimate", and the five units that exist worldwide are found in Chile (Fig. 1.22b):

(a) *Tropical macrobioclimate*: it extends from the border with Perú at 17°35′S towards the south till a diagonal limit at 23°S at the coast and at 31°S in the high Andes. The southern limit reflects on the one side the maximal influence of the polar fronts coming from the SW (Fig. 1.22b) and on the other side the maximal influence of the tropical moisture that reaches the Altiplano and the northern high Andes during the austral summer. Within this zone lies the Atacama Desert.

(b) *Mediterranean-type macrobioclimate*: this macrozone is one of the most characteristic features of Chile, as one of only five regions at the global scale that share this type of climate, characterized mainly tdue to the marked seasonality in the thermal and precipitation regimes (Di Castri 1981). The limits of this macrobiolimate in Chile have been controversial, but the proposal of Luebert and Pliscoff (2006) is concordant with the findings of Amigo and Ramírez (1998). It extends from the diagonal limit with the tropical bioclimate towards the South,

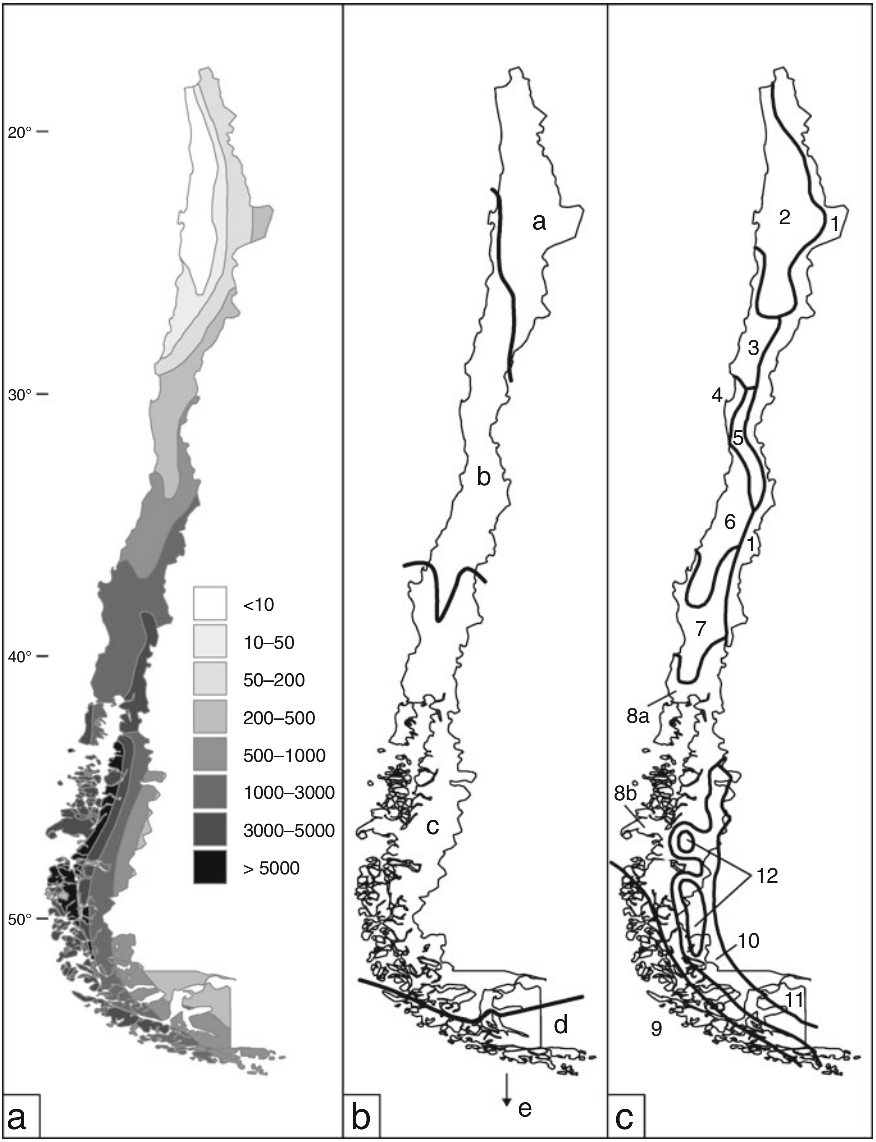

Fig. 1.22 **a** Annual precipitation, based on Schmithüsen (1956) updated with current available data; **b** five Chilean macro-bioclimates (adapted from Luebert and Pliscoff 2006); **c** distribution of vegetation formations according Schmithüsen (1956): *1*= Andean vegetation; *2*= desert core; *3*= semi-desertic scrub; *4*= xeric scrub and Fray Jorge fog-forest; *5*= woody savanna; *6*= sclerophyllous matorral; *7*= deciduous (maulino) forest with conifers; *8a*= Valdivian rainforest; *8b*= northpatagonic rainforest; *8c*=subantarctic rainforest; *9*= subantarctic moorlands; *10*=subantarctic deciduous forest, *11*=east-patagonic steppe; *12*=Campos de Hielo

till 37°S at coast and Andes, and till 39°S in the Central Depression. The Mediterranean-type macrobioclimate appears also in disjunct patches further South around 46–47°S, related to the western limit of the Patagonian steppe.

(c) *Temperate macrobioclimate*: it occupies the major area in continental Chile, from the limit with the Mediterranean-type one at 37–39°S up to western Patagonia and the Magallanes region in the southern territories. It is thermally most homogeneous and precipitation can reach more than 5,000 mm on the southwestern fjordland and island groups more exposed to the humid westerlies.

(d) *Antiboreal macrobioclimate*: it occupies a restricted portion of the southernmost continental extreme, affecting the Magellanic archipelagos and the southern part of Tierra del Fuego. Precipitation decreases notably toeads the east and temperature decreases towards the south.

(e) *Polar bioclimate*: with increasing thermal cold conditions, it occupies the territory outside the American continent towards Antarctica.

1.3.2 Vegetation Formations

Schmithüsen (1956) provided one of the most sinthetical and comprehensive accounts of the Chilean vegetation, valid till today (Fig. 1.22c). He also illustrated magistrally the latitudinal versus altitudinal distribution of the vegetation formations (Fig. 1.23).

The principal vegetation formations and their main characteristics will be briefly described here, based on Schmithüsen (1956) and Luebert and Pliscoff (2006) (Figs. 1.22c, 1.23 and Fig. 1.24).

(a) The hyperarid *desert* formation or desert core extends from 18°S along the coast and interior zones towards the south till around 24°. Approaching the border with Peru, vegetation is restricted to the deep valleys of Azapa

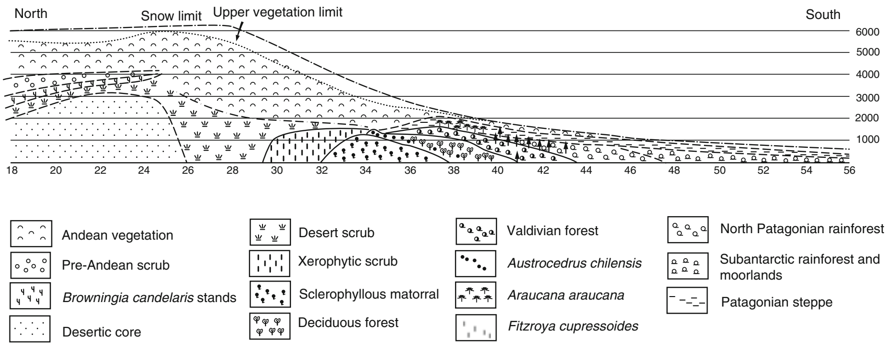

Fig. 1.23 Distribution of vegetation formations along the altitudinal profile according Schmithüsen (1956)

Fig. 1.24 Chilean vegetation: **a** high-Andean vegetation, *Azorella compacta* at Parinacota (18°30′S); **b** high-Andean vegetation, vegas de Zapaleri, border with Bolivia at 22°50′S; **c** *Puya coerulea*, characteristic of the xeric matorral at Cerro La Campana (33°S); **d** sclerophyllous forest at Río Clarillo (33°47′S); **e** temperate forest at Navarino island (55°S); **f** conifer forest (*Araucaria*) with *Nothofagus* at El Cañi, Pucón (39°20′S) (photo credits: **a** Walter Welss; **b**–**f** A. Moreira-Muñoz)

and Camarones, related to agriculture. At the heart of the Atacama, vegetation is almost completely lacking; nevertheless, there are stands of natural and human induced forests of *Prosopis tamarugo* = Pampa del Tamarugal. Towards the Andes, scrub vegetation consists mainly of a low scrub (matorral) of *Adesmia atacamensis, Cistanthe salsoloides, Atriplex imbricata,* and *Acantholippia deserticola*. In a very thin belt between 2,000 and 2,800 m asl, big cacti of *Browningia candelaris* bear out the landscape (Fig. 7.1).

(b) The sparse coastal shrub vegetation, also characteristic for coastal southern Peru, is called the "Lomas" formation, and consists of a rich assemblage of *Eulychnia*, *Nolana*, *Heliotropium*, *Tetragonia*, and *Euphorbia* species. This formation is highly dependent on fog and humidity to some extent related to the El Niño phenomenon (Box 7.1).

The desert coastal scrub extends into the land's interior between 24 and 32°S, generating a transition zone from the desert towards the winter-wet Mediterranean climate of Central Chile. It encompasses an open scrub (matorral) composed by *Adesmia* spp., *Bulnesia, Balbisia*, and *Heliotropium* species. At 30°S, the vegetation gradually changes to a xerophytic scrub composed of *Haplopappus* spp., *Porlieria chilensis*, *Flourensia thurifera*, *Colliguaja odorifera*, *Trichocereus* cacti, and *Puya* species. This zone harbours one of the most interesting botanical phenomena, the "desierto florido" (Box 7.1), and a plant geographical icon = the fog forest of Fray Jorge, where the northernmost remnants of southern floristic elements are to be found (see Box 3.1).

(c) The *Andean vegetation* is the formation occupying extreme, high environments, ranging from 17°30′S to ca. 40°S along the western Andean slope. This wide latitudinal extension encompasses a very different composition along the North-South profile, and in the altitude. The intermediate altitudinal belts show the structurally most developed vegetation: the lowest belts are affected by the aridity, the highest by low temperature. These intermediate belts are composed by tolares, dominated by *Parastrephia* species and pajonales (cushion grasses) of *Festuca orthophylla*. Stands of *Polylepis tarapacana* trees are to be found. Precordilleran belts are dominated by *Fabiana ramulosa* and *Diplostephium meyenii*. Above 4,700 m asl bofedales (high Andean wetlands) support the long tradition of Andean llama and alpaca pasture. Approaching the most arid part of the Atacama Desert there are shrubs of *Fabiana* and *Baccharis*, together with *Atriplex* and *Acantholippia* in the lower belts. Towards the south, sparse vegetation is composed of *Jarava frigida* cushion grasses, several *Adesmia* species, with the addition of *Mulinum*, and *Urbania* species. The treeline changes constantly along the latitude gradient: in the north it is composed by queñoales = *Polylepis tarapacana* and *P. rugulosa*, in the central-north it is replaced by *Adesmia* shrubs with *Ephedra* between 31 and 34°S the treeline reappears by means of *Kageneckia angustifolia* accompanied by *Guindilia trinervis*. At this latitudinal range the Andean scrub is composed of *Adesmia* species, *Tetraglochin alatum*, *Mulinum spinosum*, and cushion Apiaceae like *Azorella* spp. and *Laretia acaulis*. From 32°60′ to the South, at the lower limit of the Andean formation, appears the conifer *Austrocedrus chilensis* (Fig. 2.18). The

Andean formation disappears at around 37°S, where it is replaced by deciduous forests.

(d) Entering into the Mediterranean climate zone the vegetation changes to a sclerophyllous high scrub or *matorral esclerófilo*. On favorable South oriented slopes this scrub shows characteristics of woodland, with trees reaching 20–25 meter in height. Typical species of the Central Chilean matorral are *Peumus boldus*, *Cryptocarya alba*, *Quillaja saponaria*, *Maytenus boaria*. In the quebradas, i.e. more humid stands, there appears a more hygrophyllous forest composed of *Crinodendron patagua*, *Beilschmiedia miersii*, *Drimys winteri*, and *Persea lingue*. In contrast, the most exposed and plain areas contain a woody savanna (*espinal*) mainly composed of *Acacia caven* and *Prosopis chilensis*. North exposed slopes show a rich array of annual species and characteristic bromeliads, *Puya chilensis, P. berteroniana* and *P. coerulea*, together with the cactus *Trichocereus chiloensis*.

(e) Around 33° the coastal cordillera reaches far inside the continent, and above 1,200 m asl, the sclerophyllous woodland leaves space for a deciduous forest composed of deciduous *Nothofagus* species. The northernmost populations at 33°S seem to be remnants of an ancient distribution of the genus (Chap. 9). Deciduous forests dominate along the Andes and the coast towards the South, surrounding the Central Depression. The core of the deciduous forest between 35 and 36°S is known as the *maulino forest*, a mesic forest type, dominated by the two broadleaved deciduous species *Nothofagus alessandrii* and *N. glauca* (San Martín and Donoso 1996). At around 38°S, this forest shows signs of the transition towards the temperate macrobiolimate, with the remarkable presence of the resinous or *conifer forests* of *Araucaria araucana* at the coast (Nahuelbuta) and the Andes. Deciduous forests turn often into a krummholz of *Nothofagus antarctica* and *N. pumilio* composes the treeline along the Andes all the way to the Cape Horn.

(f) Located well into the temperate macrobioclimate, and related to high precipitation levels (>2,000 mm/year) is the broad-leaved (laurifolious) forest, also known as the *Valdivian forest*. It shows, same as the maulino forest, a "U" shape with a coastal and an Andean branch between 39° and 42°S. The history of this forest has been vastly debated, and some of its components, like *Aextoxicon punctatum, Laureliopsis philippiana, Dasyphyllum diacanthoides* (Fig. 8.2)*, Luma apiculata, Laurelia sempervirens, Eucryphia cordifolia,* and *Weinmannia trichosperma* seem to be old remnants of Palaeogene floras (Sect. 1.2).

(g) At around 41°S on the Andes and 41°30′ on the coast, broad-leaved forests are replaced by an evergreen northpatagonian rainforest mainly composed of large trees pertaining to the Nothofagaceae: *Nothofagus dombeyi*, *N. nitida*, and *N. betuloides*. These rainforests are intermingled with the conifer forests of *Podocarpus nubigenus*, *Fitzroya cupressoides* and *Pilgerodendron uviferum*. These evergreen forests dominate at the coast and interior, being replaced in altitude by the deciduous forest.

(h) As the landscape gets more and more fragmented into fjords and little islands south of 47°, and the precipitation exceeds the 4,000 mm/year the vegetation turns to a low physiognomy of moorlands, dominated by *Astelia pumila, Donatia fascicularis, Oreobolus obtusangulus*. Towards the East the moorlands get less humid and dominated by the moss *Sphagnum magellanicum*. Most of the interior of Patagonia is covered by the two wide icefielkds Campo de Hielo Norte and Campo de Hielo Sur. To the South of this last icefield, the deciduous forest of *Nothofagus* reappears, together with the subantarctic evergreen rainforest. In accordance with the marked precipitation gradient ranging from 4,000 mm at the western side to 300 mm at the eastern side of the low Andes in southern Patagonia and Tierra del Fuego, a gramineous steppe of *Festuca* spp. dominates the landscape.

The scheme presented here, based on Schmithüsen (1956) and Luebert and Pliscoff (2006) corresponds to the potential vegetation, but all the formations and most of the vegetation belts that compose the Chilean vegetation are to a high degree affected by the long history of human occupation, from localized mining impacts in the north to extended forest substitutions in the south. The core of the deciduous forest at around 38°S to 41°S has been transformed into agriculture, and in the Central Derpression only remnants of sclerophyllous forests remain in this mainly cultural landscape (Chap. 6).

References

Amigo J, Ramírez C (1998) A bioclimatic classification of Chile: woodland communities in the temperate zone. Plant Ecol 136:9–26

Andersen BG, Denton GH, Heusser CJ, Lowell TV, Moreno PI, Hauser A, Heusser LE, Schluchter C, Marchant D (1995) Climate, vegetation, and glacier fluctuations in Chile between 40°30′ and 42°30′s latitude: a short review of preliminary results. Quat Int 28:199–201

Anderson JM, Anderson HM, Archangelsky S, Bamford M, Chandra S, Dettmann M, Hill R, McLoughlin S, Rösler O (1999) Patterns of Gondwana plant colonisation and diversification. J Afr Earth Sci 28:145–167

Artabe AE, Morel EM, Spalletti LA (2003) Characterization of the phytogeographic Triassic provinces from extratropical Gondwana. Ameghiniana 40:387–405

Artabe AE, Ganuza DG, Spalletti LA, Zúñiga A, Morel EM (2005) Revisión de la paleoflora del cerro La Brea (Jurásico Temprano), provincia de Mendoza, Argentina. Ameghiniana 42: 429–442

Ashworth AC, Markraf V, Villagrán C (1991) Late Quaternary climatic history of the Chilean Channels based on fossil pollen and beetle analysis, with an analysis of the modern vegetation and pollen rain. J Quat Sci 6:279–291

Astini RA, Benedetto JL, Vaccari NE (1995) The early Paleozoic evolution of the Argentine Precordillera as a Laurentian rifted, drifted, and collided terrane: a geodynamic model. Geol Soc Am Bull 107:253–273

Barichivich J, Sauchyn DJ, Lara A (2009) Climate signals in high elevation tree-rings from the semiarid Andes of north-central Chile: responses to regional and large-scale variability. Palaeogeogr Palaeoclimatol Palaeoecol 281:320–333

Barreda V, Archangelsky S (2006) The southernmost record of tropical pollen grains in the mid-Cretaceous of Patagonia, Argentina. Cretaceous Res 27:778–787

Barreda VD, Anzótegui LA, Prieto AR, Aceñolaza PG, Bianchi MM, Borromei AM, Brea M et al. (2007) Diversificación y cambios de las angiospermas durante el Neógeno en Argentina. In: Archangelsky S, Sánchez T, Tonni EP (eds) Ameghiniana 50° aniversario, Publicación Especial 11:173–191

Barrientos SE (2007) Earthquakes in Chile. In: Moreno T, Gibbons W, (eds) The geology of Chile. Geological Society, London, pp 263–287

Beerling DJ (2002) Low atmospheric CO_2 levels during the Permo-Carboniferous glaciation inferred from fossil lycopsids. Proc Natl Acad Sci 99:12567–12571

Benton MJ, Twitchett RJ (2003) How to kill (almost) all life: the end-Permian extinction event. Trends Ecol Evol 18:358–365

Berry EW (1922a) Contributions to the paleobotany of Peru, Bolivia and Chile. The John Hopkins Press, Baltimore.

Berry EW (1922b) The flora of Concepción-Arauco coal measures of Chile. Stud Geol (John Hopkins Univ) 4:73–142

Betancourt JL, Saavedra B (2002) Rodent middens, a new method for Quaternary research in arid zones of South America. Rev Chil Hist Nat 75:527–546

Brea M, Zucol AF (2006) Leños fósiles de Boraginaceae de la Formación Peñas Coloradas (Paleoceno superior), Puerto Visser, Chubut, Argentina. Ameghiniana 43:139–146

Cecioni G, (ed) (1968) El Terciario de Chile: zona central. Editorial Andrés Bello, Santiago.

Charrier R (1988) Condiciones Paleoclimáticas para el Carbonífero Superior y Pérmico Inferior en la mitad austral de América del Sur. Bol Mus Nac Hist Nat (Chile) 41:105–116

Charrier R, Pinto L, Rodríguez M (2007) Tectono-stratigraphic evolution of the Andean orogen in Chile. In: Moreno T, Gibbons W, (eds) The geology of Chile. The Geological Society, London, pp 21–116

Chumakov NM, Zharkov MA (2003) Climate of the Late Permian and Early Triassic: general inferences. Stratigr Geol Correl 11:361–375

Convey P, Gibson JAE, Hillenbrand C-D, Hodgson DA, Pugh PJA, Smellie JL, Stevens MI (2008) Antarctic terrestrial life – challenging the history of the frozen continent? Biol Rev 83:103–117

Cúneo RC (1989) Phytogeography and paleoecology of Late Paleozoic Floras from Southern South America and their relationship with other floral realms. Abstracts, 28th International Geological Congress, p 351

Cúneo RN, Johnson K, Wilf P, Gandolfo MA, Iglesias A (2007) A preliminary report on the diversity of Latest Cretaceous floras from Northern Patagonia, Argentina. Abstract GSA Denver Annual Meeting

Denton GH, Heusser CJ, Lowell TV, Moreno PI, Andersen BG, Heusser LE, Schlüchter C, Marchant DR (1999) Interhemispheric linkage of paleoclimate during the last glaciation. Geogr Ann 81A:107–153

Di Castri F (1968) Esquisse écologique du Chili. In: Delamanre-Debouteville C, Rapoport E, (eds) Biologie del’ Amérique Australe, 4. Editions du Centre National de la Recherce Scientfique, Paris, pp 6–52

Di Castri F (1981) Mediterranean-type shrublands of the world. In: Di Castri F, Goodall DW, Specht RL, (eds) Mediterranean-type Shrublands. Ecosystems of the World vol 11. Elsevier, Amsterdam, pp 1–52

Di Castri F, Hajek E (1976) Bioclimatología de Chile. Vicerrectoría Académica, Universidad Católica de Chile, Santiago.

DiMichele WA, Pfefferkorn HW, Gastaldo RA (2001) Response of late carboniferous and early permian plant communities to climate change. Annu Rev Earth Planet Sci 29:461–487

Dowsett HJ, Barron JA, Poore RZ, Thompson RS, Cronin TM, Ishman SE, Willard DA (1999) Middle pliocene paleoenvironmental reconstruction: PRISM2. US Geological Survey Open File Report, 99–535. http://pubs.usgs. gov/of/1999/of99-535/

Dunai TJ, González López GA, Juez-Larré J (2005) Oligocene–Miocene age of aridity in the Atacama Desert revealed by exposure dating of erosion-sensitive landforms. Geology 33:321–324

Dusén P (1907) Über die Tertiäre Flora der Magellansländer. In: Nordenskjold O (ed) Wissenschaftlichen Ergebnisse der Schwedischen Expedition nach der Magellansländern, 1895–1897, vol I, pp 84–108

Emck P, Moreira-Muñoz A, Richter M (2006) El clima y sus efectos en la vegetación. In: Moraes M, Øllgaard B, Kvist LP, Borchsenius F, Balslev H, (eds) Botánica Económica de los Andes Centrales, Universidad Mayor de San Andrés, La Paz, pp 11–36

Encinas A, Maksaev V, Pinto L, Le Roux JP, Munizaga F, Zentilli M (2006) Pliocene lahar deposits in the Coastal Cordillera of central Chile: implications for uplift, avalanche deposits, and porphyry copper systems in the Main Andean Cordillera. J S Am Earth Sci 20:369–381

Endlicher W, Santana A (1988) El clima del sur de la Patagonia y sus aspectos ecológicos: un siglo de mediciones climatológicas en Punta Arenas. An Inst De La Patagonia (Chile) 18:57–86

Engelhardt H (1891) Über Tertiärpflanzen von Chile. Abh Senckenb Naturforsch Ges 16:629–692

Fickert T, Friend D, Grüninger F, Molnia B, Richter M (2007) Did debris covered glaciers serve as Pleistocene refugia for plants? A new hypothesis derived from observations of recent plant growth on Glacier surfaces. Arct Antarct Alp Res 39:245–257

Fosdick JC (2007) Late Miocene exhumation of the Magallanes Basin and sub-Andean fold belt, southern Chile: new constraints from apatite U-Th/He thermochronology. Abstracts 2007 GSA Denver Annual Meeting

Frakes LA, Francis JE, Syktus JI (1992) Climate modes of the Phanerozoic. Cambridge University Press, Cambridge.

Fuenzalida H (1938) Las capas de Los Molles. Bol Mus Nac Hist Nat 16:67–92

Fuenzalida H (1966) Historia vegetacional de Chile. Estudios geográficos . Facultad de Filosofía y Educación, Universidad de Chile, Santiago, pp 21–39

Gajardo R (1994) La vegetación natural de Chile: clasificación y distribución geográfica. Ed. Universitaria, Santiago.

Gallagher SJ, Wagstaff BE, Baird JG, Wallace MW, Li CL (2008) Southern high latitude climate variability in the Late Cretaceous greenhouse world. Glob Planet Change 60:351–364

Gandolfo MA, Zamaloa MC (2003) Evolution of Upper Cretaceous and Tertiary Angiosperm floras of Patagonia. 12°Simposio Argentino de Paleobotánica y Palinología (Buenos Aires), Resúmenes, pp 40–41

Gandolfo MA, Gonzalez CC, Zamaloa MC, Cúneo NR, Wilf P, Johnson K (2007) Eucalyptus (Myrtaceae) macrofossils from the early Eocene of Patagonia, Argentina. 5° Southern Connection Conference, Adelaide, Australia, Abstracts p 32

Garreaud RD, Aceituno P (2007) Atmospheric circulation over South America: mean features and variability. In: Veblen T, Young K, Orme A, (eds) The physical geography of South America. Oxford University Press, Oxford, pp 45–66

Garreaud RD, Muñoz R (2004) The diurnal cycle of circulation and cloudiness over the subtropical southeast Pacific: a modeling study. J Clim 17:1699–1710

Garreaud RD, Vuille M, Compagnucci R, Marengo J (2009) Present-day South American climate. Paleogeogr Paleoclimatol Paleoecol doi: 10.1016/j.palaeo.200710.032

Garzione CN, Hoke GD, Libarkin JC, Withers S, MacFadden B, Eiler J, Ghosh P, Mulch A (2008) Rise of the Andes. Science 320:1304–1307

Gayó E, Hinojosa LF, Villagrán C (2005) On the persistence of tropical paleofloras in central Chile during the Early Eocene. Rev Palaeobot Palynol 137:41–50

Ghosh P, Garzione NC, Eiler JM (2006) Rapid uplift of the Altiplano revealed through 13C-18O bonds in paleosol carbonates. Science 311:511–515

González CC, Gandolfo MA, Zamaloa MC, Cúneo NR, Wilf P, Johnson KR (2007) Revision of the Proteaceae macrofossil record from Patagonia, Argentina. Bot Rev 73:235–266

González-Ferrán O (1994) Volcanes de Chile. Instituto Geográfico Militar (IGM), Santiago.

Gradstein FM, Ogg JG, Smith AG et al (2004) A geologic time scale 2004. Cambridge University Press, Cambridge.

Gregory-Wodzicki KM (2000) Uplift history of the central and northern Andes: a review. Geol Soc Am Bull 112:1091–1105

Hartley AJ (2003) Andean uplift and climate change. J Geol Soc 160:7–10

Hartley AJ, Chong G (2002) A late Pliocene age for the Atacama Desert: implications for the desertification of western South America. Geology 30:43–46

Haywood AM, Francis JE, Sellwood BW (2002) Global middle Pliocene biome reconstruction: a data/model synthesis. Geochem Geophys Geosy 3:1–18

Herbst R, Troncoso A (1996) La tafoflora de Juan de Morales del Jurásico Medio (Formación Chacarilla), Región de Tarapacá, Chile. Rev Geol Chile 23:3–15

Hesse M, Zetter R (2005) Ultrastructure and diversity of recent and fossil zona-aperturate pollen grains. Plant Syst Evol 255:145–176

Heusser CJ (1997) Deglacial setting of the southern andes following the last glacial maximum: a short review. An Inst Patagonia Serie Cienc Nat 25:89–103

Heusser CJ (2003) Ice age southern andes: a chronicle of paleoecological events. Developments in Quaternary Science 3. Elsevier, Amsterdam.

Hinojosa LF (2005) Cambios climáticos y vegetacionales inferidos a partir de paleofloras cenozoicas del sur de Sudamérica. Rev Geol Chile 32:95–115

Hinojosa LF, Armesto JJ, Villagrán C (2006) Are Chilean coastal forests pre-Pleistocene relicts? Evidence from foliar physiognomy, paleoclimate, and paleobiogeography. J Biogeogr 33: 331–341

Hoke GD, Garzione CN (2008) Paleosurfaces, paleoelevation, and the mechanisms for the late Miocene topographic development of the Altiplano plateau. Earth Planet Sci Lett 271:192–201

Holderegger R, Thiel-Egenter C (2009) A discussion of different types of glacial refugia used in mountain biogeography and phylogeography. J Biogeogr 36:476–480

Iglesias A, Wilf P, Johnson KR, Zamuner AB, Matheos SD, Cúneo RN (2007) Rediscovery of Paleocene Macrofloras in Central Patagonia, Argentina. GSA Denver Annual Meeting (28–31 October 2007)

IGM (2005) Atlas de Chile. Instituto Geográfico Militar, Santiago.

Illies H (1959) Die Entstehungsgeschichte eines Maares in Süd-Chile: ein aktuo-geologischer Beitrag zum Problem des Maar-Vulkanismus. Int J Earth Sci 48:232–247

Jasper A, Guerra-Sommer M, Cazzulo-Klepzig M, Iannuzzi R (2003) Biostratigraphic and paleoclimatic significance of *Botrychiopsis* fronds in the Gondwana realm. In: Wong TE (ed) Proceedings of the XVth International Congress on Carboniferous and Permian Stratigraphy, Utrecht, 10–16 August 2003

Klicka J, Zink RM (1997) The importance of recent ice ages in speciation: a failed paradigm. Science 277:1666–1669

Knapp S, Mallet J (2003) Refuting refugia? Science 300:71–72

Köppen W (1930) Die Klimagebiete nach Köppens Klassifikation. In: Knoch K (ed) Klimakunde von Südamerika vol. 2. Handbuch der Klimatologie (ed. by W Köppen, Geiger R), Berlin, part G, pp 242–329

Looy CV, Twitchett RJ, Dilcher DL, Van Konijnenburg-Van Cittert JHA, Visscher H (2001) Life in the end-Permian dead zone. Proc Natl Acad Sci 14:7879–7883

Lowell TV, Heusser CJ, Andersen BG, Moreno PI, Hauser A, Denton GH, Heusser LE, Schluchter C, Marchant D (1995) Interhemispheric correlation of Late Pleistocene Glacial events. Science 269:1541–1549

Luebert F, Pliscoff P (2006) Sinopsis bioclimática y vegetacional de Chile. Editorial Universitaria, Santiago.

Maldonado A, Betancourt JL, Latorre C, Villagrán C (2005) Pollen analyses from a 50 000-yr rodent midden series in the southern Atacama Desert (25 degrees 30’s). J Quat Sci 20:493–507

Massaferro JI, Moreno PI, Denton GH, Vandergoes M, Dieffenbacher-Krall A (2009) Chironomid and pollen evidence for climate fluctuations during the Last Glacial termination in NW Patagonia. Quat Sci Rev 28:517–525

McAllister Rees P, Ziegler AM, Valdes PJ (2000) Jurassic phytogeography and climates: new data and model comparisons. In: Huber BT, Macleod KG, Wing SL, (eds) Warm climates in earth history. Cambridge University Press, Cambridge, pp 297–318

McAllister Rees P, Ziegler AM, Gibbs MT, Kutzbach JE, Behling PJ, Rowley DB (2002) Permian phytogeographic patterns and climate data/model comparisons. J Geol 110:1–31

McElwain JC, Punyasena SW (2007) Mass extinction events and the plant fossil record. Trends Ecol Evol 22:548–557

McLoughlin S (2001) The breakup history of gondwana and its impact on pre-Cenozoic floristic provincialism. Aust J Bot 49:271–300

McLoughlin S, Carpenter RJ, Jordan GJ, Hill RS (2008) Seed ferns survived the end-Cretaceous mass extinction in tasmania. Am J Bot 95:465–471

Milleron M, Gallo LA, Marchelli P (2008) The effect of volcanism and postglacial migration and seed dispersal. A case study in Southern South America. Tree Genet Genomes 4:435–444

Moore DM (1983) Flora of Tierra del Fuego. Missouri Botanical Garden, St. Louis, MO.

Moreno FP (1882) Patagonia, resto de un antiguo continente hoy sumergido. An Soc Cient Argent 14:97–131

Moreno PI (2004) Millennial-scale climate variability in northwest Patagonia over the last 15 000 yr. J Quat Sci 19:35–47

Moreno PI, Jacobson GL, Lowell TV, Denton GH (2001) Interhemispheric climate links revealed by a late-glacial cooling episode in southern Chile. Nature 409:804–808

Nalpas T, Dabard M-P, Ruffet G, Vernon A, Mpodozis C, Loi A, Hérail G (2008) Sedimentation and preservation of the Miocene Atacama Gravels in the Pedernales–Chañaral area, Northern Chile: climatic or tectonic control? Tectonophysics 459:161–173

Nishida M (1984) The anatomy and affinities of the petrified plants from the tertiary of Chile, III. Petrified woods from Mocha Island, Central Chile. In: Nishida M, (ed). Contributions to the Botany in the Andes, I. Academia Scientific Books, Tokyo, pp 98–110

Oberdorfer E (1960) Pflanzensoziologische Studien in Chile. Ein Vergleich mit Europa. Flora Et Vegetatio Mundi 2:1–208

Ochsenius CC (1891) Über Tertiärpflanzen von Chile von H. Engelhardt (Nachtrag). Abh Senckenb Naturforsch Ges 16:1–4

Okuda M, Nishida H, Uemura K, Yabe A (2006) Paleocene/Eocene pollen assemblages from the Ligorio Márquez Formation, Central Patagonia, XI Region, Chile. In: Nishida H, (ed) Post-Cretaceous floristic changes in southern patagonia, chile. Chuo University, Tokyo, pp 37–43

Orme AR (2007) The tectonic framework of South America; tectonism, climate, and landscape change. In: Veblen TT, Young KR, Orme AR, (eds) The physical geography of South America. Oxford University Press, New York, NY, pp 3–44

Palazzesi L, Barreda V (2007) Major vegetation trends in the Tertiary of Patagonia (Argentina): a quatitative paleoclimatic approach based on palynologial evidence. Flora 202:328–337

Pankhurst RJ, Hervé F (2007) Introduction and overview. In: Moreno T, Gibbons W, (eds) The geology of Chile. The Geological Society, London, pp 1–4

Pankhurst RJ, Rapela CW, Fanning CM, Márquez M (2006) Gondwanide continental collision and the origin of Patagonia. Earth Sci Rev 76:235–257

Pastorino MJ, Gallo LA (2002) Quaternary evolutionary history of *Austrocedrus chilensis*, a cypress native to the Andean–Patagonian forest. J Biogeogr 29:1167–1178

Pisano E (1954) Fitogeografía. La vegetación de las distintas zonas geográficas chilenas. Rev Geogr Terra Australis 11:95–107

Prámparo MB, Quattrocchio M, Gandolfo MA, Zamaloa MC, Romero E (2007) Historia evolutiva de las angiospermas (Cretácico-Paleógeno) en Argentina a través de los registros paleoflorísticos. In: Archangelsky S, Sánchez T, Tonni EP (eds) Ameghiniana 50° aniversario, Publicación Especial 11:157–172

Premoli AC, Kitzberger T, Veblen TT (2000) Isozyme variation and recent biogeographical history of the long-lived conifer Fitzroya cupressoides. J Biogeogr 27:251–260

Quattrocchio ME, Martínez MA, Volkheimer W (2007) Las floras jurásicas de la Argentina In: Archangelsky S, Sánchez T, Tonni EP (eds) Ameghiniana 50° aniversario, Publicación Especial 11: 87–100

Quintanilla V (1974) La carta bioclimática de Chile Central. Rev Geogr Valparaíso 5:33–58

Quintanilla V (1983) Biogeografía. Colección Geografía de Chile. Instituto Geográfico Militar (IGM), Santiago.

Ramos VA (2008) Patagonia: a paleozoic continent adrift? J S Am Earth Sci 26:235–251

Ramos VA (2009) Anatomy and global context of the Andes: main geological features and the Andean orogenic cycle. Gsa Memoirs 204:31–65

Ramos VA, Aleman A (2000) Tectonic evolution of the Andes. In: Cordani UJ et al (eds) Tectonic evolution of South America, International Geological Congress, 31st, Rio de Janeiro (2000), pp 635–685

Ranero CR, von Huene R, Weinrebe W, Reichert C (2006) Tectonic processes along the Chile convergent margin. In: Oncken O, Chong G, et al (eds) The Andes: Active Subduction Orogeny. Springer, Berlin, pp 91–121

Rapalini AE (2005) The accretionary history of southern South America from the latest Proterozoic to the Late Palaeozoic: some palaeomagnetic constraints. In: Vaughan APM, Leat PT, Pankhurst RJ, (eds) Terrane processes at the margins of Gondwana, 246. Geological Society, London, Special Publications, pp 305–328

Raymond A, Gensel PG, Stein WE (2006) Phytogeography of Late Silurian macrofloras. Rev Paleobot Palynol 142:165–192

Reiche C (1907) Grundzüge der Pflanzenverbreitung in Chile. In Series: Engler A, Drude O, (eds) Die Vegetation der Erde: Sammlung Pflanzengeographischer Monographien, vol. VIII. Verlag von V. Engelmann, Leipzig.

Rivas-Martínez S, Rivas-Sáenz S (1996–2009) World Bioclimatic Classification System. Phytosociological Research Center, Spain. http://www.globalbioclimatics.org

Romero EJ (1986) Paleogene phytogeography and climatology of South Maerica. Ann Mol Bot 73:449–461

Romero EJ (1993) South American paleofloras. In: Goldblatt P, (ed) Biological relationships between Africa and South America. Yale University Press, New Haven, CT/London, pp 62–85

San Martín J, Donoso C (1996) Estructura florística e impacto antrópico en el bosque maulino de Chile. In: Armesto JJ, Villagrán C, Arroyo MK, (eds) Ecología de los bosques nativos chilenos. Editorial Universitaria, Santiago, pp 153–167

Schmithüsen J (1956) Die räumliche Ordnung der chilenischen Vegetation. Bonn Geogr Abh 17:1–86

Scotese CR, Boucot AJ, McKerrow WS (1999) Gondwanan palaeogeography and palaeoclimatology. J Afr Earth Sci 28:99–114

Simpson BB (1971) Pleistocene changes in the fauna and flora of South America. Science 173:771–780

Stern C, Moreno H, López-Escobar L, Clavero J, Lara LE, Naranjo JA, Parada MA, Skewes MA (2007) Chilean volcanoes. In: Moreno T, Gibson W, (eds) The geology of Chile. The Geological Society, London, pp 147–178

Storey BC (1995) The role of mantle plumes in continental breakup: case histories from Gondwanaland. Nature 377:301–308

Subercaseaux B (1940) Chile o una loca geografía. Ercilla S, (ed). English translation from 1943: Chile, a geographic extravaganza. Macmillan Co., New York, NY

Thiel M, Macaya EC, Acuna E, Arntz WE, Bastias H et al. (2007) The humboldt current system of northern and central Chile. Oceanogr Mar Biol 45:195–344

Torres T, Rallo M (1981) Anatomía de troncos fósiles del Cretácico Superior de Pichasca en el norte de Chile. Anais II Congreso Latinoaméricano Paleontología. Porto Alegre, Brasil 2: 385–398

Tremetsberger K, Stuessy TF, Guo Y-P, Baeza CM, Weiss H, Samuel RM (2003) Amplified Fragment Length Polymorphism (AFLP) variation within and among populations of *Hypochaeris acaulis* (Asteraceae) of andean southern South America. Taxon 52:237–245

Trewartha G (1961) The Earth's problem climates. University of Wisconsin Press, Madison, WI.

Troncoso A, Encinas A (2006) La tafoflora de cerro Centinela (Chile, VI Región): vegetación y clima de Chile central a fines del Mioceno-comienzos del Plioceno. Ameghiniana 43: 171–180

Troncoso A, Romero EJ (1998) Evolución de las comunidades florísticas en el extremo sur de Sudamérica durante el Cenofítico. In: Fortunato R, Bacigalupo N (eds) Proceedings of the Congreso Latinoamericano de Botánica, Monographs in Systematic Botany from the Missouri Botanical Garden 6: 149–172

Troncoso A, San Martín A (1999) Presencia del género *Escallonia* (Magnoliopsida, Escalloniaceae) en el Terciario de Chile Central. Bol Mus Nac Hist Nat (Chile) 48:29–36

Troncoso A, Suarez M, De La Cruz R, Palma-Heldt S (2002) Paleoflora de la Formación Ligorio Márquez (XI Región, Chile) en su localidad tipo: sistemática, edad e implicancias paleoclimáticas. Rev Geol Chile 29:113–135

Truswell EM (1990) Cretaceous and tertiary vegetation of Antarctica: a palynological perspective. In: Taylor TN, Taylor EL, (eds) Antarctic paleobiology: its role in the reconstruction of Gondwana. Springer-Verlag, New York, pp 71–88

Veblen TT, Young KR, Orme AR, (eds) (2007) The physical geography of South America. Oxford University Press, Oxford.

Vega JC, Archangelsky S (1997) The first Gondwana Carboniferous compound cupules and associated seeds. A preliminary note. Rev Palaeobot Palynol 99:55–59

Villagrán C, Le-Quesne C, Aravena JC, Jiménez H, Hinojosa F (1998) El rol de los cambios de clima del Cuaternario en la distribución actual de la vegetación de Chile central-sur. Bamberg Geogr Schr 15:227–242

Villagrán C, León A, Roig FA (2004) Paleodistribución del alerce y ciprés de las Guaitecas durante períodos interestadiales de la Glaciación Llanquihue: provincias de Llanquihue y Chiloé, Región de Los Lagos, Chile. Rev Geol Chile 31: 133–151

Vuille M, Baumgartner MF (1998) Monitoring the regional and temporal variability of winter snowfall in the arid andes using digital NOAA/AVHRR data. Geocarto Int 13:59–67

Weischet W (1970) Chile: seine länderkundliche individualität und struktur. Wissenschaftliche Buchgesellschaft, Darmstast.

Wilf P, Johnson KR, Cúneo NR, Smith ME, Singer BS, Gandolfo MA (2005) Eocene plant diversity at Laguna del Hunco and Río Pichileufú, Patagonia, Argentina. Am Nat 165:634–650

Wilf P, Gandolfo MA, Johnson KR, Cúneo R (2007) Biogeographic significance of the Laguna del Hunco flora, Early Eocene of Patagonia, Argentina. Abstract GSA Denver Annual Meeting (28–31 October 2007)

Willis KJ, McElwain JC (2002) The evolution of plants. Oxford University Press, Oxford.

Willis KJ, Niklas KJ (2004) The role of Quaternary environmental change in plant macroevolution: the exception or the rule? Philos Trans R Soc Lond B 359:159–172

Windhausen A (1931) Geología Argentina. Geología Histórica y Regional del Territorio Argentino, Buenos Aires.

Wnuk C (1996) The development of floristic provinciality during the Middle and Late Paleozoic. Rev Palaeobot Palynol 90:5–40

Zachos J, Pagani M, Sloan L, Thomas E, Billups K (2001) Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292:686–693

Chapter 2
Getting Geobotanical Knowledge

Abstract The history of the discovery of the Chilean plant world can be traced back to the Magallanes voyage around the globe. Since then dozens of naturalists and botanists contributed to build the corpus of the geobotanical knowledge of the country. According to most recent updates, the Chilean flora is composed of 56 orders, 171 families, 837 genera, and about 4,295 species. This includes 4 endemic families, 84 endemic genera, and 1,936 species endemic to the Chilean continental and oceanic territory. Richest families in genera and species numbers are the Asteraceae, the Poaceae, the Fabaceae, and the Solanaceae, while the species-richest genera are *Senecio, Adesmia, Viola*, and *Carex*.

A detailed revision of early collectors, botanists, and naturalists that contributed to the description of the Chilean flora and geobotany was done by Reiche (1907). Newer references to geobotanical works appear in Marticorena's taxonomic and botanical blibliography (Marticorena 1992, 1996). For the current *Flora de Chile*, he also provided an updated revision (Marticorena 1995). Some highlights and principal actors in the discovery of the Chilean plant world are briefly exposed here.

2.1 Romancing the South: The Discovery of a Virgin World

The discovery of the Strait of Magellan by Hernando de Magallanes and his crew (21 October 1520) set the starting point for the European exploration of South America. Magallanes gave the name "Cabo de Las Vírgenes" to the eastern Cape that allowed them to get into the Strait. During the first days of exploration, the observations are about a native wood to make fire of which the smoke smelled well. They refer undoubtedly to the wood of "canelo", *Drimys winteri*. The sailors early noted the properties of canelo's bark and herbs like *Cardamine* and *Apium* against scurvy (Pigafetta 1536). The first notes from sailors refer of course the medicinal, nutritional and wooden properties of the new plants found.

During the long conquest of Chile, many chroniclers referred to the cultivated and natural plants and their properties, such as Gerónimo de Bibar, who accompanied Pedro de Valdivia's enterprise writing his *Crónica y Relación copiosa y verdadera*

A. Moreira-Muñoz, *Plant Geography of Chile*, Plant and Vegetation 5,
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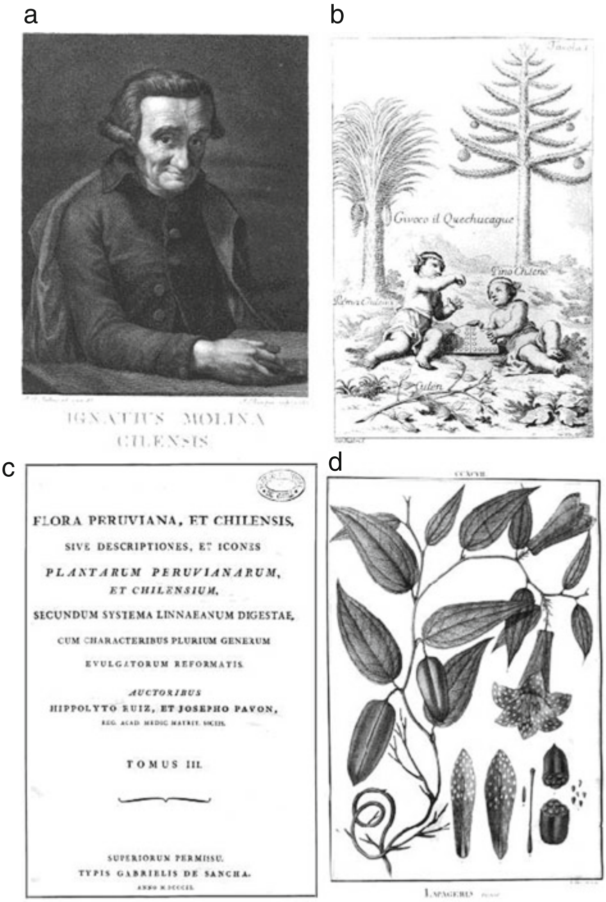


FLORA PERUVIANA, ET CHILENSIS,
SIVE DESCRIPTIONES, ET ICONES
PLANTARUM PERUVIANARUM,
ET CHILENSIUM,
SECUNDUM SYSTEMA LINNAEANUM DIGESTAE,
CUM CHARACTERIBUS PLURIUM GENERUM
EVULGATORUM REFORMATIS

AUCTORIBUS
HIPPOLYTO RUIZ, ET JOSEPHO PAVON,
REG. ACAD. MEDIC. MATRIT. SOCIIS.

TOMUS III.

SUPERIORUM PERMISSU.
TYPIS GABRIELIS DE SANCHA.
ANNO M.DCCCII.

Fig. 2.1 **a** Juan Ignacio Molina; **b** illustration in Molina's work: mapuche kids and native plants: "araucaria" (*Araucaria araucana*), "palma" (*Jubaea chilensis*), and "culén" (*Otholobium glandulosum*); **c** cover of *Flora Peruviana et Chilensis* from Ruiz and Pavón; **d** *Lapageria rosea* in Ruiz and Pavón's work

del Reyno de Chile between 1539 and 1558 (Muñoz-Schick 1975). During the seventeenth century, important advances in the description of the territory and their plant world were made by Jesuits such as Alonso de Ovalle in his *Histórica Relación del Reyno de Chile*, or Diego de Rosales in his *Historia General del Reino de Chile, Flandes Indiano*. This tradition continued with the Jesuit Juan Ignacio Molina (1737–1829) who is considered the first Chilean naturalist (Fig. 2.1a). After the expulsion of the Jesuit Company from America (1768), Molina published in Italy his *Compendio della storia geografica, naturale, e civile del Regno del Chile* (Molina 1776). This and later works (Molina 1782, 1810) were for a long time the main sources of knowledge on natural sciences of Chile.

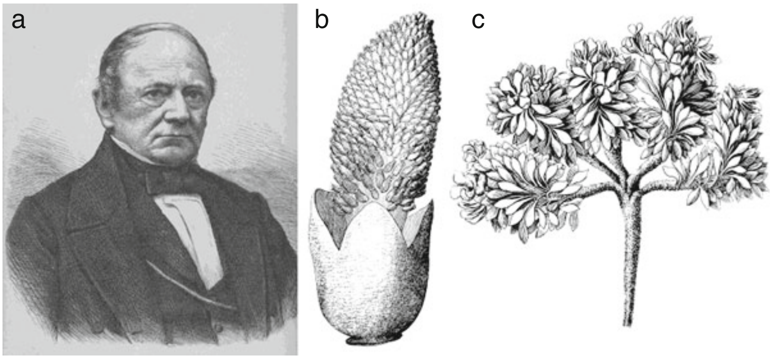


Fig. 2.2 **a** Eduard Poeppig; **b** *Ombrophytum subterraneum*; **c** *Viola cotyledon* from Poeppig and Endlicher (1835–1845)

Towards the end of the eighteenth century, and with the purpose of extending the collections of the Real Botanical Garden of Madrid, King Carlos III of Spain sent several naturalist expeditions to different countries; Peru and Chile were assigned to Hipólito Ruiz and José Pavón. They made collections at some localities between Talcahuano and Santiago between 1782 and 1783. Their work *Flora Peruviana et Chilensis* was published in 3 volumes and contains more than 300 illustrations, including the copihue, *Lapageria rosea*, that was later declared as the national flower (Fig. 2.1c, d).

In 1827 the German naturalist Eduard Poeppig arrived in Chile (Fig. 2.2). He explored the country for two years and it was the first time that a foreign naturalist stayed in Chile for a long period. He also visited other countries of South America, and his work of 3 volumes and 300 illustrations included for the first time colour paintings (Poeppig and Endlicher 1835–1845). During the night of 9th to 10th of January 1827 Poeppig for the first time crossed the equator aboard the ship *Gulnare*: "The day we left the northern hemisphere was one of the most important in my long life of travel... I had the feeling of entering into a new world and also into a new life..." (after Morawetz and Röser 1998).

The English naturalist Joseph Dalton Hooker (1817–1911) accompanied the expedition to the South Pole of John Clark Ross (1839–1843). He was the first who collected intensively in the southern lands: Kerguelen Islands, Tasmania, New Zealand, Falkland (Malvinas) Islands, and Tierra del Fuego. He rapidly noticed the close floristic relationships between these territories. His *Botany of the Antarctic Voyage* was published in three volumes between 1844 and 1859 (Fig. 9.1)

Charles Darwin (1809–1882) travelled around the globe aboard the Beagle from 1832 to 1836. He stayed in Chile from 1834 to 1835 and collected almost 1,500 plant specimens from Argentina, Falkland (Malvinas) Islands and Chile that were later studied by W.J. Hooker, G.A.W. Arnott and J.D. Hooker. It is widely believed that his visit to the southern territories and his impressions about the southern biota and geology were fundamental for his later writings on the theory of evolution (Box 2.1).

Box 2.1 Darwin's Impressions from Central Chile

"We spent the day on the summit, and I never enjoyed one more thoroughly. Chile, bounded by the Andes and the Pacific, was seen as in a map. The pleasure from the scenery, in itself beautiful, was heightened by the many reflections which arose from the mere view of the grand range, with its lesser parallel ones, and of the broad valley of Quillota directly intersecting the latter. Who can avoid admiring the wonderful force which has upheaved these mountains, and even more so the countless ages which it must have required, to have broken through, removed, and leveled whole masses of them?" Darwin (1839), from his diary while climbing the Cerro La Campana in Central Chile (33°S) (Fig. 2.3).

Homenaje a Carlos Darwin
"PASAMOS EL DIA EN LA CIMA DEL MONTE, Y NUNCA ME HA PARECIDO EL TIEMPO MAS CORTO; CHILE SE EXTIENDE A NUESTROS PIES COMO UN PANORAMA INMENSO LIMITADO POR LOS ANDES Y EL OCEANO PACIFICO."
Carlos Darwin
("Mi viaje alrededor del mundo")
17 de Agosto de 1834
La Sociedad Científica de Valparaíso,
la Colonia Británica y
sus admiradores.
17-8-1935.

Fig. 2.3 Memorial tablet dedicated to Ch. Darwin, approaching the top of Cerro La Campana

After its Independence from the Spanish dominion in 1810, the young Republic of Chile had to better know its natural resources. The French professor of natural sciences, Claudio Gay (1800–1873), already living in Chile, was contracted by the government to do the first intensive scientific exploration of the territory (Fig. 2.4). He intensively travelled between Copiapó and Chiloé (1830–1842) (Muñoz Pizarro 1944). Afterwards he published his masterpiece *Historia Física y Política de Chile*, which consists of 28 volumes (8 on botany) and 2 illustration atlases (one cultural

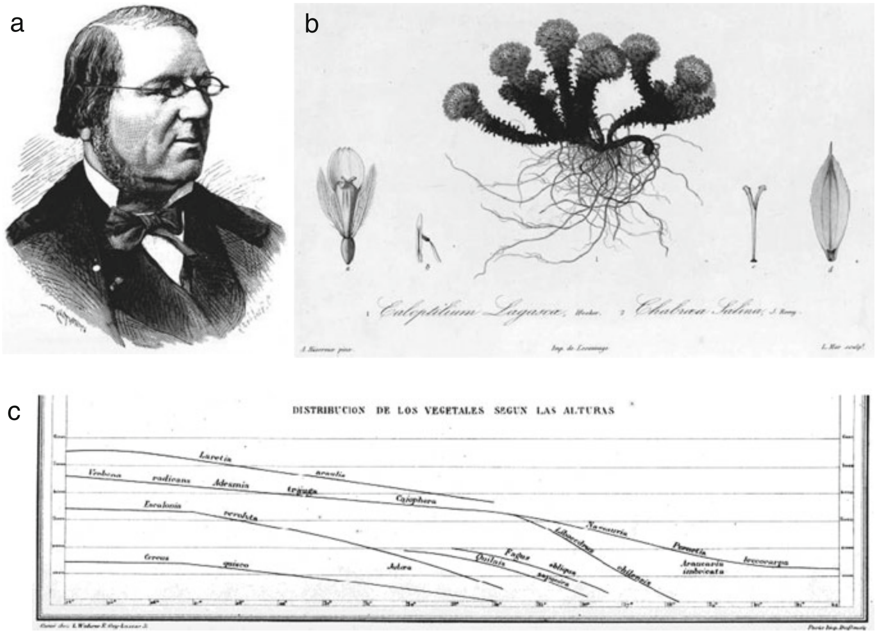
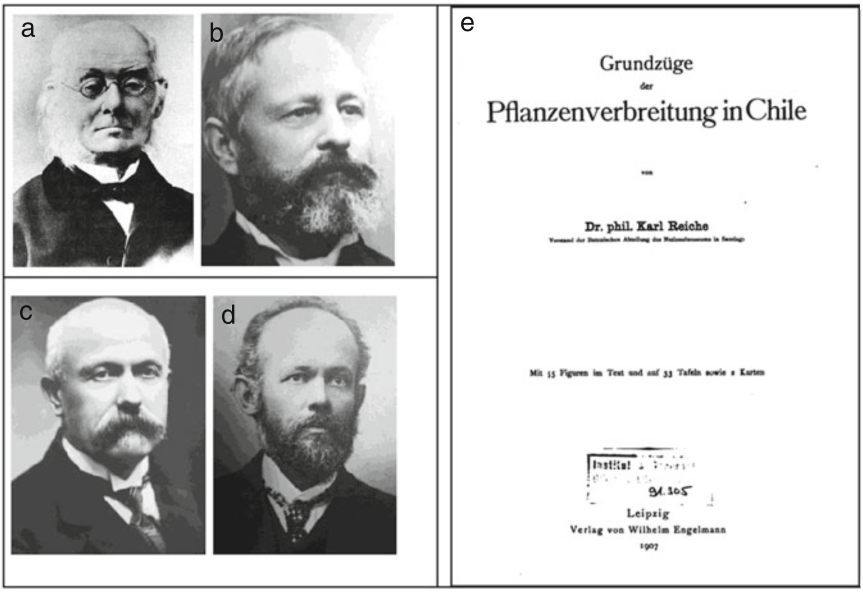


Fig. 2.4 **a** Claudio Gay; **b** illustration of *Nassauvia lagascae* in Gay's Atlas; **c** species altitudinal limits from Pissis (1875) (www.memoriachilena.cl)

and one physical) (Gay 1845–1854, reprint 2010). This was a work without precedents in America to that date. The mission that the Government of Chile had trusted on him also included the formation of a Cabinet of Natural Sciences. That became the basis of the Museo Nacional de Historia Natural (Box 2.2). Before Gay, the flora of Chile was almost unknown, consisting of only ca 300 species; Gay's compilation numbered 3,767 species. More than 600 were described by himself and his collaborators.

The *Historia Física*... of Gay, including both illustrated Atlases, is one of the most important milestones in the development of Chilean natural history. Naturalists coming after him could count on this truly basal study, and it allowed them to rapidly develop many research fields: botany and zoology by R.A. Philippi, geology by I. Domeyko, geography by A. Pissis. It is worth mentioning that these advances were not only basic for the scientific development in Chile, but also were fundamental for the consolidation of the Republic (Saldivia Maldonado 2003). Moreover, according to Stuardo and Feliú (1973, p 318), Gay's writings on Chilean plant geography were the first American advances in the field after the milestone of Alexander von Humboldt and Aimé Bonpland *Essai sur la Géographie des Plantes* of 1805 (Chap. 4). The first representation of altitudinal and latitudinal limits of several plants is the profile accompanying the Geographical Atlas from Pissis (1875) (Fig. 2.4c).



Grundzüge
der
Pflanzenverbreitung in Chile
von
Dr. phil. Karl Reiche

Mit 55 Figuren im Text und auf 33 Tafeln sowie 2 Karten

91.105
Leipzig
Verlag von Wilhelm Engelmann
1907

Fig. 2.5 **a** Rodulfo Amando Philippi; **b** Federico Philippi; **c** Federico Johow; **d** Carlos Reiche; **e** cover of *Gründzuge der Pflanzenverbreitung in Chile*

Rudolf Amandus Philippi (1808–1904) (Fig. 2.5a) arrived in Chile in 1851 with a recommendation from A. von Humboldt to the epoch's government. He rapidly began exploring the territory making discoveries and descriptions in botany, zoology, geology, paleontology, and ethnology. He gave a large impulse to the Museo Nacional de Historia Natural, getting the palace that harbours till today the main natural history collections of Chile (Box 2.2).

RA Philippi got the collaboration of his son Federico Philippi (1838–1910) (Fig. 2.5b), exploring vast regions in Chile and the *Norte Grande*, territories just annexed to Chile (Taylor and Muñoz-Schick 1994). RA Philippi's (1860) description of the botanical exploration of the Atacama is a vivid document of the practical issues to solve at those early stages of botanical development. RA Philippi described more than 3,750 plant species! and is recognized as the main naturalist in the history of Chilean science (Castro et al. 2006). The Museum conserves 90% of Philippi's type exemplars.

Federico Johow (1859–1933) (Fig. 2.5c) arrived in Chile in 1889 to teach natural sciences at the Instituto Pedagógico, Instituto Nacional and at the Universidad de Chile. He is the author of the milestone *Estudios sobre la flora de las Islas de Juan Fernández*, still an obligate reference for the islands (Johow 1896) (Chap. 5).

Carlos Reiche (1860–1929) (Fig. 2.5d), a German professor of natural sciences, was appointed at the botanical section of the Museo Nacional de Historia Natural in 1897 by Federico Philippi, when the last took the direction of the Museo. Reiche published the second *Flora de Chile* (after Gay) in 6 volumes (Reiche 1894–1911).

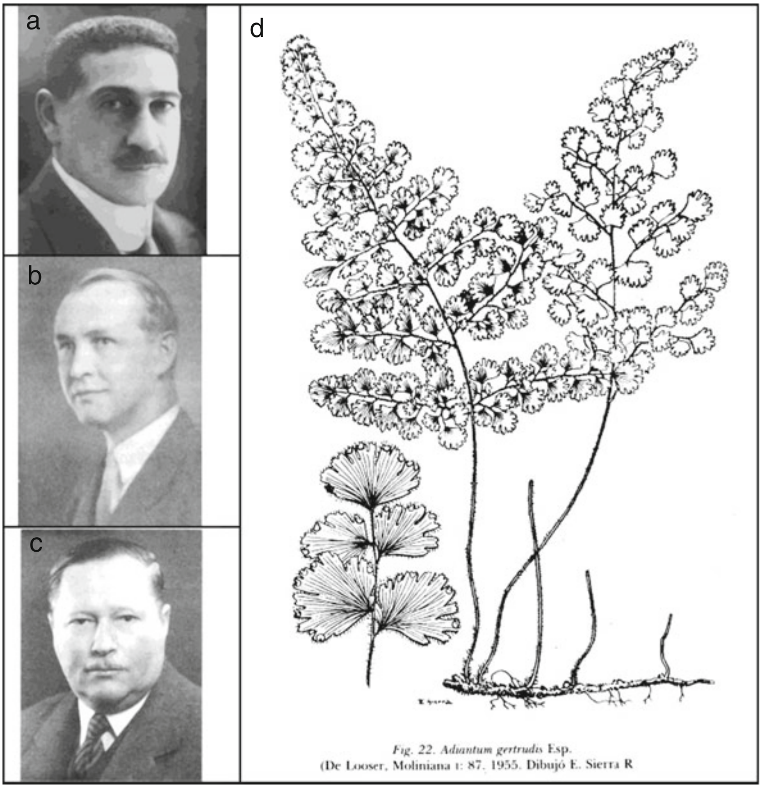


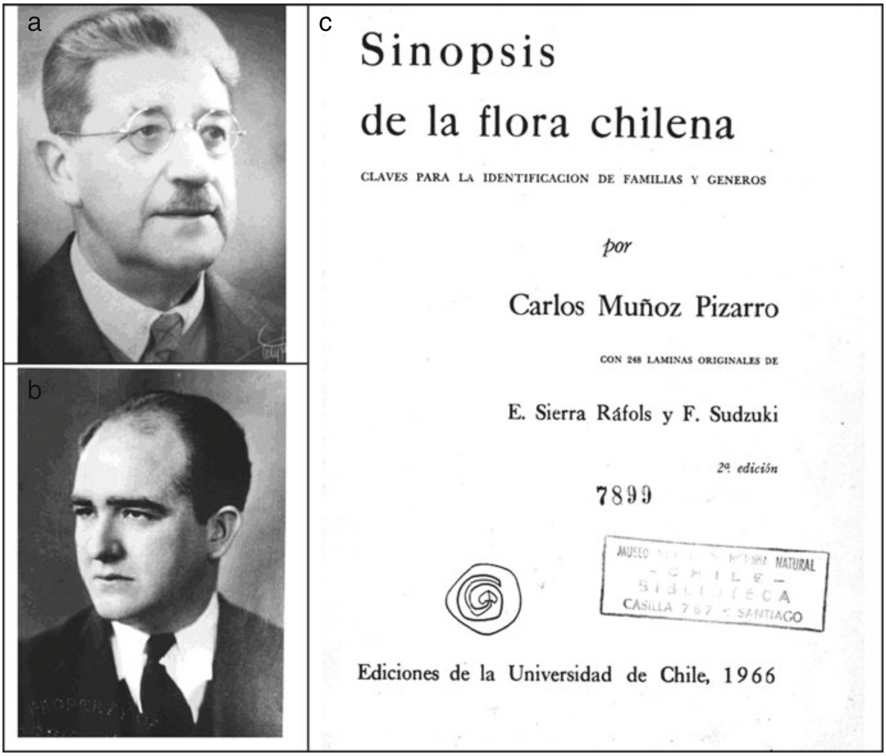
Fig. 2.6 **a** Francisco Fuentes; **b** Ivan Murray Johnston; **c** Gualterio Looser; **d** *Adiantum gertrudis* illustrated by E. Sierra for Looser's publications

He also explored intensively the Chilean territory and published the first plant geography of Chile: *Gründzuge der Pflanzenverbreitung in Chile* in 1907 (Fig. 2.5e).

Francisco Fuentes (1879–1934) (Fig. 2.6a) was in charge of the National Herbarium in 1911, as Carlos Reiche left the country accepting an appointment in Mexico. Fuentes made the first study on plants of Easter Island (Fuentes 1913) (Chap. 5) and on Monocots that had not been treated in Reiche's Flora.

Ivan Murray Johnston (1898–1960) (Fig. 2.6b), prominent US botanist, studied the coastal desert flora and vegetation. His papers *The coastal flora of the departments of Chañaral and Taltal*, and *The flora of the Nitrate Coast* (1929a, b), are considered classical studies of the northern Chilean coast, where vegetation is rather sparse but the flora is one of the most interesting at all.

Gualterio Looser (1898–1982) (Fig. 2.6c), showed a wide interest in the natural sciences, having been appointed as chief of Anthropology at the National Museum. After a journey to Juan Fernández in 1925 he demonstrated more interest in botany, publishing till 1971 about 140 works mostly dedicated to ferns. He became the national authority in this field. He also made big efforts in the translation into



Sinopsis
de la flora chilena
CLAVES PARA LA IDENTIFICACION DE FAMILIAS Y GENEROS

por

Carlos Muñoz Pizarro

CON 248 LAMINAS ORIGINALES DE

E. Sierra Ráfols y F. Sudzuki

2ª edición

7899

Ediciones de la Universidad de Chile, 1966

Fig. 2.7 **a** Carl Skottsberg; **b** Carlos Muñoz Pizarro; **c** cover of *Sinopsis de la Flora Chilena*

Spanish of main texts from C. Reiche and C. Skottsberg, including Reiche's *Plant Geography*, translated into Spanish as *Geografía Botánica de Chile* (1934–1937, reprint 2010).

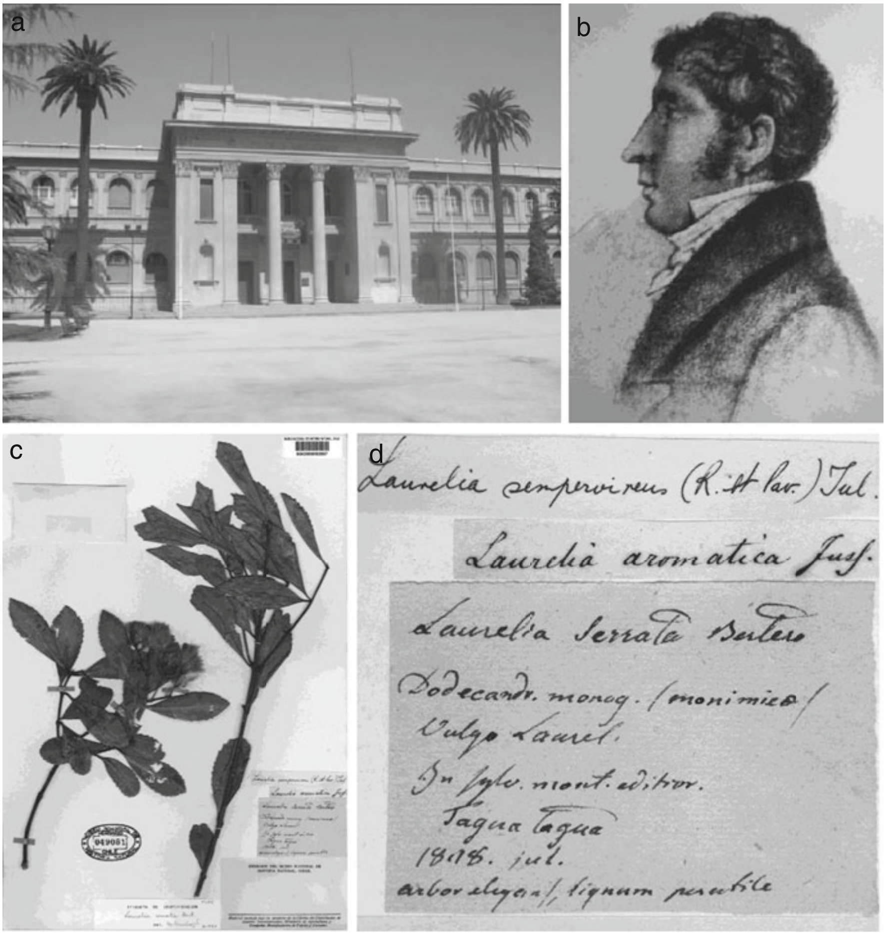
Carl Skottsberg (1880–1963) (Fig. 2.7a), Swedish botanical eminence, president of the 7th International Botanical Congress in 1950, came first with the Swedish expedition to the South Pole, between 1901 and 1903 and afterwards several times explored Patagonia and the Pacific islands. He published about 128 articles and several books about Chilean botany and plant geography. His *Vegetations-verhältnisse längs der Cordillera de los Andes südlich von 41 Grad…* (1916) and his *Natural History of Juan Fernandez and Easter Island* (1920–1956) are till today the most complete works that treat these territories (see Chaps. 4 and 5).

Carlos Muñoz Pizarro (1913–1976) (Fig. 2.7b) was a student of Francisco Fuentes. After a Guggenheim scholarship in the USA, under the direction of IM Johnston, he became in charge of the Botanical Section at the Museo Nacional de Historia Natural in 1942. He initiated a program of organization of the collections: around 30,700 specimens were revised, catalogued and organized. In 1961, with a grant from the Rockefeller Foundation, Muñoz Pizarro explored, together with his wife Ruth Schick, the principal European herbaria, carrying out the photographic registry of the type collections of Chilean plants. The acquired knowledge allowed him to publish several important books: *Sinopsis de la Flora Chilena* (1959, 2nd ed. 1966) (Fig. 2.7c), the principal synthetical work on the Chilean flora still in use; *Flores Silvestres de Chile* (1966); *Chile: Plantas en extinción* (1973) (see Sect. 6.1).

To this brief revision of the most prominent "Chilean" botanists we should add Edmundo Pisano (1919–1997), one of the most prolific plant researchers of Patagonia and Magallanes, and Otto Zöllner (1909–2007), indefatigable collector, professor and connoisseur of the plants of Central Chile. Finally, we should not forget to mention the national and international collaborators to the current *Flora de Chile*, a continuing work in progress directed by the Universidad de Concepción (Marticorena and Rodríguez 1995 onwards). This University contains one of the most important Herbarium in Chile (CONC) with 175.000 specimens, initiated by A. Pfister and continued by M. Ricardi, C. Marticorena and R. Rodríguez. Chilean botanists recently collaborated in the great effort that represented the compilation of the *Catálogo de las Plantas Vasculares del Cono Sur*, an up to date checklist encompassing Argentina, Chile, Paraguay, Uruguay, and southern Brazil (Zuloaga et al. 2008) (Sect. 2.2).

Box 2.2 The National Herbarium (SGO)

The National Herbarium (SGO in the international code) is strongly related to the discovery and description of the Chilean plants (Muñoz-Schick 1991). Is it located in Santiago in the Museo Nacional de Historia Natural (Fig. 2.8). The National Herbarium has increased its collections under the curatorship of Mélica Muñoz-Schick, daughter of C. Muñoz Pizarro. Today it contains almost 81,000 specimens which are a sample of the entire vascular plant diversity of the country. Bryophytes, Fungi and Algae are also well represented in the Herbarium. The museum holds also a palaeobotanical collection. Museums and Herbaria have funding problems everywhere, but their role in systematic biology and nowadays in conservation is increasingly being recognized (e.g. Graham et al. 2004; Wake et al. 2009). Together with a constant increase of collections, the daily work in the Herbarium comprises organization, identification, digitizing and georeferencing of the specimens. In accordance with the global trend, digitalization of the specimens is actually on its way. This considers the scanning of more than 4,000 type specimens, including the first collections of Carlo G. Bertero from 1828. These are the first steps towards a Virtual Herbarium (Muñoz-Schick and Moreira-Muñoz 2008), a challenge taken up by many countries worldwide (Wang and Qin 2008).



Laurelia sempervirens (R. et Pav.) Tul.
Laurelia aromatica Juss.
Laurelia serrata Bertero
Dodecandr. monog. (monimiea)
Vulgo Laurel.
In sylv. mont. editior.
Tagua Tagua
1828. jul.
arbor elegans, lignum perutile

Fig. 2.8 **a** View of the old palace containing the Museo Nacional de Historia Natural since R.A. Philippi's directorship; **b** early collector C.G. Bertero; **c** type Specimen from *Laurelia sempervirens*, collected by C.G. Bertero in the year 1828

2.2 Classification and Phylogeny of the Chilean Vascular Flora

While preparing the new *Flora de Chile,* Reiche's account on the Chilean Flora comprised 141 families and 716 genera (Reiche 1907). The previous account by F Philippi numbered a total of 863 genera (Philippi 1881) (Table 2.1). Muñoz Pizarro (1959) in his *Sinopsis de la Flora Chilena* gave a number of 182 families and 960 native genera, and Marticorena's (1990) checklist comprised 175 families and 827 genera (Table 2.1).

For his *Flora de Chile*, Reiche (1894–1911) followed Engler and Prantl's classification system. For his *Sinopsis*, Muñoz Pizarro (1959) followed Christensen

Table 2.1 Historical numbers for the Chilean native vascular plants

	Orders	Families	Genera
F. Philippi (1881)	–	–	863
Reiche (1907)	–	141	716
Muñoz Pizarro (1966)	91	182	960[a]
Marticorena (1990)	–	175	827

[a] Including many naturalized taxa.

(1934) for the Pteridophyta, Engler and Diels (1936) for the Gymnosperms, and Hutchinson (1926, 1934) for the Angiosperms. Marticorena and Quezada (1985), and Marticorena (1990) presented their checklists in alphabetic order following the criteria of several authors, like Cronquist (1981). The permanent revision of taxa under the current cladistic paradigm leads to drastic changes in the traditional classification of ferns and fern allies (Smith et al. 2006; Pryer and Schuettpelz 2009) and angiosperms (APGII 2003, APGIII 2009; Stevens 2001 onwards). Gymnosperms are more constant in their classification, although relationships between main groups are not resolved (Renner 2009).

According to these modern classification schemes, a comprehensive and updated checklist of the Chilean flora is presented here. The basis for this account has been the Southern Cone Checklist (Zuloaga et al. 2008), which has been revised and updated according to Hassler and Swale (2002), Pryer et al. (2004) and Smith et al. (2006) for the ferns and fern allies; and according to APGIII (2009) for the angiosperms. Families' classification differs slightly from APGIII (2009), considering the opinion of several experts. The resulting checklist is presented as Appendix, including accepted genera and their global distribution, latitudinal range in Chile, and the number of native and endemic species (not including infraspecific taxa). According to this revision, the extant Chilean vascular native flora consists of *56* orders, *171* families, *837* genera, and about *4,295* species. Among the latter, ca. *1,936* species (45%) are endemic to the Chilean territory (continental or oceanic). Numbers for traditional groups are presented in Table 2.2.

Table 2.2 Summary of Chilean vascular plants (updated January 2010)

	Orders	Families	Genera	Native species	Endemic species
Ferns and fern allies	11	22	52	146	38
Gymnosperms	2	4	9	16	3
Monocots	6	28	176	906	330
Dicots	37	117	600	3,227	1,565
Total	56	171	837	4,295	1,936

This account includes the offshore oceanic flora. Pacific genera not represented on the continent, many of them endemic to the islands, plus two endemic families (in bold), are listed in Table 2.3 (see Chap. 5).

Table 2.3 Genera not found in continental Chile

		Genera (family)
Juan Fernández Islands	ferns and fern allies	*Dicksonia* (Dicksoniaceae)[a] *Thyrsopteris* (**Thyrsopteridaceae**)[a] *Arthropteris* (Tectarinaceae)[a]
	Gymnosperms	–
	Monocots	*Juania* (Arecaceae) *Machaerina* (Cyperaceae) *Megalachne* (Poaceae) *Podophorus* (Poaceae)
	Dicots	*Centaurodendron* (Asteraceae) *Dendroseris* (Asteraceae) *Robinsonia* (Asteraceae) *Yunquea* (Asteraceae) *Selkirkia* (Boraginaceae) *Haloragis* (Haloragaceae) *Cuminia* (Lamiaceae) *Lactoris* (**Lactoridaceae**)[a] *Zanthoxylum* = *Fagara* (Rutaceae) *Coprosma* (Rubiaceae) *x Margyracaena* (Rosaceae) *Santalum* (Santalaceae) (1 *extinct species*) *Boehmeria* (Urticaceae)
Desventuradas Islands	Ferns and fern allies	–
	Gymnosperms	–
	Monocots	–
	Dicots	*Lycapsus* (Asteraceae) *Thamnoseris* (Asteraceae) *Nesocaryum* (Boraginaceae) *Sanctambrosia* (Caryophyllaceae)
Isla de Pascua	Ferns and fern allies	*Davallia* (Davalliaceae)[a] *Microlepia* (Dennstaedtiaceae) *Diplazium* (Woodsiaceae) *Dryopteris* (Dryopteridaceae) *Microsorum* (Polypodiaceae) *Psilotum* (Psilotaceae)[a] *Vittaria* (Pteridaceae) *Doodia* (Blechnaceae)
	Gymnosperms	–
	Monocots	*Kyllinga* (Cyperaceae) *Pycreus* (Cyperaceae) *Axonopus* (Poaceae) *Stipa* (Poaceae)
	Dicots	*Triumfetta* (Malvaceae) *Ipomoea* (Convolvulaceae)

[a] Families absent from continental Chile.

2.2.1 Rich Families and Genera

As in many floras (e.g. Flora of Ecuador, see Table 2.8), most families and genera are represented by a few species: 41 families (24%) are represented by only one species and 80 families (47%) contain 14 or fewer species. Fifty families (29%) have 15 or more species (Fig. 2.9a). The reduced number of species is most marked at the genus level: most genera (381) are represented by only one species (46%), and almost the same percentage of genera contains 14 or fewer species (389 genera, 46%). Only 67 genera (8%) have 15 or more species (Fig. 2.9b).

The Asteraceae, usually the largest family in floras of arid or semi-arid regions (Goldblatt and Manning 2000), is also the most species- and generic-rich family in the Chilean flora (Table 2.4) (Chap. 8) (Fig. 8.1). The second largest family is

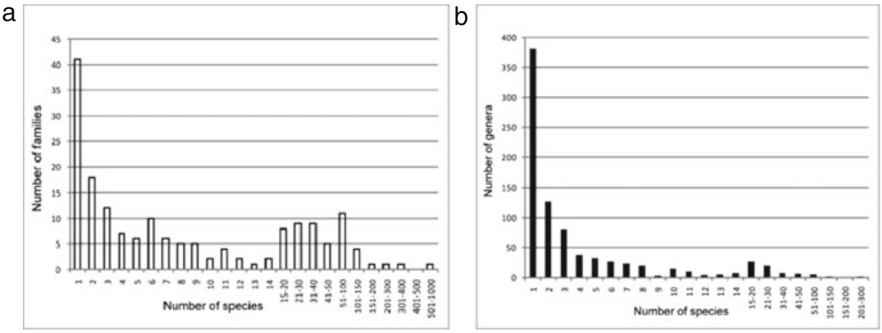


Fig. 2.9 **a** Number of families (*white bars*) versus the number of species; **b** number of genera (*black bars*) versus the number of species

Table 2.4 Ranking of the 20 largest families in the Chilean flora by size

Family	Native species	Endemic species
Asteraceae	838	374
Poaceae	380	73
Fabaceae	280	152
Solanaceae	169	87
Cyperaceae	150	32
Brassicaceae	145	66
Cactaceae	112	88
Boraginaceae	103	64
Apiaceae	99	42
Malvaceae	75	37
Violaceae	73	50
Caryophyllaceae	72	32
Calceolariaceae	63	45
Verbenaceae	60	18
Orchidaceae	56	32
Portulacaceae	55	22
Amaranthaceae	54	23
Oxalidaceae	53	26
Veronicaceae	53	13
Loasaceae	46	22

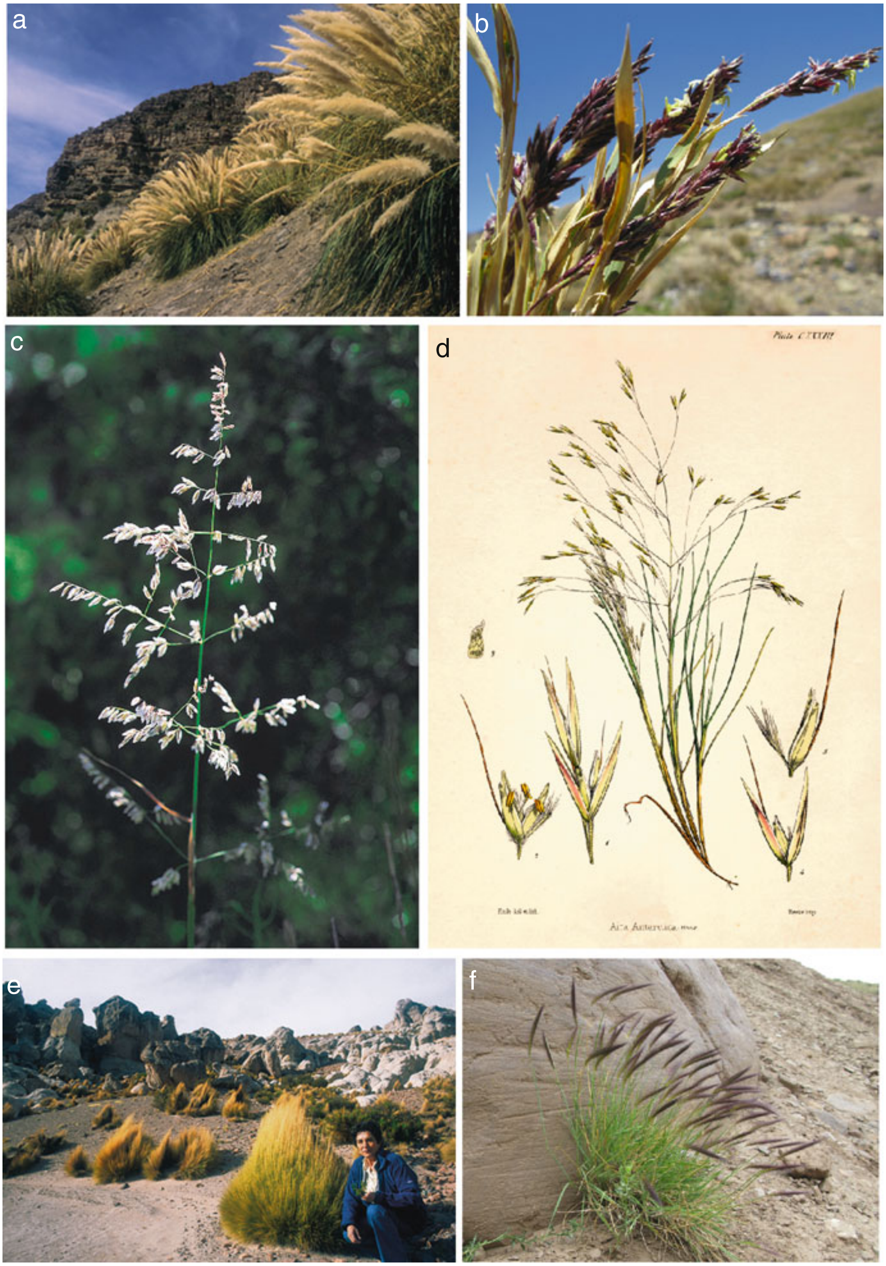


Fig. 2.10 Genus-rich families, representative species of the Poaceae: **a** *Cortaderia atacamensis*, Chusmiza; **b** *Chusquea cumingii*, Lircay; **c** *Melica argentata*, Cerro La Campana; **d** *Deschampsia antarctica*; **e** *Festuca ortophylla* and Mélica Muñoz-Schick, Colchane; **f** *Hordeum comosum*, Juncal (photo/illustration credits: **a**–**c**, **e** A. Moreira-Muñoz; **d** plate 133 in J.D. Hooker (1847))

Fig. 2.11 Genus-rich families, representative species of the Fabaceae: **a** *Balsamocarpon brevifolium*, Cuesta Pajonales; **b** *Anarthrophyllum cumingii*, Laguna Negra; **c** *Astragalus cruckshanksii*, Portillo; **d** *Adesmia argentea*, southern Atacama; **e** *Geoffroea decorticans,* Cuesta Pajonales (photo credits: **a**, **b**, **d**, **e** A. Moreira-Muñoz; **c** Sergio Moreira)

the Poaceae, as can be expected from the global richness of the family (Fig. 2.10). Fabaceae, Solanaceae, Cyperaceae, and Brassicaceae follow in size (Figs. 2.11, 2.12).

The species-richest genera are *Senecio, Adesmia, Viola*, *Carex, Calceolaria, Haplopappus* (Table 2.5). Some of these genera are cosmopolitan species-rich

Fig. 2.12 Genus-rich families, representative species of the Solanaceae: **a** *Schizanthus hookeri*, Portillo; **b** *Lycium chilense*, Concón; **c** *Salpiglossis sinuata*, Rio Clarillo; **d** *Nolana coelestis*; Cuesta Buenos Aires (photo credits: **a**, **c**, **d** A. Moreira-Muñoz; **b** S. Elórtegui Francioli)

genera (e.g. *Senecio, Carex, Viola*), while others are strictly neotropical genera (e.g *Haploppapus, Calceolaria*). *Adesmia* is a notable case, being the species-richest genus restricted to the southern Andes of Chile/Argentina (with little representation in Perú and southern Amazonas). *Senecio* and *Adesmia* are also ahead in endemic species numbers.

Table 2.5 Ranking of the 20 largest genera in the Chilean flora

Genus	Family	Species	Endemic species
Senecio	Asteraceae	224	103
Adesmia	Fabaceae	130	85
Viola	Violaceae	72	50
Carex	Cyperaceae	67	16
Calceolaria	Calceolariaceae	60	42
Haplopappus	Asteraceae	54	42
Oxalis	Oxalidaceae	53	26
Astragalus	Fabaceae	49	23
Nolana	Solanaceae	44	40
Solanum	Solanaceae	44	19
Valeriana	Valerianaceae	44	21
Poa	Poaceae	42	7
Leucheria	Asteraceae	42	16
Baccharis	Asteraceae	40	11
Cryptantha	Boraginaceae	40	31
Chaetanthera	Asteraceae	38	16
Dioscorea	Dioscoreaceae	36	34
Alstroemeria	Alstroemeriaceae	33	26
Chloraea	Orchidaceae	32	18
Loasa	Loasaceae	31	18

2.2.2 Endemic Families

The Chilean flora comprises four endemic families: Gomortegaceae, Francoaceae (Fig. 2.13), Thyrsopteridaceae and Lactoridaceae, the latter two endemic to Juan Fernández (Table 2.6) (Chap. 5). The flora also contains several subendemic families, restricted to Chile and adjacent territories in Argentina and/or Peru: Aextoxicaceae, Quillajaceae, Misodendraceae, Philesiaceae, and Malesherbiaceae (Table 2.7); and one subendemic family restricted to Chile and Australia: Berberidopsidaceae. The Chilean flora harbours 84 endemic genera, which are discussed in Sect. 3.1.

The high level of endemism at the family and genus level is remarkably, even resting the Francoaceae (Table 2.6). As a comparison, Argentina harbours one endemic family (Halophytaceae) and 45 endemic genera (Zuloaga et al. 1999). The flora of Perú, composed of more than 17,000 species, and around 2,400 native genera, has 51 endemic genera but none endemic family (Brako and Zarucchi 1993, not considering ferns). The flora of Ecuador (2,110 native genera, and around 15,300 species), has 23 endemic genera and also none endemic family (Jørgensen and León-Yáñez 1999) (Table 2.8). Other distant territories worth of interest due to their biogeographical relationships are New Zealand and the Cape Floristic Region, which contain respectively 48 and 160 endemic genera (Table 2.8). Compared to all

Table 2.6 Endemic families of the Chilean flora[a]

Family	Genera	N° species
Gomortegaceae	*Gomortega*	1
Francoaceae[a]	*Francoa, Tetilla*	2
Lactoridaceae	*Lactoris*	1 (Juan Fernández)
Thyrsopteridaceae	*Thyrsopteris*	1 (Juan Fernández)

[a] Francoaceae has been alternatively included in Melianthaceae (APGIII 2009).

Table 2.7 Subendemic families of the Chilean flora

Family	Genera	N° species	N° species Chile	Distribution
Aextoxicaceae	*Aextoxicon*	1	1	Chile/Argentina
Philesiaceae	*Lapageria*	1	1	Chile/Argentina
	Philesia	1	1	
Misodendraceae	*Misodendrum*	8	8	Chile/Argentina
Quillajaceae	*Quillaja*	2	1	Chile/Arg/Brazil/Uruguay
Malesherbiaceae[a]	*Malesherbia*	24	18	Chile/Perú/Argentina
Berberidopsidaceae	*Berberidopsis*	2	1	Chile/E Australia

[a] Alternatively considered in the Passifloraceae by APG III (2009).

Table 2.8 Generic and familiar endemism in several vascular floras

Country	N° native families	Endemic families	N° native genera	Endemic genera	Native species	Endemic species	Sources
Chile	171	4	837	84	4,293	1,933	Updated here from Zuloaga et al. (2008)
Argentina	~ 250	1	900	45	~ 9,000	1,760	Zuloaga et al. (1999) and (2008))
Perú	~ 200	0	2,400	51	~ 15,000	5,354	Brako and Zarucchi (1993) (not considering ferns)
Ecuador	254	0	2,110	23	15,306	4,173	Jørgensen and León-Yáñez (1999)
New Zealand	90	0	446	49	1,936	1,591	Wilton and Breitwieser (2000) and De Lange et al. (2006)
Cape Floristic Region	178	5	994	160	9,000	6,210	Goldblatt and Manning (2000)

Note: This comparison must be taken as illustrative but not definitive, since each of these floras follows its own classification system.

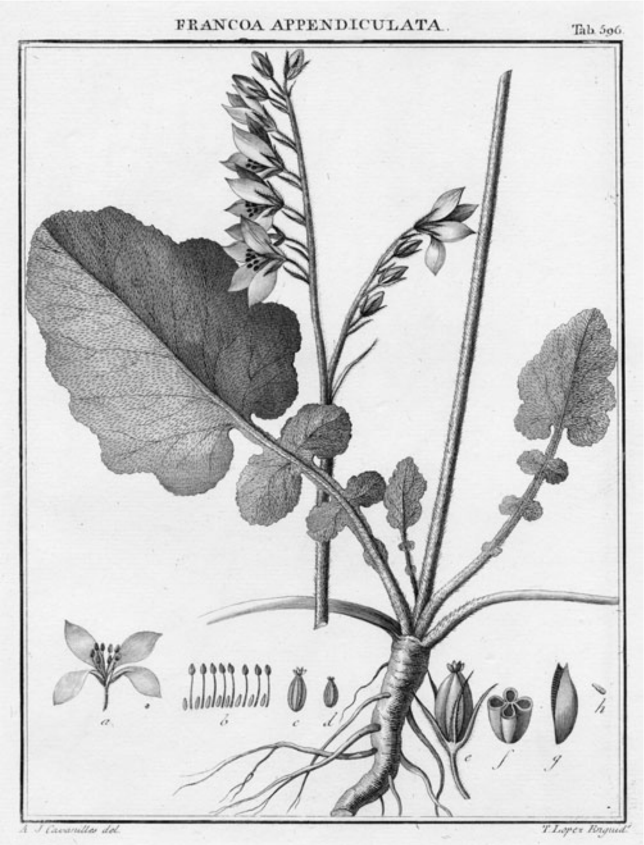


Fig. 2.13 *Francoa appendiculata*, illustrated in Cavanilles (1801)

these territories, the Chilean flora has a remarkable floristic identity, not equalling the overwhelming Cape flora, but surpassing most species-rich South American countries as regards endemism at genus and family levels.

2.2.3 Phylogenetic Groups

The systematic arrangement of the plant world has seen a dramatic improvement during the last decade, under the current paradigm of cladistics. The monophyly of the land plants is nowadays well supported by morphological and molecular characters (Magallón and Hilu 2009) (Fig. 2.15). Living land plants have been placed in four major clades: antocerophytes (hornworts, ca. 100 species), bryophytes (mosses, ca. 13,000 species), marchantiophytes (liverworts; 5,000–8,000 species), and tracheophytes (vascular plants: ca. 285,000 species) (Magallón and Hilu 2009) (Fig. 2.15).

Vascular plant evolution has been viewed traditionally as “a successive series of incremental increases in complexity, from simple bryophytic ancestors through vascularized spore producers, more complex seed plants, and ultimately to angiosperms” (Pryer et al. 2004, p 1582) (Box 2.3).

Box 2.3 Origin of the Vascular Plants

The time of the origin of the early vascular plants can be the Mid-Ordovician (ca. 475 mya) (Wellman et al. 2003) or the Late Silurian (ca. 425 mya) (Gensel 2008). A deep phylogenetic dichotomy occurred in the early-mid Devonian (ca. 400 mya), separating the lycophytes from the euphyllophytes (Gensel and Berry 2001; Pryer et al. 2004). Monilophytes have been dated back to the Late Devonian (ca. 370 mya). The earliest known occurrence of fossil leptosporangiate ferns is in the Early Carboniferous (Galtier and Phillips 1996); by the end of the Carboniferous six families were present. In subsequent major radiations in the Permian, Triassic, and Jurassic, several families with extant representatives replaced these Carboniferous families (e.g. Osmundaceae, Schizaceae, Matoniaceae, and Dipteridaceae) (Rothwell 1987). The more derived polypod ferns dramatically diversified in the Cretaceous, accompanying the great angiosperm diversification (Schneider et al. 2004) (see Sect. 1.2).

Molecular dating results are giving much older dates for the land plant crown group, from the Ordovician, ca. 490 mya (Sanderson 2003), to the Precambrian (Heckman et al. 2001). This result contrasts sharply with palaeobotanical estimates (Kenrick and Crane 1997; Wellman et al. 2003). The extant seed plants have been shown to be a monophyletic group, but exact relationships among these lineages and the pattern and chronology of divergence remain unclear, despite of the recent accumulation of molecular data sets and techniques to analyse them (e.g. Burleigh and Mathews 2004) (see Box 3.3).

Gnetales and modern conifer families appeared in the Triassic to Jurassic, and angiosperms on the boundary of the Jurassic/Cretaceous periods. From the Permian through the late Jurassic many seed plant lineages went extinct, including lyginopterids, medullosans, Callistophytaceae, Glossopterids, Cordaitales, and Voltziales (Stewart and Rothwell 1993), and their relationships with extant groups remain poorly resolved. During the Cretaceous and Cenozoic, the diversity of all surviving seed plant lines, except angiosperms, decreased (Knoll 1984; Willis and McElwain 2002) (Fig. 2.14).

During the past 20 years the phylogenetic relationships are beginning to be clearer and the predominant paraphyletic former scheme is changing to a more com-

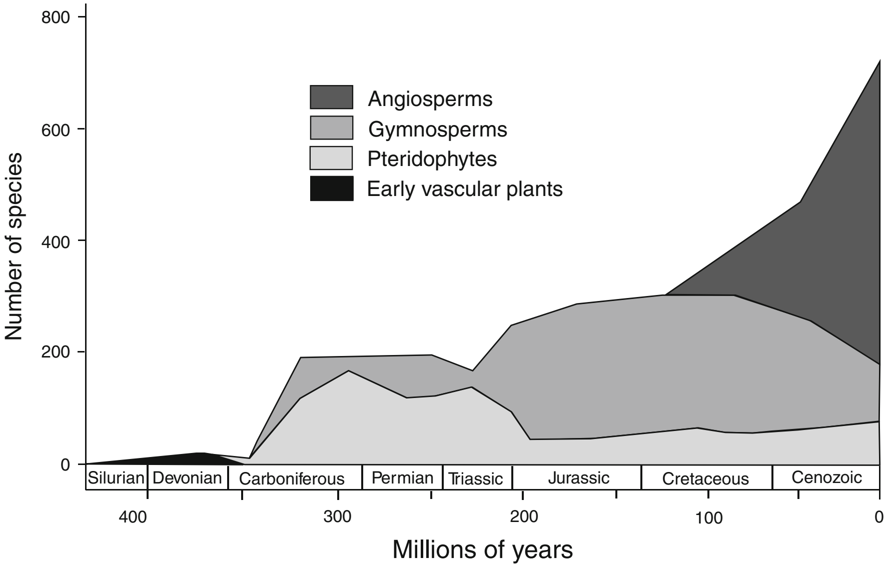


Fig. 2.14 Species richness of different vascular plant groups from the Silurian into the Cenozoic (from Willis and McElwain (2002), by permission of Oxford University Press)

prehensive system of evolutionary relationships (Pryer et al. 2004). Monilophytes and lycophytes are all spore bearing and "seed-free", and therefore, were traditionally lumped under terms like "pteridophytes" or "ferns and fern allies", that united paraphyletic assemblages of plants (Pryer et al. 2004). Now there is the tendency to differentiate the earliest diverging lineage Lycopsida or lycophytes from the real ferns or monilophytes (Fig. 2.15). The vascular plants (Tracheophyta) are classified in four main groups: lycophytes, ferns, Gymnosperms and Angiosperms. Lycophytes all possess lycophylls (leaves with an intercalary meristem) and comprise three main clades: homosporous Lycopodiales (club-mosses), heterosporous Isoetales (quillworts) and Selaginellales (spikemosses) (Fig. 2.15). Extant lycophytes are mostly diminute plants, but fossil members that dominated the Carboniferous landscape (like *Lepidodendron*) were huge arborescent forms. These are today the major component of coal deposits (Stewart and Rothwell 1993) (see Sect. 1.2).

2.2.3.1 Lycophytes

Lycophytes constitute the earliest diverging lineage under the vascular plants, and are consequently the most "primitive" plants in the Chilean extant vascular flora. They comprise two orders (Lycopodiales and Isoetales), two families (Lycopodiaceae and Isoetaceae), three genera (*Isoetes, Huperzia, Lycopodium*), and

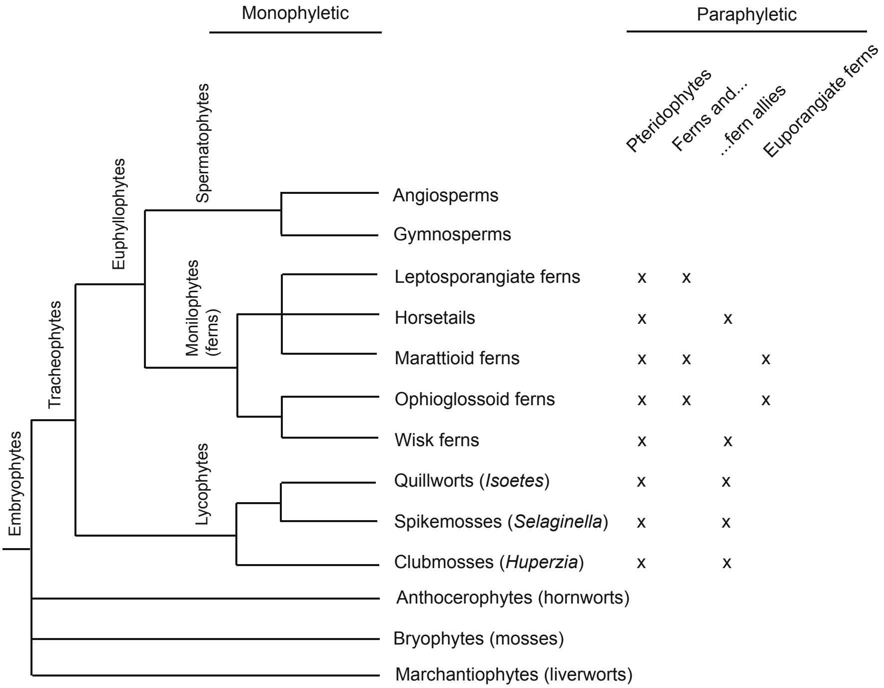


Fig. 2.15 Cladogram showing relationships among major lineages of vascular plants as currently and formerly understood (i.e. monophyletic v/s paraphyletic) (adapted from Pryer et al. 2004; Magallón and Hilu 2009)

11 species. *Huperzia* appears in Chile only at subantarctic latitudes (Fig. 1.20), while *Isoetes* and *Lycopodium* are to be found further north to 37ºS.

2.2.3.2 Monilophytes

Living euphyllophytes belong to two major clades (Fig. 2.15): seed plants (spermatophytes) and monilophytes (Kenrick and Crane 1997; Pryer et al. 2004). Monilophytes, ferns s. str., include most former groups recognized as "fern and fern allies". Ferns are represented in the Chilean flora by 9 orders, 20 families, 49 genera, and 135 species. Among the last, the Chilean flora comprises 38 endemic fern species. Basal classes among ferns s. str. are Psilotopsida, Equisetopsida, and Marattiopsida (Fig. 2.16), represented in Chile by three families: Ophioglossaceae (genera *Botrychium* and *Ophioglossum*), Psilotaceae (only *Psilotum* from Isla de Pascua), and Equisetaceae (*Equisetum*). The Order Marattiales does not show modern representatives in Chile, but is represented in the fossil record by the genus *Asterotheca* for the Upper Triassic of the La Ternera formation (Copiapó province,

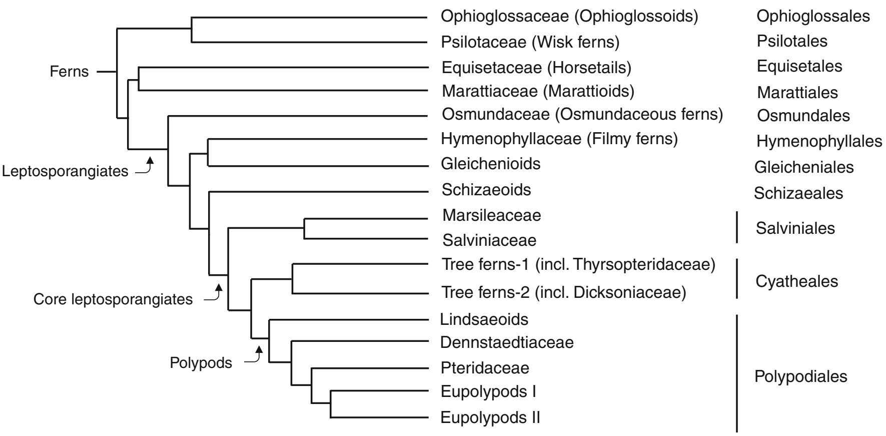


Fig. 2.16 Relationships between main fern groups (adapted from Smith et al. 2006; Pryer and Schuettpelz 2009, by permission of Oxford University Press)

Herbst et al. 1998), and the genera *Asterotheca* and *Rienitsia* for the Upper Triassic of the Biobío province (Leppe et al. 2006).

The most diverse of the monilophytes are the leptosporangiate ferns, a group of more than 9,000 extant species (Pryer and Schuettpelz 2009), represented in Chile by 125 species. The species-richest family is the Pteridaceae, with 10 genera and 26 species. The species-richest genus in Chile is *Hymenophyllum* (filmy ferns), comprising 19 species. The closely related monospecific genera *Hymenoglossum* and *Serpyllopsis* are considered by Ebihara et al. (2006) as nested within *Hymenophyllum.* Important to mention is the high fern species-richness in the oceanic islands, especially Juan Fernández and Rapa Nui. The Juan Fernández archipelago harbours 55 native fern species, of which 50% are endemic to the islands (Marticorena et al. 1998). A very remarkably species is *Thyrsopteris elegans*, the only representative of the tree fern family Thyrsopteridaceae (Smith et al. 2006) (Table 2.6, Fig. 5.8). Rapa Nui lacks such a huge species richness, but contains several tropical genera that are not represented in the rest of the Chilean territory, like *Davallia, Diplazium*, and *Vittaria* (Table 2.3). In the continent, ferns occupy most habitats from the coast to the Andes, and from the arid North (e.g. *Equisetum giganteum*) to the humid South (e.g. *Lophosoria quiadripinnata*). The generic fern richness concentrates in Chile between 35 and 45°S.

2.2.3.3 Spermatophytes

The seed plants (spermatophytes) (Fig. 2.15) are the most diverse vascular plant group in the world. Spermatophytes comprise Gymnosperms and angiosperms. Extant seed plants likely number between 250,000 and 300,000 species (Scotland and Wortley 2003). In Chile the seed plants are represented by 45 orders, 149 families, 785 genera and 4,144 species (Appendix A).

2.2.3.4 Gymnosperms

The seed-bearing plants or gymnosperms are characterized, contrary to the angiosperms, by the presence of ovules on the edge of an open sporophyll. Gymnosperms are classified into four main groups: conifers, cycads, ginkgos, and Gnetales. Gymnosperms as a whole are recognized as being monophyletic, but the relationships between the groups remain unresolved (Renner 2009) (Fig. 2.17).

The Chilean Flora is lacking extant cycads or Ginkgoales, but they were characteristic of the Triassic and Jurassic landscapes (see Sect. 1.2).

Fossil cycads have been reported from the Triassic of the Santa Juana Formation at the lower Biobío (Leppe and Moisan 2003; Nielsen 2005), from the Panguipulli Formation (Zavattieri et al. 2003), and the La Ternera formation (also Triassic) (Herbst and Troncoso 2000).

Ginkgoales are also found in the Chilean Triassic floras, like the ones from Copiapó and Los Molles (Troncoso and Herbst 1999), from La Ligua (Torres and Philippe 2002), and from the Lake District (39º30′ S) (Herbst et al. 2005). This last palaeoflora is composed of ca. 25 vascular plant species, including representatives from the Apocalamitaceae, Asterothecaceae, Gleicheniaceae, Corystospermaceae (*Dicroidium*), Peltaspermaceae, Cycadophyta, and Coniferales (Podocarpaceae and Voltziaceae).

Chilean *Gnetales* are represented by the family Ephedraceae, with the genus *Ephedra* comprising 7 species, 2 of them endemic.

Conifers harbour a rich fossil record that goes back to the Late Carboniferous, ca 300 mya (Hilton et al. 2003). Traditionally the conifers have been considered as the sister clade to Ginkgophyta and Cycadophyta, but this relationship

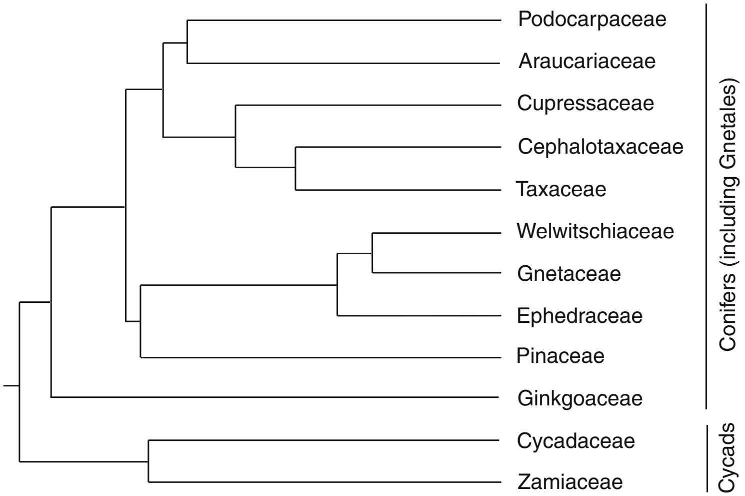


Fig. 2.17 Putative relations between main groups of gymnosperms (from Renner 2009, by permission of Oxford University Press)

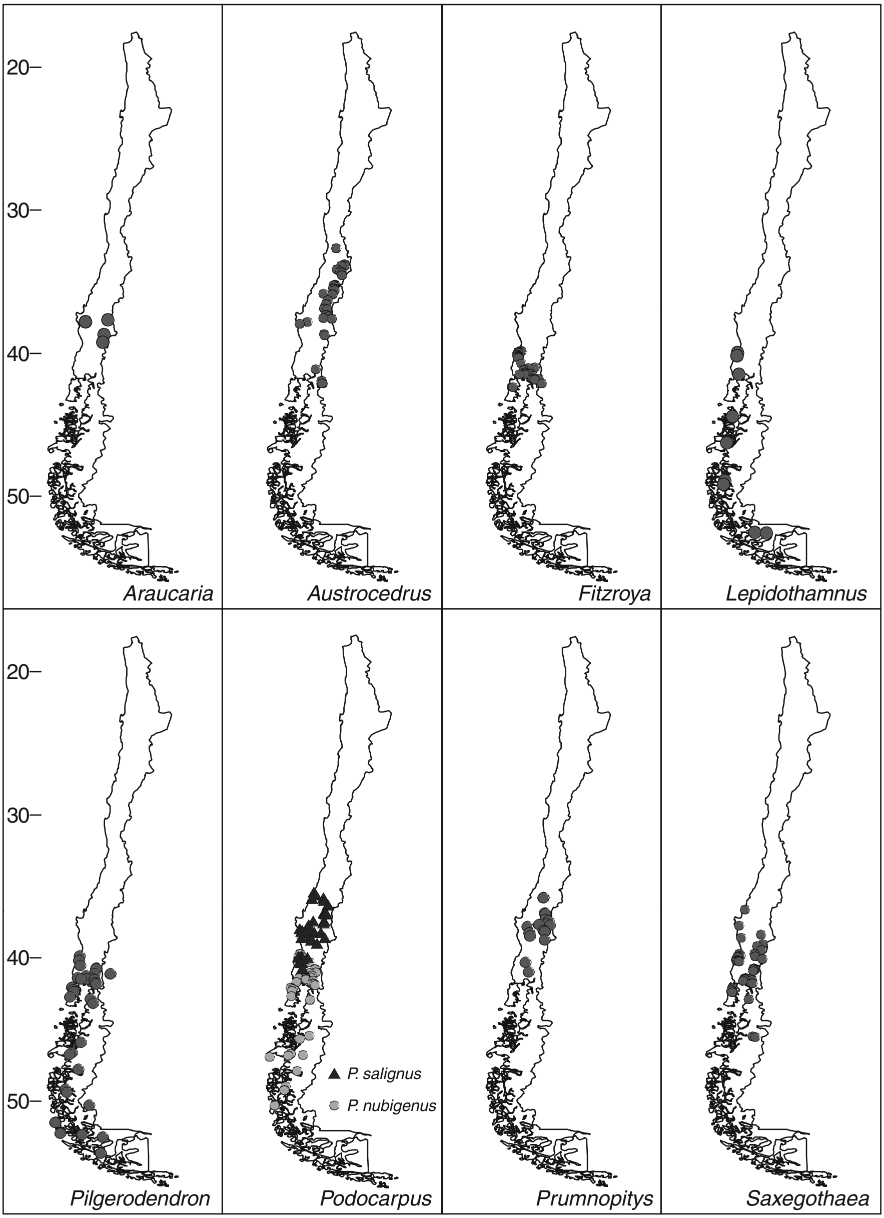


Fig. 2.18 Distribution maps of Chilean conifers (SGO collections)

has been constantly challenged (Henry 2005); new proposals place the Pinaceae as sister to the Gnetales and both as sister to the other conifers (Renner 2009) (Fig. 2.17). Conifers are a main issue in some of the most characteristic Chilean landscapes, especially in the temperate rainforests. They are represented in the

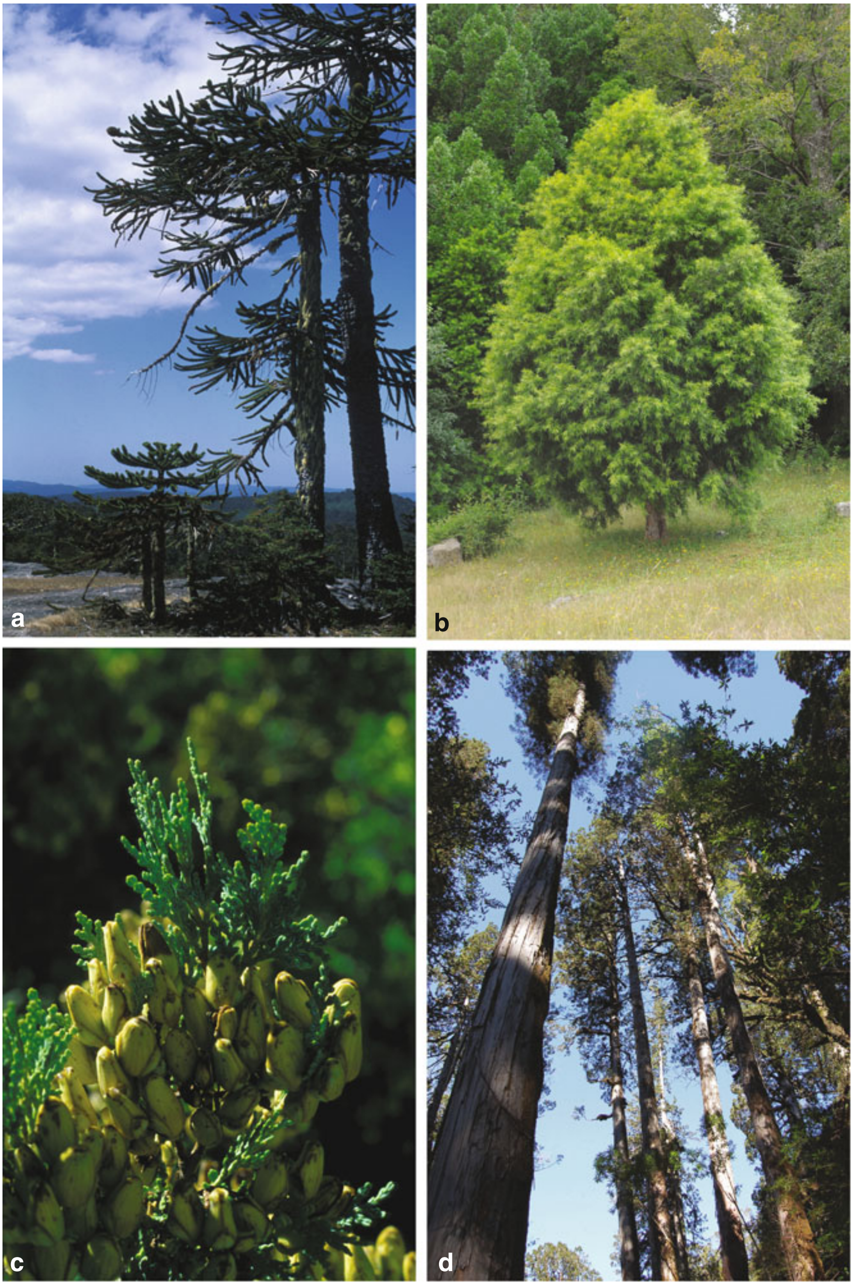


Fig. 2.19 Chilean conifers: **a** *Araucaria araucana*, Nahuelbuta; **b** *Podocarpus salignus*, Antuco; **c** *Austrocedrus chilensis*, Antuco; **d** *Fitzroya cupressoides*, continental Chiloé (photo credits: **a**–**c** A. Moreira-Muñoz; **d** María Castro)

extant flora by 3 families and 8 genera: *Araucaria* (Araucariaceae); *Lepidothamnus, Saxegothaea, Podocarpus, Prumnopitys* (Podocarpaceae); *Austrocedrus, Fitzroya, Pilgerodendron* (Cupressaceae) (Fig. 2.18) (Fig. 2.19).

The Araucariaceae are a family that is abundant worldwide in deposits from the Mesozoic (Stockey 1982) and became restricted to the southern hemisphere (Gondwana) from the end of the Mesozoic (fine distribution map in Golte 1993). The family expanded and diversified in both hemispheres in the Jurassic and Early Cretaceous and remained a significant component of Gondwanan vegetation until the end of the Cenozoic (see Sect. 1.2). The development of angiosperms in the Middle Cretaceous probably assisted in the demise of some araucarian components but there was also evolution of new genera. Recorded diversity in the early Cenozoic of Australia is as high as it was in the Early Cretaceous (Kershaw and Wagstaff 2001). *Araucaria araucana* distribution in Chile shows a disjunction between the coastal cordillera (Nahuelbuta) and the Andes, that is also expressed in the specie's genetic diversity (Ruiz et al. 2005).

2.2.3.5 Angiosperms

Flowering plants or Angiosperms, defined as plants with ovules enclosed in a carpel, are the most intensively studied group due to their predominance in modern terrestrial ecosystems (Palmer et al. 2004; Magallón 2009). They comprise around 223,000–260,000 living species classified in 61 orders and ca. 450 families (Scotland and Wortley 2003; APGIII 2009). The fossil record of the angiosperms extends back at least to the early Cretaceous, conservatively 130 mya (Crane et al. 2004). Molecular dating has but pushed this age to the Early – Middle Jurassic (ca 170 mya) (Wikström et al. 2001; Magallón 2009) (Box 2.4). Relationships between Angiosperm orders are presented in Fig. 2.20, including numbers of Chilean representatives.

2.2.3.6 Magnoliids

The most basal groups with representatives in Chile correspond to the *magnoliid* clade, including Piperales, Laurales, Canellales and Magnoliales (this latter with no presence in Chile). Chileans representatives of these basal orders are the Lactoridaceae, Piperaceae, Aristolochiaceae, Winteraceae, Lauraceae, Monimiaceae, Gomortegaceae, and Atherospermataceae.

Monimiaceae and Lauraceae were widespread by the Upper Cretaceous. The oldest fossil of the Lauraceae has been dated at 109 mya (Crane et al. 1994) and of the Monimiaceae at 83 mya (Poole and Gottwald 2001). Chilean *Peumus* supposedly diverged from a *Monimia/Palmeria* line some 76 mya, perhaps by disruption of a once continuous range that stretched from Chile across Antarctica and the Kerguelen plateau to Madagascar (Renner 2004). *Laurelia sempervirens* seems to have been present already since some 80 mya, while *Gomortega keule* is considered a relict species that has been in existence without modification for 100 my (Renner

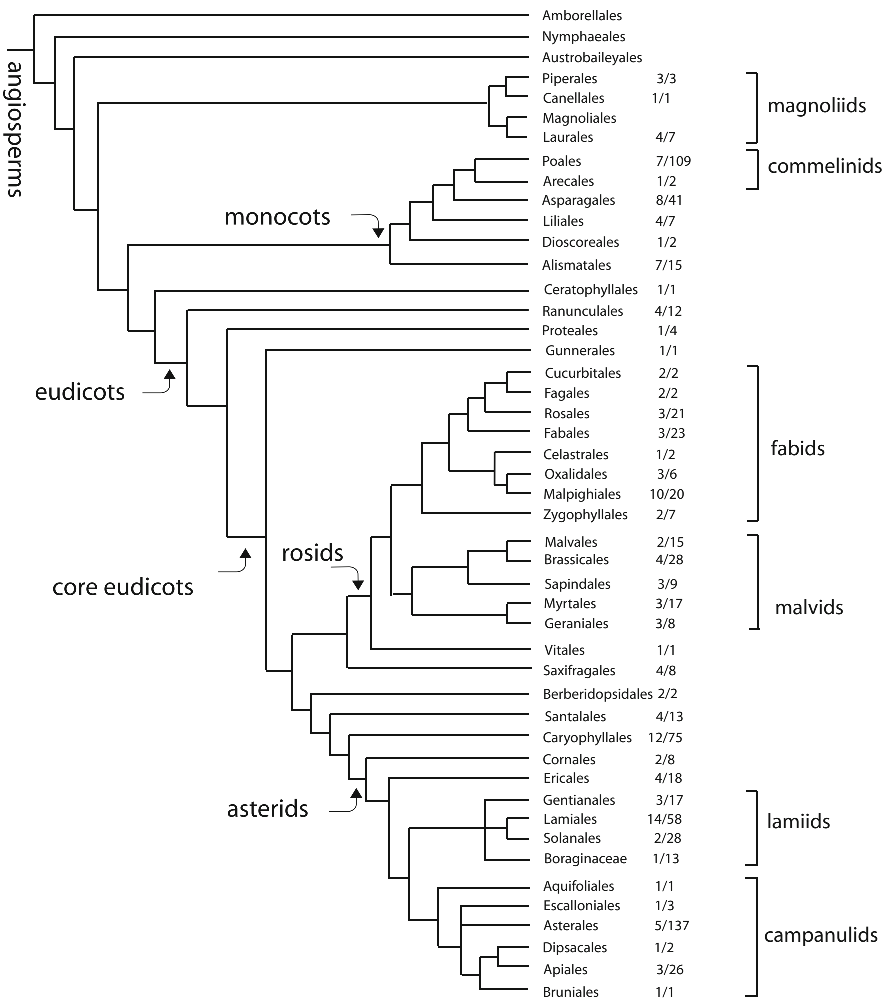


Fig. 2.20 Cladogram showing relationships between angiosperm orders (adapted from Stevens 2001 onwards, APG III 2009). Numbers represent native families/genera present in Chile; only basal orders not present in Chile are shown (without numbers)

2004) (see Sect. 3.3). The Lactoridaceae is a monospecific family endemic to Juan Fernández, constituting a real biogeographic enigma (Chap. 5).

Monocots

Regarding the Monocots, considerable diversification took place during the Early Cretaceous, with most families already present at the Cretaceous-Cenozoic boundary (Janssen and Bremer 2004). Basal within the Monocots are the

Acorales and Alismatales, the former being absent from Chile and the latter present by means of 6 families, 15 genera and 29 (mostly aquatic) species. Dioscoreales are represented by the sole family Dioscoreaceae, with 2 genera and 39 species. Liliales diverged from their sister-group in the Early Cretaceous, 117 mya (Bremer 2000). Among them are the Chilean national species *Lapageria rosea*, and species-rich Alstroemeriaceae (Table 2.5, Muñoz-Schick and Moreira-Muñoz 2003). Monogeneric Luzuriagaceae has been recently treated as nested within Alstroemeriaceae (APGIII 2009). Asparagales encompass also a big amount of Chilean Monocots (8 families, 41 genera, 195 species, and within them, 133 endemics). According to APGIII (2009), Asparagaceae may include Laxmanniaceae (*Trichopetalum*), and Xanthorrhoeaceae shall include Hemerocallidaceae (*Pasithea*). There is also the proposal to include Alliaceae into the Amaryllidaceae, but this is not followed by Anderson and Janssen (2009). Janssen and Bremer (2004) found an unexpected old age of 111 mya for the Orchidaceae: "Traditionally, this family has been looked at as a very specialized and hence, probably, a young group… Orchid diversity is not necessarily due to a rapid and recent radiation" (Janssen and Bremer 2004).The Tecophilaeaceae are represented in Chile by three endemic genera: *Conanthera, Tecophilaea,* and *Zephyra* (see Sect. 4.3). The rest of the Monocots have been grouped in a clade called the Commelinids that comprises four orders: under them is the Poales, which comprises in Chile 7 families, 109 genera, 596 species, of which 128 endemic species, mostly from the Poaceae and Cyperaceae. Poales has been dated at ca 115 mya (Mid-Cretaceous) (Bremer 2000). Bromeliaceae also appear to date back to the Cretaceous (Linder and Rudall 2005), but the uncertainties in dating the Bromeliaceae are considerable (Bremer 2002).

Eudicots

The probable sister of the eudicots is *Ceratophyllum* (Ceratophyllaceae), as apparent from APGIII (2009), but alternative models propose a closer relationship with Magnoliids (Goremykin et al. 2009). Ranunculales is the first diverging clade in the eudicots, followed by Proteales. These basal eudicots comprise in Chile 5 families, 16 genera, 71 species, and among the Ranunculales, 18 endemic species. Most genera in the Proteaceae show a Gondwanic relationship with Australasia (Chap. 3).

The Gunnerales is the first diverging lineage in the core eudicots (APGIII 2009; Forest and Chase 2009). Pantropical Gunneraceae are represented in southern Chile and Juan Fernández by 11 species, 6 of them endemic. Relationships within the rest of the core eudicots are getting clearer: Saxifragales appears as sister to the newly recognized Vitales + Rosids. Saxifragales are represented by the Saxifragaceae and to a less extent by the Haloragaceae and Grossulariaceae. Berberidopsidales appear as sister to Santalales + Caryophyllales + Asterids. The recently recognized order Berberidopsidales (APG III 2009) is composed of two monotypic families from Central Chile/Australia (Berberidopsidaceae) and Central

Chile/Argentina (Aextoxicaceae) (Table 2.7). Santalales are represented, together with the Santalaceae, by several parasitic Loranthaceae mainly from North-central Chile, and the Misodendraceae, distributed from 33ºS to the South as parasites of extant *Nothofagus* species (Chap. 9). Caryophyllales is one of the orders with the highest presence in Chile, encompassing 12 families that include the species-rich Cactaceae in North-central Chile (Chap. 7), and the related Portulacaceae, as well as several rich families like the Caryophyllaceae and Polygonaceae (72 and 32 species respectively). The Molluginacea and Nyctaginaceae are more sparsely represented.

Rosids

Rosids have been recently organized in two main clades: fabids and malvids, incorporating as sister clade the newly recognized Vitales (APG III 2009). These last are represented in Chile only by *Cissus striata* (Vitaceae), a liana from central Chilean sclerophyllous forests. **Fabids** are represented in Chile by 8 orders: Zygophyllales (comprising the Zygophyllaceae and Krameriaceae), Celastrales (including the Lepuropetalaceae under the Celastraceae), Oxalidales (including the Cunoniaceae, Elaeocarpaceae, Oxalidaceae), Malpighiales (including 10 Chileans families), Cucurbitales, Fabales, Fagales, and Rosales. Under the fabids, the best representation in Chile rests on the Fabales, that comprises the largest Fabaceae, the third largest family of angiosperms, comprising more than 19,000 species (Lewis et al. 2005). Chilean species-richest genera from the Fabaceae are *Adesmia* and *Astragalus* (Table 2.5). The Fabales also includes the Polygalaceae and Quillajaceae, this latter comprising just two species from South America (Kubitzki 2007), being the Chilean endemic *Quillaja saponaria* one of the most characteristic trees of Mediterranean Chile. The Fagales is represented in Chile by the Myricaceae and Nothofagaceae, the latter represented by10 species that are highly characteristic of Central/South Chilean landscapes (Chap. 9). The Rosales are represented in Chile by 3 families, 21 genera and 71 species. The Malpighiales are represented by 10 families, with most genera (7) in the Euphorbiaceae. The Passifloraceae consist in Chile of only one species, while the monogeneric Malesherbiaceae is represented by 16 species, 13 of them endemic. The Malpighiaceae are represented by two endemic genera, *Dinemandra* and *Dinemagonum.* Within Malpighiales the species-rich genus *Viola* (Violaceae) also is remarkable (Table 2.5).

Malvids are represented in Chile by 5 orders: Geraniales, Myrtales, Malvales, Brassicales, and Sapindales. The Geraniales includes the Geraniaceae, Vivianiaceae, and Meliathaceae. This last one shall include the endemic Chilean Francoaceae, according to APGIII (2009) (Table 2.6). Within the Malvales, the Malvaceae comprise 75 species. The Sapindales include the Sapindaceae, Anacardiaceae, Rutaceae. The Brassicaceae is the richest family in the Brassicales, with 145 Chilean species.

Asterids

This clade constitues one if the major lineages within the Angiosperms. It comprises about 100 families and more than 80,000 species (Bremer 2009). Asterids have been recently organized in two main clades: lamiids and campanulids. Sister to them are the Cornales and Ericales (APG III 2009), both with representatives in Chile (47 and 31 species respectively). Former Empetraceae are considered as nested within the Ericaceae (Kron and Luteyn 2005).

Lamiids include in Chile the Gentianales, Lamiales, Solanales, and the Boraginaceae. In Chile one of the species-richest order is the Lamiales, that comprises 14 families, 58 genera, and 270 species (124 endemics). Species-rich families are the newly recognized Calceolariaceae (Olmstead et al. 2001), the Verbenaceae, and the Veronicaceae (Table 2.4). Veronicaceae is an alternative name to Plantaginaceae (Tank et al. 2006), and resulted from the disintegration of the former Scrophulariaceae. Most Chilean former Scrophulariaceae have been transferred to the Calceolariaceae (*Calceolaria, Jovellana*), Linderniaceae (*Lindernia*), Phrymaceae (*Mimulus*), Orobanchaceae (*Agalinis, Bartsia, Castilleja, Euphrasia, Orobanche*), or Veronicaceae (14 genera, see Appendix). The Scrophulariaceae still conserve the genera *Alonsoa, Bluddleja* (formerly Buddlejaceae), and *Limosella*.

The Solanales comprise only two families (Convolvulaceae and Solanaceae), but 28 genera, and 193 species (93 endemics). The species-rich genus *Nolana* (Table 2.5), formerly pertaining to the Nolanaceae, is considered currently as part of the Solanaceae (Dillon et al. 2009).

The Boraginaceae have not yet gained order status, and comprise in Chile 13 genera and 103 species (66 endemic).

Campanulids comprise the Aquifoliales (including *Citronella* in the Cardiopteridaceae, formerly classified in the Icacinaceae); the big Asterales, Escalloniales, Bruniales, Dipsacales, and Apiales.

The Asterales include 11families, five of them present in Chile: Asteraceae, Calyceraceae, Campanulaceae (including Lobeliaceae), Goodeniaceae, and Stylidiaceae (including Donatiaceae). No wonder that the Asterales are the best represented order in the flora of Chile, with 137 genera, and 883 species (395 of them endemic); the sole presence of representatives of the Asteraceae and the closely related Calyceraceae and Goodeniaceae compose much of these numbers (Table 2.4, Chap. 8). The Escalloniales consists of the family Escalloniaceae, represented in Chile by 3 genera (*Escallonia, Tribeles, Valdivia*), and 16 species (7 endemic). Chilean Campanulaceae consist of 6 genera; remarkably are the endemic genus *Cyphocarpus* from the Atacama Desert, and *Wahlenbergia*, with several species endemic to Juan Fernández. The Bruniales include the monospecific family Desfontainiaceae, alternatively nested within Columelliaceae (APGIII 2009). The Dipsacales include the Chilean Valerianaceae (genera *Stangea* and *Valeriana*), alternatively classified under the Caprifoliaceae (APGIII 2009). The Chilean Apiales include three families (Apiaceae, Araliaceae, and Griseliniaceae), comprising 26 genera, and 106 species (46 endemic).

Box 2.4 Angiosperms Temporal and Spatial Origin(s)

The origin of the flowering plants is considered as the "Holy Grail" of botany (Miller 2009), or "Darwin's abominable mystery" (Crepet 1998, Davies et al. 2004). From fossil evidence, a major radiation of angiosperms is obvious in the mid-Cretaceous, (ca. 130 mya) (Lidgard and Crane 1990).

The fossil record is but not unequivocal: *Sanmiguelia*, a Late Triassic fossil described by Brown (1956), has been interpreted by Cornet (2002) as a very primitive angiosperm that combines both monocot and dicot characters, but this interpretation has been ignored by other palaeobotanists. Even the genus *Archaefructus* proposed as a Jurassic primitive angiosperm (Sun et al. 1998, 2002) has been very controversial. In this respect there is still a high level of uncertainty: the Holy Gray of botany is still a great mystery (Frohlich and Chase 2007). "If the gymnosperms are indeed monophyletic, their sister-group the angiosperms must date from the same period, the Carboniferous. This leaves a gap of over 150 million years with no fossil record of angiosperms – a period longer than their entire known fossil history. This could be either because the gymnosperms are not a natural group or because the stem lineage of the angiosperms lacked distinguishing angiosperm synapomorphies" (Hill 2005).

Molecular dating shows a middle Jurassic origin of flowering plants (ca 175 mya) (Wikström et al. 2001; Magallón 2009), suggesting that the angiosperms may be older than the fossil record indicates, and "predating the oldest unequivocal fossil angiosperms by about 45 million years" (Bell et al. 2005). Other molecular dating analyses even suggest a pre-Mesozoic age for the divergence of the angiosperm lineage from other seed plants (Miller 2009). This is an old idea: "The angiosperms undoubtedly originated long before the Cretaceous period. The specialised character and astonishingly modern facies of many Cretaceous angiosperms confirm our belief in an antiquity of angiosperms antedating by many millions of years, probably by several geologic periods, the first appearance of recognisable pioneers of the present ruling dynasty in the modern world" (Seward 1933 as quoted by Takhtajan 1961, p 122). Early authors postulated a Triassic or even Permo-Triassic origin (Wieland 1933; Camp 1947; Zimmermann 1959): "Angiosperms originated during the Permian as the aftermath of the so called Permo-Carboniferous Glaciations" (Croizat 1960, p 1735).

Regards the geographic origin of the angiosperms, high contrasting views developed (Axelrod 1952; Retallack and Dilcher 1981; Lu and Tang 2005). Stebbins (1974) proposed that alpine biomes of northern latitudes might have been the centre of early radiation of angiosperms. An eastern Asian centre of origin was put forth by Sun et al. (2001, 2008). Others postulated that flowering plants evolved from multiple, unrelated seed plant lineages and areas, i.e. a polyphyletic-polychromic-polytopic hypothesis (Wu et al. 2002).

Stuessy (2004) proposed that angiosperms evolved slowly from seed ferns in the Jurassic, beginning first with the carpel, followed later by double fertilization, and lastly by the appearance of flowers. These three fundamental transitions may have taken more than 100 million years to complete! This topic is far from been solved, and others maintain that it is an illusion the search for a strict centre of origin (see Sect. 3.3).

References

APG II [Angiosperm Phylogeny Group II] (2003) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APGII. Bot J Linn Soc 141: 399–436

APG III (2009) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APGIII. Bot J Linn Soc 161:105–121

Anderson CL, Janssen T (2009) Monocots. In: Hedges SB, Kumar S, (eds) The timetree of life. Oxford University Press, New York, pp. 203–212

Axelrod AJ (1952) A theory of angiosperm evolution. Evolution 6:29–60

Bell ChD, Soltis DE, Soltis PS (2005) The age of the angiosperms: a molecular timescale without a clock. Evolution 59:1245–1258

Brako L, Zarucchi JL (1993) Catalogue of the flowering plants and gymnosperms of Peru. Reprint 1996. Monographs in Systematic Botany from the Missouri Botanical Garden, vol. 45. Missouri Botanical Garden, St. Paul, MO, 1–1286

Bremer K (2000) Early Cretaceous lineages of monocot flowering plants. PNAS 97:4707–4711

Bremer K (2002) Gondwanan evolution of the grass alliance of families (Poales). Evolution 56:1374–1387

Bremer B (2009) Asterids. In: Hedges SB, Kumar S, (eds) The timetree of life. Oxford University Press, New York, pp. 177–187

Brown RW (1956) Palm-like plants from the Dolores Formation (Triassic), southwestern Colorado. US Geol Surv Prof Pap 274:205–209

Burleigh JG, Mathews S (2004) Phylogenetic signal in nucleotide data from seed plants: implications for resolving the seed plant tree of life. Am J Bot 91:1599–1613

Camp WH (1947) Distribution patterns in modern plants and the problem of ancient dispersals. Ecol Monogr 17:159–183

Castro SA, Camousseight A, Muñoz-Schick M, Jaksic FM (2006) Rodulfo Amando Philippi, el naturalista de mayor aporte al conocimiento taxonómico de la diversidad biológica de Chile. Rev Chil Hist Nat 79:133–143

Cavanilles AJ (1801) Del género Nuevo *Francoa*. An Cienc Nat 4:236–239

Christensen C (1934) Index filicum. Copenhagen

Cornet B (2002) Last updated on 10/10/2008. When Did Angiosperms First Evolve? (http://www.sunstar-solutions.com/sunstar/Why02/why.htm)

Crane PR, Friis EM, Pedersen KR (1994) Palaeobotanical evidence on the early radiation of magnoliid angiosperms. Plant Syst Evol 8(Suppl):51–72

Crane PR, Herendeen P, Friis EM (2004) Fossils and plant phylogeny. Am J Bot 91:1683–1699

Crepet WL (1998) The abominable mystery. Science 282:1653–1654

Croizat L (1960) Principia Botanica. Published by the author. Caracas, Venezuela

Cronquist A (1981) An integrated system of classification of flowering plants. Columbia University Press, Nueva York

Darwin C (1839) Narrative of the surveying voyages of His Majesty's Ships Adventure and Beagle between the years 1826 and 1836, describing their examination of the southern shores of South America, and the Beagle's circumnavigation of the globe. Henry Colburn, London

Davies TJ, Barraclough TG, Chase MW, Soltis PS, Soltis DE, Savolainen V (2004) Darwin's abominable mystery: Insights from a supertree of the angiosperms. Proc Natl Acad Sci USA 101:1904–1909

De Lange PJ, Sawyer JWD, Rolfe JR (2006) New Zealand indigenous vascular plant checklist. New Zealand Plant Conservation Network, Wellington

Dillon MO, Tu T, Xie L, Quipuscoa Silvestre V, Wen J (2009) Biogeographic diversification in Nolana (Solanaceae), a ubiquitous member of the Atacama and Peruvian Deserts along the western coast of South America. J Syst Evol 47:457–476

Ebihara A, Dubuisson J-Y, Iwatsuki K, Hennequin S, Ito M (2006) A taxonomic revision of hymenophyllaceae. Blumea 51:221–280

Engler A, Diels L (1936) Syllabus der Pflanzenfamilien, 11th ed. Gebrüder Borntraeger, Berlin

Forest F, Chase MW (2009) Eudicots. In: Hedges SB, Kumar S, (eds) The timetree of life. Oxford University Press, New York, pp 169–176

Frohlich MW, Chase MW (2007) After a dozen years of progress the origin of angiosperms is still a great mystery. Nature 450:1184–1189

Fuentes F (1913) Reseña botánica sobre la Isla de Pascua. Bol Mus Nac Hist Nat 5:320–337

Galtier J, Phillips TL (1996) Structure and evolutionary significance of palaeozoic ferns. In: Camus JM, Johns RJ, Gibby M (eds) Pteridology in perspective: pteridophyte symposium "95. Proceedings of the Holttum memorial pteridophyte symposium, Kew 1995. Royal Botanic Gardens Kew, pp 417–433

Gay C (1845–1854) Historia Física y Política de Chile según documentos adquiridos en esta República durante doce años de residencia en ella y publicada bajo los auspicios del Supremo Gobierno (including two illustrated atlases). Paris

Gensel PG (2008) The earliest land plants. Annu Rev Ecol Evol Syst 39:459–477

Gensel PG, Berry CM (2001) Early lycophyte evolution. Am Fern J 91:74–98

Goldblatt P, Manning J (2000) Cape plants: a conspectus of the Cape Flora of South Africa. Strelitzia (National Botanical Institute of South Africa) 9:1–743

Golte W (1993) Araucaria: Verbreitung und Standortanspruche einer Coniferengattung in vergleichender Sicht. Erdwissenschaftliche Forschung vol 27. Steiner Verlag, Stuttgart

Goremykin VV, Viola R, Hellwig FH (2009) Removal of noisy characters from chloroplast genome-scale data suggests revision of phylogenetic placements of amborella and ceratophyllum. J Mol Evol 68:197–204

Graham CH, Ferrier S, Huettmand F, Moritz C, Townsend Peterson A (2004) New developments in museum-based informatics and applications in biodiversity analysis. Trend Ecol Evol 19: 497–503

Hassler M, Swale B (2002 onwards) Checklist of World Ferns. (http://homepages.caverock.net.nz/~bj/fern/list.htm)

Heckman-enlargethispage-12pt DS, Geiser DM, Eidell BR, Stauffer RL, Kardos NL, Hedges SB (2001) Molecular evidence for the early colonization of land by fungi and plants. Science 293:1129–1133

Henry RJ (2005) Plant diversity and evolution. CABI Publishing, Cromwell Press, London

Herbst R, Melchor R, Troncoso A (1998) Las Pteridophyta y el paleoambiente de la parte media de la Formación La Ternera (Triásico Superior), en Quebrada La Cachivarita, III Región, Chile. Rev Geol Chile 25:85–107

Herbst R, Troncoso A (2000) Las Cycadophyta del Triásico de las Formaciones La Ternera y El Puquén (Chile). Ameghiniana 37:283–292

Herbst R, Troncoso A, Muñoz J (2005) Las Tafofloras Triásicas de la Región de Los Lagos, Xma Región, Chile. Ameghiniana 42:377–394

Hill K (2005) Diversity and evolution of gymnosperms. In: Henry RJ, (ed) Plant diversity and evolution: genotypic and phenotypic variation in higher plants. CABI Publishing, Cromwell Press, London, pp 25–44

Hilton J, Wang S-J, Tian B, Li C-H (2003) Evidence for conifer origins and early evolution from the Late Palaeozoic Cathaysian flora of South East Asia. Acta Hort 615:59–65

Hooker JD (1844–1859) The botany of the Antarctic voyage of H.M. Discovery ships Erebus and Terror in the years 1839–1843. Under the command of Captain Sir James Clark Ross/by Joseph Dalton Hooker. Reeve, London

Hutchinson J (1926) The families of flowering plants. Vol I Dicotyledons. The Macmillan Co, London

Hutchinson J (1934) The families of flowering plants. Vol II Monocotyledons. The Macmillan Co, London

Janssen T, Bremer K (2004) The age of major monocot groups inferred from 800 rbcL sequences. Bot J Linn Soc 146:385–398

Johnston IM (1929a) The coastal flora of the departments of Chañaral and Taltal. Contributions from the Gray Herbarium of Harvard University 85:1–137

Johnston IM (1929b) The flora of the Nitrate Coast. Contributions from the Gray Herbarium of Harvard University 85:138–163

Johow F (1896) Estudios sobre la flora de las Islas de Juan Fernández. Imprenta Cervantes, Santiago

Jørgensen PM, León-Yáñez S, (eds) (1999) Catalogue of the vascular plants of Ecuador. Monographs in Systematic Botany vol 75. Missouri Botanical Garden, St. Paul, MO, pp 1–1182

Kenrick P, Crane PR (1997) The origin and early diversification of land plants: a cladistic study. Smithsonian Institution Press, Washington DC

Kershaw P, Wagstaff B (2001) The southern conifer family Araucariaceae: history, status, and value for paleoenvironmental reconstruction. Annu Rev Ecol Evol Syst 32:397–414

Knoll AH (1984) Patterns of extinction in the fossil record of vascular plants. In: Nitecki MH, (ed) Extinctions. University of Chicago Press, Chicago, pp 21–68

Kron KA, Luteyn JL (2005) Origins and biogeographic patterns in Ericaceae: new insights from recent phylogenetic analyses. Biol Skr 55:479–500

Kubitzki K (2007) Quillajaceae. In: Kubitzki K, (ed) The families and genera of vascular plants, vol IX. Springer, Berlin, pp 407–408

Leppe M, Moisan P (2003) New records of Upper Triassic Cycadales and Cycadeoidales of Biobio river, Chile. Rev Chil Hist Nat 76:475–484

Leppe M, Moisan P, Abad E, Palma-Heldt S (2006) Paleobotánica del Triásico Superior del valle del Río Biobío, Chile: Clase Filicopsida. Rev Geol Chile 33:81–107

Lewis GP, Schrire B, Mackinder B, Lock M (2005) Legumes of the World. Royal Botanic Gardens, Kew

Lidgard SH, Crane PR (1990) Angiosperm diversification and Cretaceous floristic trends: a comparison of palynofloras and leaf macrofloras. Paleobiology 16:77–93

Linder HP, Rudall PJ (2005) Evolutionary history of Poales. Annu Rev Ecol Syst 36:107–124

Looser G (1934–1937) Geografía Botánica de Chile. Imprenta Universitaria, Santiago (reprint 2010)Translation of Reiche (1907)

Lu A-M, Tang Y-C (2005) Consideration on some viewpoints in researches of the origin of angiosperms. Acta Phytotaxonomica Sinica 43:420–430

Magallón S (2009) Flowering plants (Magnoliophyta). In: Hedges SB, Kumar S, (eds) The timetree of life. Oxford University Press, New York, pp 161–165

Magallón S, Hilu KW (2009) Land plants (Embryophyta). In: Hedges SB, Kumar S, (eds) The timetree of life. Oxford University Press, New York, pp 133–137

Marticorena C (1990) Contribución a la estadística de la flora vascular de Chile. Gayana Botánica 47:85–113

Marticorena C (1992) Bibliografía Botánica Taxonómica de Chile. Monographs in Systematic Botany vol. 41. Missouri Botanical Garden, St. Louis, MO

Marticorena C (1995) Historia de la exploración botánica en Chile. In: Marticorena C, Rodríguez R, (eds) Flora de Chile, vol 1. Universidad de Concepción, Concepción, pp 1–62

Marticorena C (1996) Bibliografía Botánica Taxonómica de Chile. Gayana Botánica 53(Suplemento 1):1–263

Marticorena C, Quezada M (1985) Catálogo de la flora vascular de Chile. Gayana Bot 42:1–157

Marticorena C, Rodríguez R, (eds) (1995 onwards) Flora de Chile, 2 vols. Universidad de Concepción, Concepcion

Marticorena C, Stuessy TF, Baeza CM (1998) Catalogue of the vascular flora of the Robinson Crusoe or Juan Fernández Islands, Chile. Gayana Bot 55:187–211

Miller JM (2009) The Origin of Angiosperms. Online, updated January 15, 2009, URL http://www.gigantopteroid.org/html/angiosperm.htm

Molina JI (1776) Compendio della storia geografica, naturale, e civile del Regno del Chile.

Molina JI (1782) Saggio sulla storia natural del Chili. Bologna, 2d edition (1810), Bologna. Spanish translation (1987) by R Jaramillo, Santiago

Morawetz W, Röser M, (eds) (1998) Eduard Friedrich Poeppig 1798–1868. Gelehrter und Naturforscher in Südamerika anlässlich seines 200. Geburtstages. Universität Leipzig, Leipzig

Muñoz Pizarro C (1944) El itinerario de don Claudio Gay. Bol Mus Nac Hist Nat (Chile) 22: 27–44

Muñoz Pizarro C (1959) Sinopsis de la Flora Chilena, 2nd ed (1966). Ediciones Universidad de Chile, Santiago

Muñoz Pizarro C (1966) Flores Silvestres de Chile. Ediciones de la Universidad de Chile, Munich

Muñoz-Schick M (1975) Geronimo de Bilbar, notable observador naturalista en la alborada de la Conquista. Bol Mus Nac Hist Nat (Chile) 34:5–27

Muñoz-Schick M (1991) 100 años de la Sección Botánica del Museo Nacional de Historia Natural (1889–1989. Bol Mus Nac Hist Nat (Chile) 42:181–202

Muñoz-Schick M, Moreira-Muñoz A (2003) Alstroemerias de Chile: diversidad, distribución y conservación. Taller La Era, Santiago

Muñoz-Schick M, Moreira-Muñoz A (2008) La colección de Tipos del Herbario SGO: avances hacia el Herbario Nacional Virtual. Resúmenes XX Reunión Nacional de Botánica, Olmué, 25–27 septiembre 2008

Nielsen SN (2005) The Triassic Santa Juana Formation at the lower Biobio River, south central Chile. J S Am Earth Sci 19:547–562

Olmstead RG, DePamphilis CW, Wolfe AD, Young ND, Elisons WJ, Reeves PA (2001) Disintegration of the Scrophulariaceae. Am J Bot 88:348–361

Palmer JD, Soltis DE, Chase MW (2004) The plant tree of life: an overview and some points of view. Am J Bot 91:1437–1445

Philippi RA (1860) Viaje al desierto de Atacama hecho por orden del Gobierno de Chile en el verano 1853–1854 por el Dr. Rodulfo Amando Philippi. E. Anton, Halle

Philippi F (1881) Catalogus plantarum vascularium chilensium adhuc descriptarum. Ann Univ Chile 59:49–422

Pigafetta A (1536) Primer Viaje en torno del globo. Spanish edition from 1963. Espasa-Calpe, Madrid

Pissis JA (1875) Atlas de Geografía Física de la República de Chile. Instituto Geográfico de Paris, Ch. Delagrave, Paris

Poeppig E, Endlicher S (1835–1845) Nova genera ac species plantarum, quas in regno Chilensi Peruviano et in terra Amazonica :annis MDCCCXXVII ad MDCCCXXXII /legit Eduardus Poeppig et cum Stephano Endlicher descripsit iconibusque illustravit. Sumptibus F. Hofmeister, Leipzig

Poole I, Gottwald H (2001) Monimiaceae sensu lato, an element of Gondwanan polar forests: evidence from the Late Cretaceous – early Tertiary wood flora of Antarctica. Aust Syst Bot 14:207–230

Pryer KM, Schuettpelz E (2009) Ferns. In: Hedges SB, Kumar S, (eds) The timetree of life. Oxford University Press, New York, pp. 153–156

Pryer KM, Schuettpelz E, Wolf PG, Schneider H, Smith AR, Cranfill R (2004) Phylogeny and evolution of ferns (monilophytes) with a focus on the early leptosporangiate divergences. Am J Bot 91:1582–1598

Reiche C (1894–1911) Flora de Chile, 6 vols. Ediciones de la Universidad de Chile, Santiago

Reiche C (1907) Grundzüge der Pflanzenverbreitung in Chile. In: Engler A, Drude O, (eds) Die Vegetation der Erde: Sammlung Pflanzengeographischer Monographien, Vol VIII. Verlag von V. Engelmann, Leipzig

Renner SS (2004) Variation in diversity among Laurales, Early Cretaceous to Present. Biol Skr 55:441–458

Renner SS (2009) Gymnosperms. In: Hedges SB, Kumar S, (eds) The timetree of life. Oxford University Press, New York, pp. 157–160

Retallack G, Dilcher DL (1981) A coastal hypothesis for the dispersal and rise to dominance of flowering plants. In: Niklas K, (ed) Paleobotany, paleoecology and evolution, vol 2. Praeger, New York, pp 27–77

Rothwell GW (1987) Complex Paleozoic Filicales in the evolutionary radiation of ferns. Am J Bot 74:458–461

Ruiz EA, Fuentes G, Samuel R, González F et al. (2005) Genetic diversity and differentiation within and among Chilean populations of *Araucaria araucana* (Araucariaceae) base don AFLP markers and allozyme variability. Abstracts XVII International Botanical Congress, Vienna, nº 13.3.5

Saldivia Maldonado Z (2003) La visión de la naturaleza en tres científicos del siglo XIX en Chile: Gay, Domeyko y Philippi. Instituto de Estudios Avanzados, Universidad de Santiago de Chile, Santiago

Sanderson MJ (2003) Molecular data from 27 proteins do not support a Precambrian origin of land plants. Am J Bot 90:954–956

Schneider H, Schuettpelz E, Pryer KM, Cranfill R, Magallón S, Lupia R (2004) Ferns diversified in the shadow of angiosperms. Nature 428:553–557

Scotland RW, Wortley AH (2003) How many species of seed plants are there?. Taxon 52:101–104

Smith AR, Pryer KM, Schuettpelz E, Korall P, Schneider H, Wolf PG (2006) A classification for extant ferns. Taxon 55:705–731

Stebbins GL (1974) Flowering plants: evolution above the species level. Belknap Press, Cambridge

Stevens PF (2001 onwards) Angiosperm Phylogeny Website. Version 9, June 2008. URL http://www.mobot.org/MOBOT/research/APweb/

Stewart WN, Rothwell GW (1993) Paleobotany and the evolution of plants, 2d ed.. Cambridge University Press, Cambridge

Stockey RA (1982) The Araucariaceae: an evolutionary perspective. Rev Palaeobot Palynol 37:133–154

Stuardo C, Feliú G (1973) Vida de Claudio Gay (1800–1873). Editorial Nacimiento, Santiago de Chile, vol 2, pp 318–329

Stuessy TF (2004) A transitional-combinational theory for the origin of angiosperms. Taxon 53: 3–16

Sun G, Dilcher DL, Zheng S-L, Zhou Z (1998) In search of the first flower: a jurassic angiosperm, *Archaefructus*, from Northeast China. Science 282:1692–1695

Sun G, Zheng S-L, Dilcher DL, Wang YD, Mei SW (2001) Early Angiosperms and their associated plants from Western Liaoning, China. Shanghai Scientific and Technological, Education Publishing House, Shanghai

Sun G, Ji Q, Dilcher DL, Zheng S-L, Nixon KC, Wang X (2002) Archaefructaceae, a new basal angiosperm family. Science 296:899–904

Sun G, Ji Q, Dilcher DL, Zheng S-L (2008) A review of recent advances in the study of early angiosperms from northeastern China. Palaeoworld 17:166–171

Takhtajan A (1961) The origin of Angiospermous Plants, 2nd ed. (original Russian edition, Moscow). Traslated as Flowering plants, origin and dispersal by C. Jeffrey, Kew (1969). Reprint 1981. Otto Koeltz Science Publishers, Koenigstein

Tank DC, Beardsley PM, Kelchner SA, Olmstead RG (2006) Review of the systematics of Scrophulariaceae s.l. and their current disposition. Aust Syst Bot 19:289–307

Taylor CM, Muñoz-Schick M (1994) The botanical works of Philippi, father and son, in Chile. Ann Mo Bot Gard 81:743–748

Torres T, Philippe M (2002) Nuevas especies de Coniferales y Ginkgoales del Lías de La Ligua (Chile) con una evaluación del registro paleoxilológico en el Jurásico de Sudamérica. Rev Geol Chile 29:151–165

Troncoso A, Herbst R (1999) Triassic Ginkgoales from northern Chile. Rev Geol Chile 26:255–273

von Humboldt A, Bonpland A (1805) Essai sur la Géographie des Plantes. Chez Levrault, Schoell et compagnie, Paris

Wake DB, Hadly EA, Ackerlya DD (2009) Biogeography, changing climates, and niche evolution. PNAS 106:19631–19636

Wang L, Qin H (2008) The Chinese Virtual Herbarium (CVH) and its future role for biogeographic research. Biogeografía 3:15–20. URL http://www.uac.pt/~seba/?q=taxonomy/term/7

Wellman CH, Osterloff PL, Mohiuddin U (2003) Fragments of the earliest land plants. Nature 425:282–285

Wieland GR (1933) Origin of Angiosperms. Nature 131:360–361

Wikström N, Savolainen V, Chase MW (2001) Evolution of the angiosperms: calibrating the family tree. Proc R Soc Lond B 268:2211–2220

Willis KJ, McElwain JC (2002) The evolution of plants. Oxford University Press, Oxford

Wilton AD, Breitwieser I (2000) Composition of the New Zealand seed plant flora. New Zealand J Bot 38:537–549

Wu Z-Y, Lu A-M, Tang Y-C, Chen Z-D, Li W-H (2002) Synopsis of a new ‘polyphyletic-polychromic-polytopic’ system of the angiosperms. Acta Phytotaxon Sin 40:289–322

Zavattieri AM, Herbst R, Muñoz BJ (2003) Microflora de la Formación Panguipulli (Triásico Superior), en Lincán Ray, Lago Calafquén, 10° Región, Chile. Ameghiniana 40:585–600

Zimmermann W (1959) Die Phylogenie der Pflanzen, 2d edn. Gustav Fischer Verlag, Stuttgart

Zuloaga FO, Morrone O, Rodríguez D (1999) Análisis de la biodiversidad en plantas vasculares de la Argentina. Kurtziana 27:17–167

Zuloaga FO, Morrone O, Belgrano MJ, (eds) (2008) Catálogo de las Plantas Vasculares del Cono Sur (Argentina, Sur de Brasil, Chile, Paraguay y Uruguay). Monographs in Systematic Botany from the Missouri Botanical Garden, vol. 107:3 vols. Missouri Botanical Garden, St. Paul, MO

Part II
Chorology of Chilean Plants

Chapter 3
Geographical Relations of the Chilean Flora

Abstract The chorological approach attempts to classify taxa according to their geographic relationships. The Chilean native genera have been classified in 7 floristic elements and 10 generalized tracks. The origin of major disjunctions in the flora is intensively discussed from the viewpoint of under contrasting biogeographic paradigms like dispersal and vicariance. Attention is also put on the influence of the Andean Dry Diagonal on the evolution of the Chilean flora and its distribution patterns.

Chorology is an old approach in biogeography that deals specifically with comparing distribution maps. In Cain's (1944) opinion, the most comprehensive concept encompassing the analysis of distributions would be the old German term *Arealkunde*, the "science of area" (*sensu* Meusel 1943; Meusel and Jäger 1992). Used more or less like a synonym, the term "chorology" is "still in use, in quite a variety of different ways, but many modern studies do appear to be within that remit" (Williams 2007, p 29). Chorology has it strength in its comparative nature . . ." area maps will actually show interesting distribution conditions, others will only obtain its value in the relationship with other areas" (Hannig and Winkler 1926–1940) (Fig. 3.1).

Chorology is in line with Parenti and Ebach's comparative biogeography (see Chap. 10), and is closer linked to systematics (Rothmaler 1955; Stuessy et al. 2003; Parenti and Ebach 2009). It is still the most suited term for remitting to the science of geographic distributions.

3.1 Floristic Elements

A product of the comparison of distribution maps is the classification of floras into floristic elements (Christ 1867; Engler 1882; Wangerin 1932; Good 1947; Takhtajan 1986). Wulff (1950) described five different approaches to define floristic elements, but recognized that "most investigators have been inclined to believe that the geographical factor is of primary importance and that the term element should

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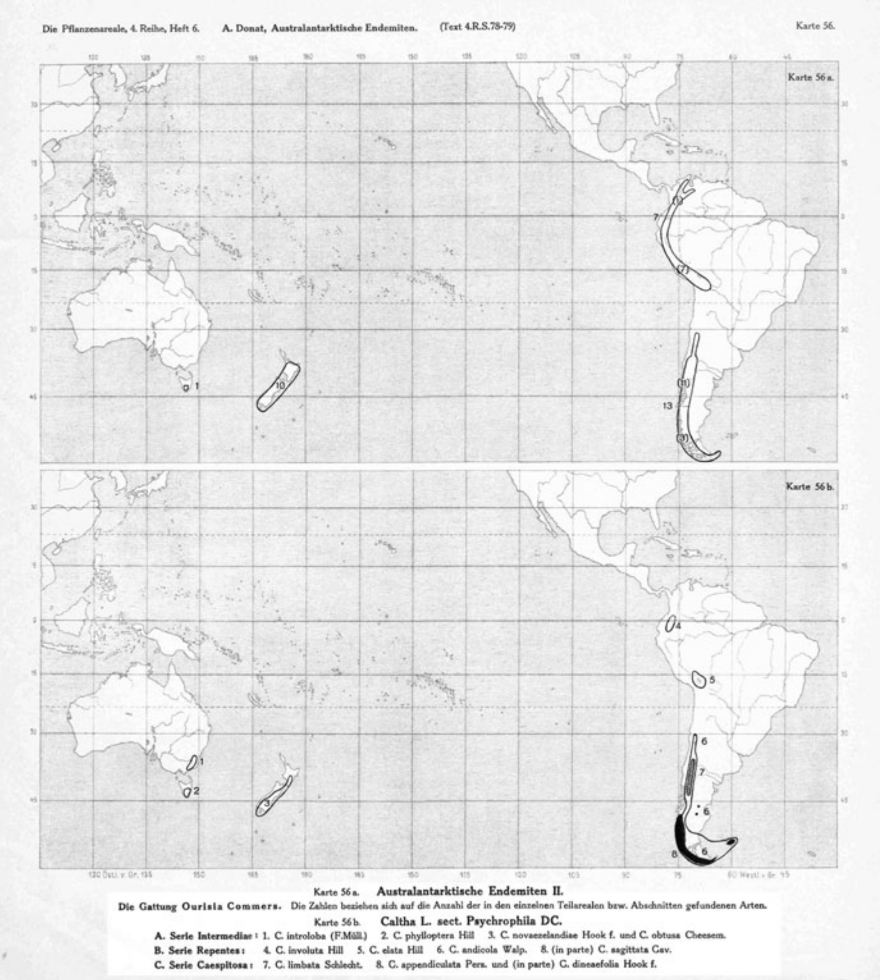

Fig. 3.1 Donat's distribution maps of the genera *Ourisia* and *Caltha*, in Hannig and Winkler (1926–1940)

be applied to it" (Wulff 1950, p 204). In any case Wulff (1950) was of the opinion that geographical [floristic] elements are fundamental for an understanding of a flora, and that an analysis of a flora should begin with these elements. Recently, floristic elements have been analysed for the North American flora north of México (Qian 1999), the East Asian flora (Qian et al. 2003), the flora of the Bolivian Andean valleys (López 2003), and the Ecuadorian superpáramo (Sklenar and Balslev 2007). In the case of the Chilean flora, the first attempt is the one of Reiche (1907). He was able to identify seven elements or *Kontingente* (Table 3.1). Later, Villagrán

Table 3.1 Floristic elements in the Chilean Flora

Kontingente (Reiche 1907)	Elements (Villagrán and Hinojosa 1997)
Tropical-American	Neotropical (wide/disjunct)
Andes Chile/Argentina	Endemic subantarctic forests/Chilean endemic
California/Mexican	–
Antarctic	Australasiatic (warm/cool)
Boreal (Europa, S Chile)	Wide
Pantropic	Pantropical
Introduced flora	–

and Hinojosa (1997) applied a similar classification to the woody genera of the Chilean temperate forests. They described eight floristic elements, including fossil taxa (Table 3.1).

A complementary approach to floristic elements is the so called "track analysis", which has been integrated into biogeographical analysis by Croizat (1952, 1958).[1] This approach has been successfully used for the analysis and interpretation of disjunct distribution patterns (see Craw et al. 1999). Worth of mention here are the assessment of the Andean biota by Katinas et al. (1999); the biogeographic analysis of the Australian flora (Crisp et al. 1999); the analysis of North American Onagraceae (Katinas et al. 2004), the analysis of the Mexican cloud forests (Luna Vega et al. 2000) and the evolution of the Andean genus *Adesmia* series *Microphyllae* (Mihoc et al. 2006).

Hereafter, Reiche's (1907) attempt to analyse the geographical relationships of the Chilean vascular flora as a whole will be replicated under current floristic and chorological knowledge. Floristic elements have been usually recognized at the genus level (e.g. Good 1947), and this approach will be followed here. The use of the genus as analytical unit is not free of critique, but has the advantage of being systematic and replicable. The global distribution for each genus has been obtained from Wielgorskaya (1995) and Mabberley (1997, 2008). These global accounts have been checked with available monographs. As resumed in Sect. 2.2, by current knowledge, the Chilean flora is composed of 837 genera. Analysing the global distribution of each genus, 7 floristic elements were identified, plus 10 generalized tracks that eminently represent wide disjunct distributions (Table 3.2 and Fig. 3.17). The geographical classification of each genus is presented in Appendix A.

The dominant element is clearly the Neotropical one, with almost one third of the genera. It is followed by the Antitropical and Cosmopolitan element. The Pantropical, South-temperate and Endemic elements are equally important

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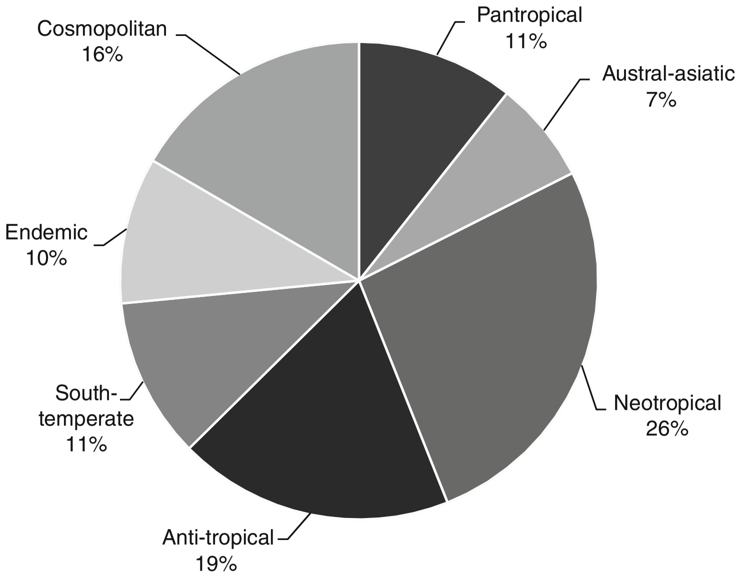
[1] Croizat apparently took the idea from van Steenis (1962) or maybe from C Skottsberg? (see Craw 1988 in Chap. 10).

Table 3.2 Floristic elements for the total vascular flora (updated January 2010)

Floristic elements	N° Genera
1. Pantropical	89
2. Australasiatic	58
3. Neotropical	221
4. Antitropical	156
5. South-temperate	91
6. Endemic	83
7. Cosmopolitan	139
Total	*837*



reasching around 10%, while the smallish element is the Australasiatic. All elements will be revised hereafter.

3.1.1 Pantropical Floristic Element

Genera grouped in this element grow mainly in tropical regions (pantropics), sometimes extending into subtropical and/or temperate areas (Fig. 3.2). This element includes 89 genera. The families with the greatest number of genera are Asteraceae (9 genera), Fabaceae (6), Poaceae and Cyperaceae (5 each). The most species-rich genera are *Dioscorea, Conyza,* and *Nicotiana*. Few genera occur over the whole country (e.g *Conyza*), other are restricted to northern Chile (e.g. *Notholaena, Spilanthes, Gomphrena*). Most are found in central-south Chile, disjunct from the rest of their distribution area (e.g. *Cryptocarya, Cissus, Glinus, Passiflora, Dodonaea, Dennstaedtia, Sigesbeckia, Pelletiera, Pouteria, Beilschmiedia, Wolffiella, Mikania*) (see examples in Fig. 3.3).

Note: *Megalastrum* and *Lippia* are included in this element despite being restricted to the American and African tropics. *Alonsoa* was included here, too, even though the majority of its species are found in the Neotropics, because two of its species occur in South Africa.

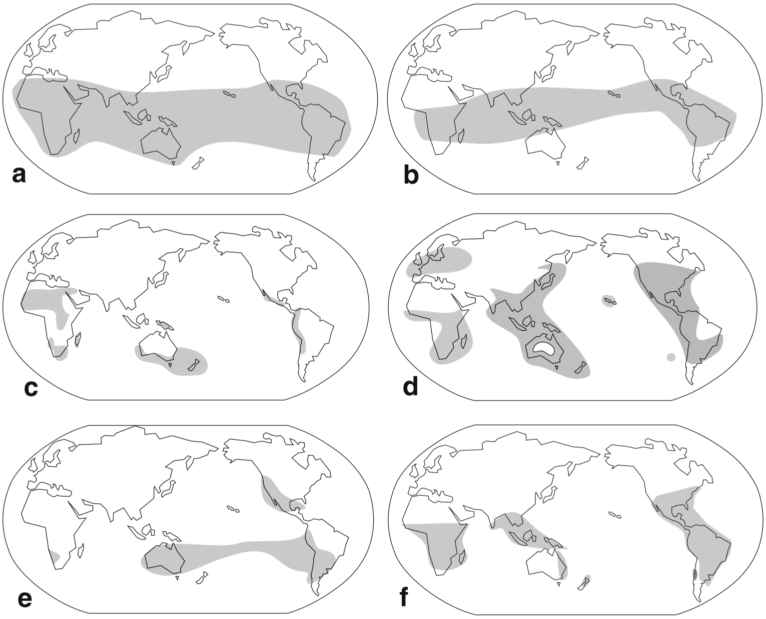


Fig. 3.2 Distribution of several genera exemplifying the pantropical floristic element: **a** *Acacia* (Fabaceae); **b** *Bacopa* (Veronicaceae); **c** *Cotula* (Asteraceae); **d** *Lobelia* (Campanulaceae); **e** *Nicotiana* (Solanaceae); **f** *Passiflora* (Passifloraceae) (diverse sources in Moreira-Muñoz (2007))

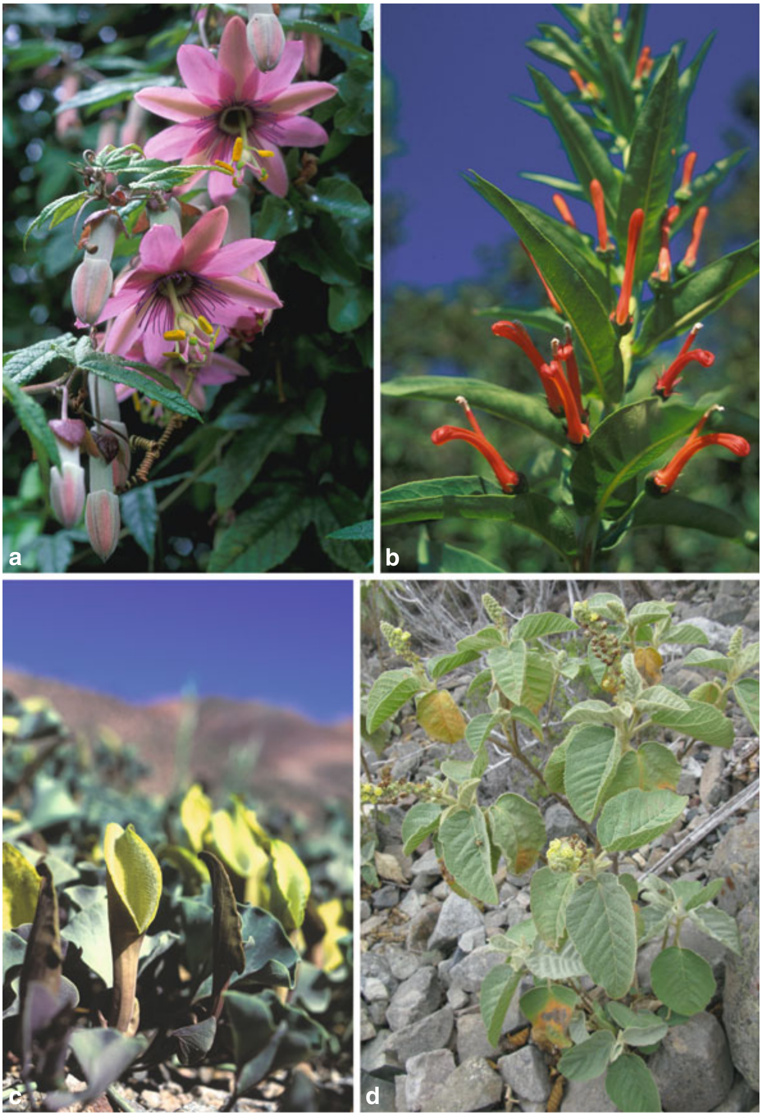


Fig. 3.3 Representative species of genera pertaining to the *pantropical* element: **a** *Passiflora pinnatistipula*, Quebrada del Tigre; **b** *Lobelia excelsa*, Ocoa; **c** *Aristolochia bridgesii*; Río Hurtado; **d** *Croton chilensis*, Paposo (photo credits: **a**–**d** A. Moreira-Muñoz)

3.1.2 Australasiatic Floristic Element

This element comprises genera from the South Pacific, i.e. Australasia as well as South America, and the Pacific islands (Fig. 3.4). Some genera are restricted to temperate subantarctic latitudes; others extend their distribution into tropical regions in South-East Asia or in South America. The components of this element

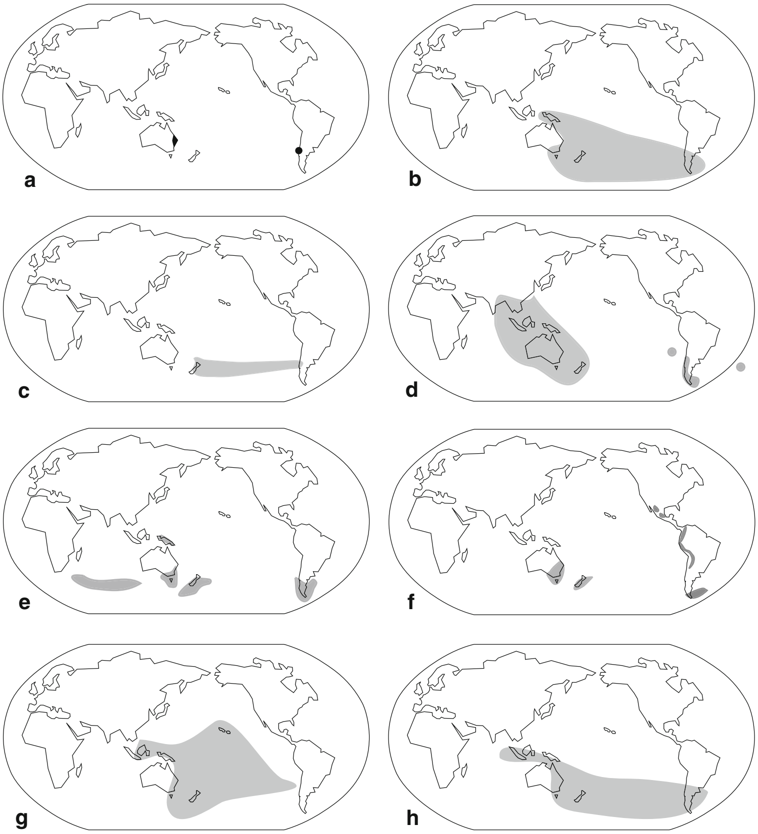


Fig. 3.4 Distribution of several genera exemplifying the australasiatic floristic element: **a** *Berberidopsis* (Berberidopsidaceae); **b** *Hebe* (Veronicaceae); **c** *Jovellana* (Calceolariaceae); **d** *Lagenophora* (Asteraceae); **e** *Leptinella* (Asteraceae); **f** *Oreomyrrhis* (Apiaceae); **g** *Coprosma* (Rubiaceae); **h** *Rytidosperma* (Poaceae) (diverse sources in Moreira-Muñoz (2007))

can be traced to the Gondwana era, as a once-continuous cool-temperate flora, now scattered into a relict distribution by tectonic movements. Therefore some authors recognize explicitly the austral floras as a "Gondwanan element" (Barlow 1981; Nelson 1981; Hinojosa 2005), building an austral floristic realm (see Sect. 4.2).

The australasiatic floristic element comprises 58 genera (see examples in Fig. 3.5). The families with the greatest number of genera are Asteraceae (4) and Poaceae, Apiaceae, Cyperacea, Rubiaceae, and Proteaceae, all with 3 genera. Within these genera, 3 generalized tracks based on superimposing distributions have been identified.

Austral-antarctic track

This track comprises genera occurring in southernmost South America, New Zealand, Eastern Australia and Tasmania. It was previously described as *South Pacific track* by Crisp et al. (1999).

Fig. 3.5 Representative species of genera pertaining to the *australasiatic* element: **a** *Berberidopsis corallina*, Concepción; **b** *Embothrium coccineum*, Vilches; **c** *Eucryphia glutinosa*, Antuco; **d** *Orites myrtoidea*, Antuco; **e** *Fuchsia magellanica*, Los Angeles (photo credits: **a** M. Muñoz-Schick; **b**–**e** A. Moreira-Muñoz)

It numbers 30 genera, e.g. *Luzuriaga, Eucryphia, Prumnopitys, Jovellana, Raukaua*. Most of these genera are restricted to the southern temperate forests, but some of them reach northernmost Chile (e.g. *Azorella, Cortaderia*). Some genera reach Central Chile, disappear in the Atacama and reappear in the northern Andes (e.g. *Fuchsia, Lomatia, Prumnopitys*). *Haloragis* is an austral genus that reaches the Juan Fernández islands, but not the continent.

Tropical Pacific track

This track comprises genera occurring in southernmost South America, New Zealand, Eastern Australia and/or Tasmania, some also extending to New Guinea, Malesia, and even to East Asia.

It numbers 24 genera, e.g. *Abrotanella, Araucaria, Nothofagus, Lagenophora, Coprosma,* and *Hebe.* Many genera are restricted to the southern temperate forests, but a few reach northernmost Chile (e.g. *Colobanthus, Muehlenbeckia*). Some reach central Chile, disappear in the Atacama and reappear in the northern Andes (e.g. *Citronella, Uncinia, Oreobolus*). *Doodia* is widespread in the Pacific till Isla de Pascua, but does not occur in continental Chile. *Dicksonia, Arthropteris, Coprosma,* and *Santalum* are austral genera that are present in the Juan Fernández Islands, and are also absent from the continent. The genus *Santalum* is considered in this account for analytical purposes, in spite of the fact that due to human pressure, *Santalum fernandezianum* is extinct from Juan Fernández (see Box 5.1).

Circum-austral track

This track comprises a few genera that extend their distribution through Australasia to southern Africa and/or Madagascar. These are only 4 genera: *Ficinia*, *Nertera, Rumohra,* and *Wahlenbergia*.

3.1.3 Neotropical (American) Floristic Element

Strictly speaking, this is an *American* element, but *Neotropical* has been used for a long time in the phytogeographical literature (Fig. 3.6). This element is the most important one in the Chilean flora: it includes 221 genera, mostly from the Asteraceae (53), followed by Cactaceae and Poaceae (each 12), Brassicaceae and Solanaceae (each 11) (see examples in Fig. 3.7). Four generalized tracks have been identified within this element:

Wide Neotropical track

This track comprises genera from South America, extending to Mexico, to the south-western USA or even to southern Canada. The main massing, however, lies in the intertropics. Many species also occur in Brazil. It numbers 65 genera, e.g. *Ageratina, Baccharis, Calceolaria, Dalea, Nasa, Nassella.* Some are found in all of Chile (e.g. *Baccharis, Gamochaeta, Calceolaria, Calandrinia*), other just in northern Chile (e.g. *Coreopsis, Bouteloua*), and many genera occur in central/south Chile, disjunct from the core neotropical

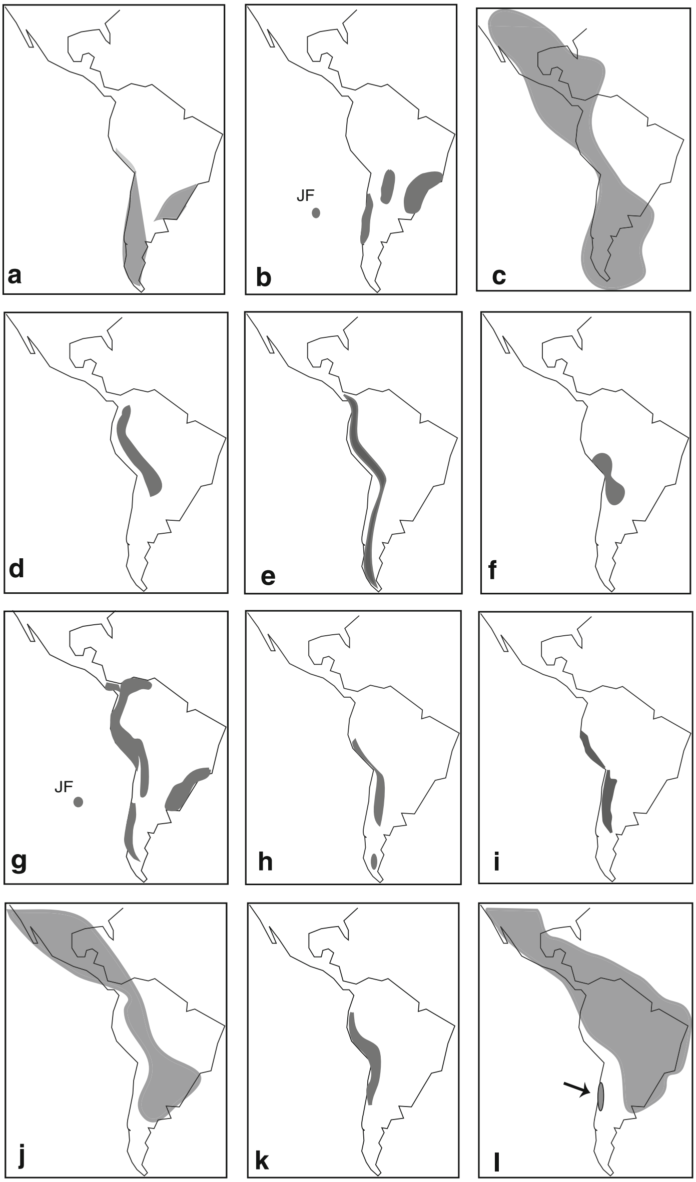


Fig. 3.6 Distribution of several genera exemplifying the neotropical floristic element: **a** *Alstroemeria* (Alstroemeriaceae); **b** *Azara* (Salicaceae); **c** *Calceolaria* (Calceolariaceae); **d** *Cremolobus* (Brassicaceae); **e** *Desfontainia* (Desfontainiaceae); **f** *Eremodraba* (Brassicaceae); **g** *Escallonia* (Escalloniaceae); **h** *Eudema* (Brassicaceae); **i** *Malesherbia* (Malesherbiaceae); **j** *Mecardonia* (Veronicaceae); **k** *Nototriche* (Malvaceae); **l** *Vasconcellea* (Caricaceae) (diverse sources in Moreira-Muñoz (2007))

Fig. 3.7 Representative species of genera pertaining to the *neotropical* element: **a** *Tweedia birostrata*, Concón; **b** *Chloraea alpina*, Vilches; **c** *Caiophora chuquitensis*, Chusmiza; **d** *Colletia ulicina*, Los Queñes; **e** *Escallonia pulverulenta*, Granizo; **f** *Mentzelia scabra*, Río Hurtado; **g** *Calceolaria cana*, Vilches (photo credits: **a** S. Elórtegui Francioli; **b–f** A. Moreira-Muñoz; **g** Francisco Casado)

distribution area (e.g. *Piptochaetium, Stenandrium, Chusquea, Calydorea, Chaptalia, Ugni*).

Wide Andean track

This track comprises genera ranging from southern Chile to Colombia (and Costa Rica), but does not reach North America. It numbers 29 genera, e.g. *Chuquiraga, Myrteola, Polylepis, Geoffroea.* Some are found in all of Chile (e.g. *Perezia, Escallonia*); others only in northernmost (*Dunalia, Cremolobus*) or north-Central Chile (*Exodeconus, Nototriche*); many distributions are disjunct between southern Chile/Argentina and northern South America (e.g. *Llagunoa, Myrcianthes, Dysopsis, Blepharocalyx, Desfontainia, Myrteola*).

Central Andean track

This track comprises genera found in the Central Andes, in Perú, Bolivia, northern Argentina and north-central Chile.

It numbers 86 genera, e.g. *Loasa, Philibertia,* and *Oxychloë,* comprising by far many Asteraceae (18 genera) and Cactaceae (11). Most genera occur in a continuous range from northern Chile to Peru/Bolivia (e.g. *Acantholippia, Balbisia, Neowerdermannia, Oreocereus, Tunilla, Pycnophyllum, Philibertia*), others occur disjunctly between central Chile/Perú (*Eccremocarpus, Kageneckia, Tetraglochin, Nassauvia, Weberbauera*). 10 genera are restricted to central/northern Chile and adjacent Argentina (e.g. *Cruckshanksia*, *Monttea, Urmenetea, Werdemannia, Lenzia, Kurzamra*).

South-Amazonian track

This track comprises genera found in central Chile, northern Argentina, Uruguay, Paraguay, and south-eastern Brazil.

It numbers 41 genera, e.g. *Colliguaja, Quillaja, Azara, Tweedia, Myrceugenia, Viviania,* and *Dasyphyllum.* Most of these genera occur disjunctly between Central Chile and SE Brazil (see Sect. 3.2).

3.1.4 Antitropical Floristic Element

This element comprises genera found both in the northern and in the southern temperate regions, but are absent from the intervening tropics. This pattern is commonly referred to as the *amphi-tropical* pattern in the literature, but as W. Welß (pers. comm.) correctly noted, the most appropriate term would be "antitropic", since "amphitropical" means "both tropics". In Cox's (1990) opinion, the most appropriate term to be used would be "amphitemperate", but since it includes subtropical distributions, the most suited term is *antitropical* (see also Wen et al. 2002; Glasby 2005; Parenti 2007) (Fig. 3.8).

This element includes 156 genera. The families with the greatest number of genera are Asteraceae (26), Poaceae (23), Fabaceae and Polemoniaceae (each 8), and Boraginaceae (7) (see examples in Fig. 3.9).

Note: *Menodora* (Oleaceae) is considered as an antitropical genus, since its distribution range includes both subtropical Americas, and subtropical South Africa (map in Muñoz-Schick et al. 2006).

One of the naturalists referring to this element was G. Treviranus (1803), even though he did not recognise it formally. While discussing the components of his *Antarktische Flor*, he noticed that there was a floristic relationship between southern South America and New Zealand, and that some of these genera have their main

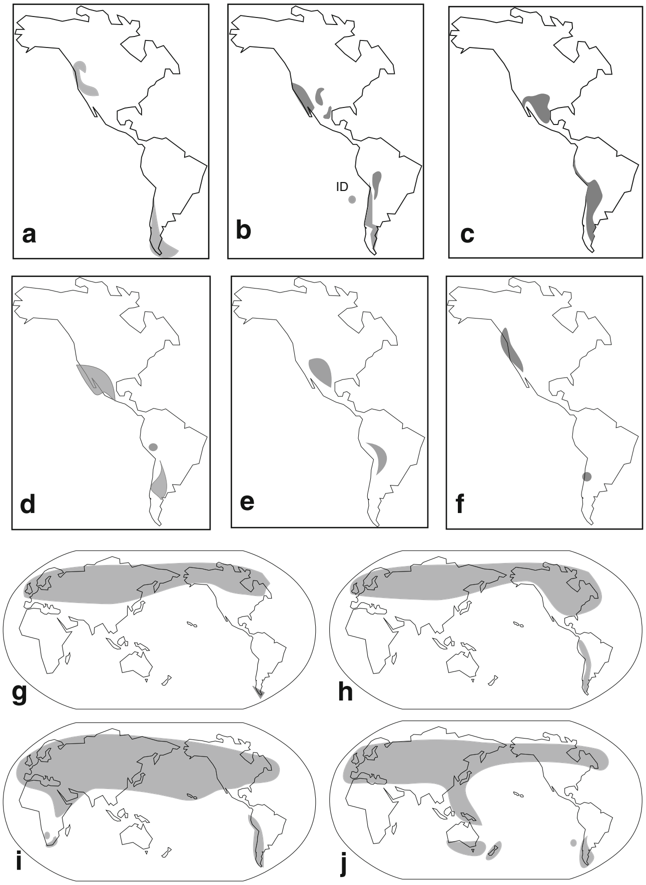


Fig. 3.8 Distribution of several genera exemplifying the antitropical floristic element: **a** *Agoseris* (Asteraceae); **b** *Frankenia* (Frankeniaceae); **c** *Hoffmannseggia* (Fabaceae); **d** *Larrea* (Zygophyllaceae); **e** *Mancoa* (Brassicaceae); **f** *Tropidocarpum* (Brassicaceae); **g** *Androsace* (Primulaceae); **h** *Antennaria* (Asteraceae); **i** *Artemisia* (Asteraceae); **j** *Euphrasia* (Orobanchaceae) (diverse sources in Moreira-Muñoz (2007))

distribution in the northern and southern temperate zones (e.g. *Pinguicula, Salix*, *Ribes*) (Treviranus 1803, pp 131–132). Du Rietz (1940) and many others called it the pattern of "bipolar plant distribution". The antitropical element was treated in depth in several papers that arose from a symposium at the beginning of the 1960s (Constance 1963) (see Sect. 3.2). The antitropical element includes many variable distribution patterns, some restricted, and others very wide. Within this element three generalized tracks were identified.

Wide antitropical track (bipolar-temperate element)

This track comprises genera found in Eurasia, North America, southern South America, some also ranging into the montane American tropics.

Fig. 3.9 Representative species of genera pertaining to the *antitropical* element: **a** *Ribes punctatum*, Rio Clarillo; **b** *Amblyopappus pusillus*, Los Vilos; **c** *Clarkia tenella*, Los Molles; **d** *Larrea nitida*, Illapel; **e** *Bahia ambrosioides*, Huentelauquén (photo credits: **a**–**e** A. Moreira-Muñoz)

It numbers 85 genera, e.g. *Astragalus, Fagonia, Valeriana, Vicia.* Many of these genera are found in all of Chile (e.g. *Hypochaeris, Cystopteris, Bromus, Valeriana*). Few are restricted to northern Chile (e.g. *Woodsia*), while most are restricted to southern Chile (e.g. *Rhamnus, Potentilla, Adenocaulon, Saxifraga*), some of them even to the southernmost Magallanes region (*Androsace, Botrychium, Chrysosplenium*).

Antitropical Pacific track

All the genera grouped in this track have a disjunct distribution between south-western North America and South America, occurring mostly in subtropical and tropical deserts.

This track numbers 58 genera, e.g. *Agalinis, Hoffmannseggia, Camissonia, Tiquilia*, and several Polemoniaceae (*Gilia, Microsteris, Ipomopsis, Leptosiphon, Navarretia*). Few genera are found along the whole latitudinal gradient in Chile (e.g. *Phacelia*). Some occur in northern Chile and the Central Andes (e.g. *Mancoa, Cistanthe, Tarasa*), but many are found only in Central Chile and south-western North America (e.g. *Blennosperma, Errazurizia, Hoffmannseggia, Lastarriaea, Navarretia, Plectritis, Tropidocarpum*).

Circum-Pacific track

This track comprises genera with a disjunct distribution in North/Central America and South America that have also representatives in Australasia. It numbers 12 genera: *Distichlis, Flaveria, Gochnatia, Gaultheria, Lilaeopsis, Microseris, Plagiobothrys, Sicyos, Soliva,* and *Weinmannia.* Only two circum-Pacific genera reach South Africa: *Acaena* and *Carpobrotus*, while *Weinmannia* reaches Madagascar.

3.1.5 South-Temperate Floristic Element

This element comprises genera found in the Andes cordillera in Chile and in adjacent Argentina (Fig. 3.10).

It includes 91 genera. The families with the greatest number of genera are Asteraceae (11), Apiaceae (6), and Alliaceae, Brassicaceae, Solanaceae (each with 4 genera) (see examples in Fig. 3.11). The half of the Chilean conifer genera belong to this element (*Austrocedrus*, *Fitzroya, Pilgerodendron, Saxegothaea*). Most genera within this element are restricted to the southern temperate forests (e.g. *Boquila, Drapetes, Embothrium, Laureliopsis*) and Patagonia (*Eriachaenium, Lecanophora, Lepidophyllum, Saxifragella, Xerodraba*). Some are represented in the temperate zone but reaching more arid environments to the north, like *Triptilion, Nastanthus, Trichopetalum*. The genus *Mulinum* reaches further north, at 21°S.

3.1.6 Endemic Floristic Element

This element comprises genera endemic to continental Chile, and the Chilean Pacific islands.

It numbers 83 genera, of which 16 pertain to the Asteraceae, 6 to the Cactaceae, and 4 to the Alliaceae (Table 3.3). Species-rich genera are *Copiapoa* (22 species), *Leucocoryne* (14),[2] *Dendroseris* (11), and *Robinsonia* (8). Remarkably, most

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[2] *Leucocoryne* is an interesting case of taxonomic inflation, because the Southern Cone Checklist mentions 45 species, most of them lacking justification.

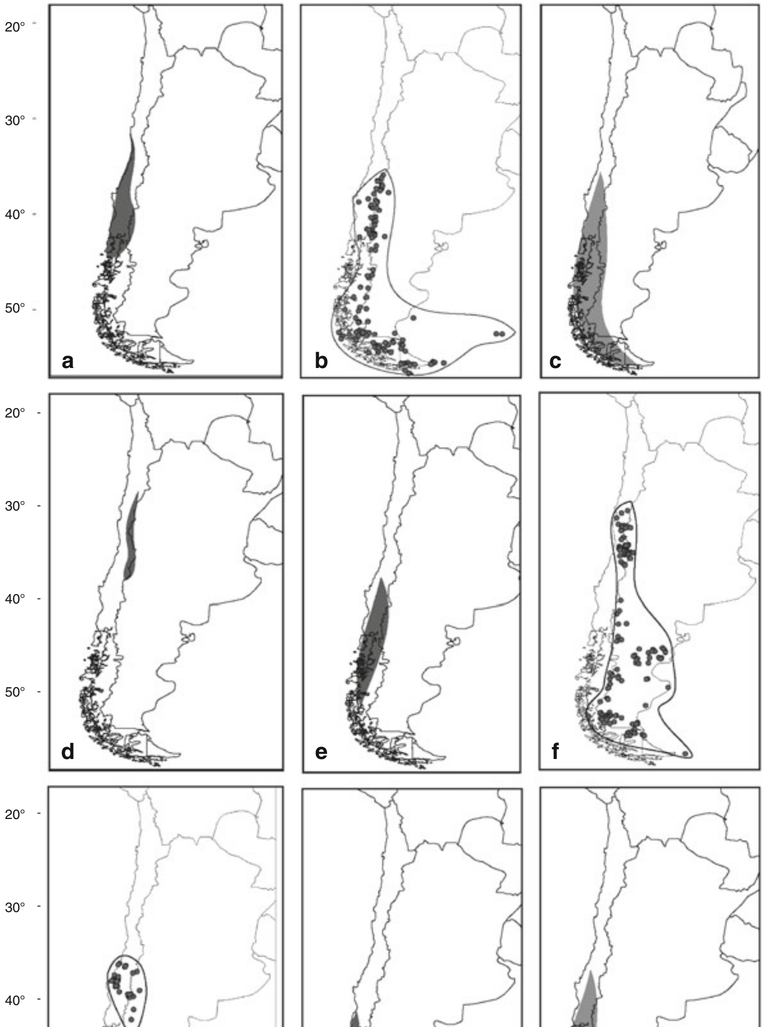

Fig. 3.10 Distribution of several genera exemplifying the South-temperate floristic element: **a** *Aextoxicon* (Aextoxicaceae); **b** *Chiliotrichum* (Asteraceae); **c** *Embothrium* (Proteaceae); **d** *Laretia* (Apiaceae); **e** *Laureliopsis* (Atherospermataceae); **f** *Nardophyllum* (Asteraceae); **g** *Notopappus* (Asteraceae); **h** *Philesia* (Philesiaceae); **i** *Tepualia* (Myrtaceae) (source: monographs and SGO collections)

Fig. 3.11 Representative species of genera pertaining to the *south-temperate* element: **a** *Schizopetalon dentatum*, Concón; **b** *Cruckshanksia pumila*, Llanos de Challe; **c** *Aextoxicon punctatum*, Fray Jorge; **d** *Philesia magellanica*. Photo/illustration credits: **a**, **b** A. Moreira-Muñoz; **c** Walter Welss; **d** illustration from Macloskie G. (1903–1906) In: Scott WB. Flora Patagonica. Reports of the Princeton University Expeditions to Patagonia, 1896–1899, Princeton

endemic genera are monospecific, an aspect that was already noticed by Reiche (1905) (Fig. 3.12) (Table 3.3).

Most genera (67) are endemic to continental Chile (e.g. *Adenopeltis, Balsamocarpon, Huidobria, Leontochir, Pitavia*) (Figs. 3.13, 3.14), while 16 genera are endemic to the Chilean Pacific islands, especially Juan Fernández (e.g. *Dendroseris, Lactoris, Cuminia, Juania*) (Chap. 5, Tables 5.2 and 5.3). The endemic element will be further discussed in Chap. 4, and the Juan Fernández flora in Chap. 5.

Table 3.3 Genera endemic to continental Chile

Genus	Family	N° species	Genus	Family	N° species
			Legrandia	Myrtaceae	1
Adenopeltis	Euphorbiaceae	1	*Leontochir*	Alstroemeriaceae	1
Anisomeria	Phytolaccaceae	2	*Leptocarpha*	Asteraceae	1
Araeoandra	Vivianiaceae	1	*Leucocoryne*	Alliaceae	14
Avellanita	Euphorbiaceae	1	*Leunisia*	Asteraceae	1
Bakerolimon	Plumbaginaceae	1	*Marticorenia*	Asteraceae	1
Balsamocarpon	Fabaceae	1	*Metharme*	Zygophyllaceae	1
Bridgesia	Sapindaceae	1	*Microphyes*	Caryophyllaceae	3
Calopappus	Asteraceae	1	*Miersia*	Alliaceae	1
Cissarobryon	Vivianiaceae	1	*Miqueliopuntia*	Cactaceae	1
Conanthera	Tecophilaeaceae	5	*Moscharia*	Asteraceae	2
Copiapoa	Cactaceae	22	*Neoporteria*	Cactaceae	6
Cyphocarpus	Campanulaceae	3	*Notanthera*	Loranthaceae	1
Desmaria	Loranthaceae	1	*Ochagavia*	Bromeliaceae	4
Dinemagonum	Malpighiaceae	1	*Oxyphyllum*	Asteraceae	1
Dinemandra	Malpighiaceae	1	*Peumus*	Monimiaceae	1
Epipetrum	Dioscoreaceae	3	*Phrodus*	Solanaceae	1
Ercilla	Phytolaccaceae	2	*Pintoa*	Zygophyllaceae	1
Eriosyce	Cactaceae	5	*Pitavia*	Rutaceae	1
Eulychnia	Cactaceae	6	*Placea*	Amaryllidaceae	5
Fascicularia	Bromeliaceae	1	*Pleocarphus*	Asteraceae	1
Francoa	Francoaceae	1	*Podanthus*	Asteraceae	2
Gethyum	Alliaceae	2	*Reicheella*	Caryophyllaceae	1
Gomortega	Gomortegaceae	1	*Sarmienta*	Gesneriaceae	1
Guynesomia	Asteraceae	1	*Scyphanthus*	Loasaceae	2
Gymnachne	Poaceae	1	*Speea*	Alliaceae	1
Gypothamnium	Asteraceae	1	*Tecophilaea*	Tecophilaeaceae	2
Hollermayera	Brassicaceae	1	*Tetilla*	Francoaceae	1
Homalocarpus	Apiaceae	6	*Thelocephala*	Cactaceae	6
Huidobria	Loasaceae	2	*Traubia*	Amaryllidaceae	1
Ivania	Brassicaceae	1	*Trevoa*	Rhamnaceae	1
Jubaea	Arecaceae	1	*Valdivia*	Escalloniaceae	1
Lapageria	Philesiaceae	1	*Vestia*	Solanaceae	1
Latua	Solanaceae	1	*Zephyra*	Tecophilaeaceae	1

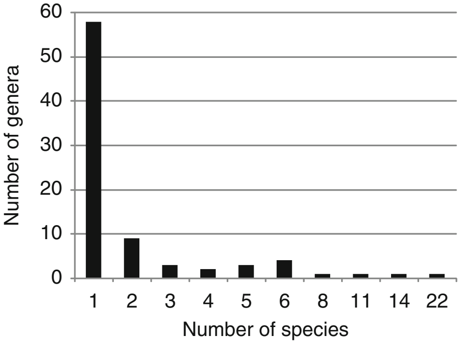

Fig. 3.12 Number of endemic genera versus the number of species

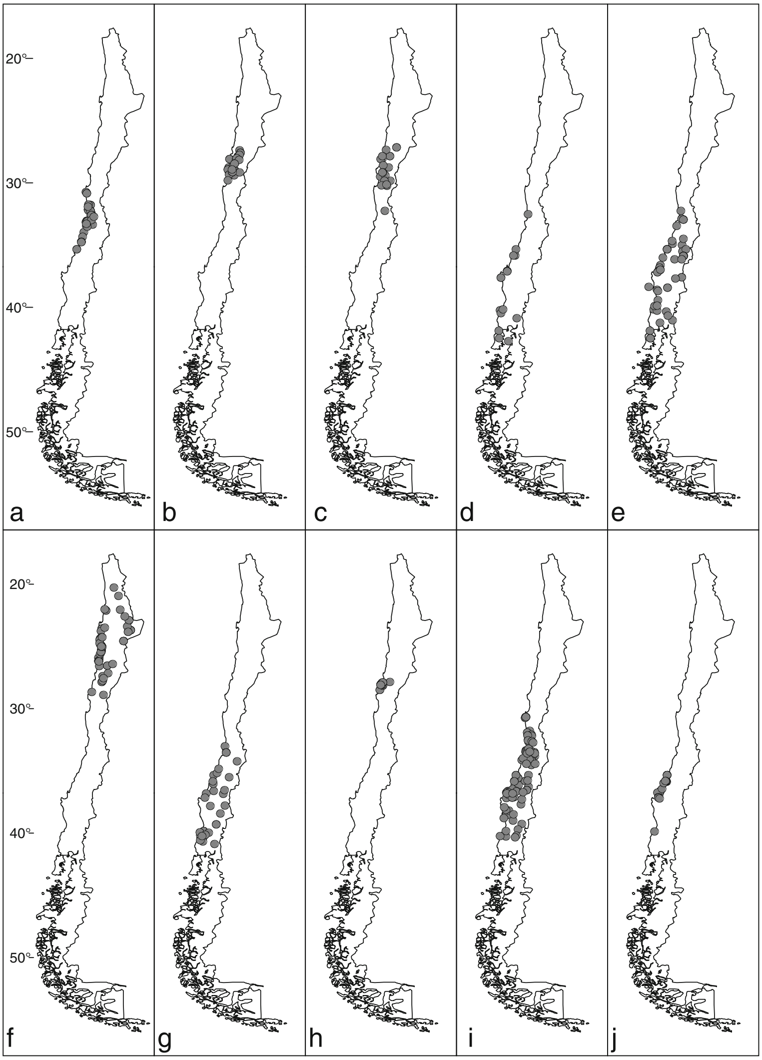

Fig. 3.13 Distribution of several genera exemplifying the endemic floristic element: **a** *Adenopeltis* (Euphorbiaceae); **b** *Balsamocarpon* (Fabaceae); **c** *Cyphocarpus* (Campanulaceae); **d** *Fascicularia* (Bromeliaceae); **e** *Francoa* (Francoaceae); **f** *Huidobria* (Loasaceae); **g** *Lapageria* (Philesiaceae); **h** *Leontochir* (Alstroemeriaceae); **i** *Peumus* (Monimiaceae); **j** *Pitavia* (Rutaceae) (source: collections SGO)

Fig. 3.14 Representative species of genera pertaining to the *endemic* element: **a** *Zephyra elegans*, Llanos de Challe; **b** *Pleocarphus revolutus*, Cuesta Pajonales; **c** *Bridgesia incisifolia*, La Serena; **d** *Leontochir ovallei*, Llanos de Challe; **e** *Speea humilis*, Caleu; **f** *Placea amoena*, Cuesta el Espino (photo credits: **a**–**f** A. Moreira-Muñoz);

3.1.7 Cosmopolitan Floristic Element

There are not many genera that can be considered as really cosmopolitan (Good 1947), e.g. some aquatic or semi-aquatic plants (*Sagittaria, Landoltia, Wolffia*),

Fig. 3.14 (continued) **g** *Jubaea chilensis,* Limache; **h** *Lapageria rosea*, Los Angeles; **i** *Gomortega keule*, specimen at the National Herbarium SGO; **j** *Scyphanthus elegans*, Concón (photo credits: **g**, **h**, **j** A. Moreira-Muñoz; **i** specimen scanned by Sergio Moreira)

some ferns and fern allies (*Adiantum, Isoetes, Lycopodium, Huperzia,*) or some really widespread terrestrial angiosperm genera like *Cyperus, Ceratophyllum, Gnaphalium, Geum, Juncus, Rubus, Ranunculus, Senecio* or *Scirpus.* Most genera included in this element have a wide distribution in more than two continents and more than two principal climatic zones (e.g. tropical and temperate) (Fig. 3.15). In fact, the element should be called *subcosmopolitan*, but *cosmopolitan* is more often used.

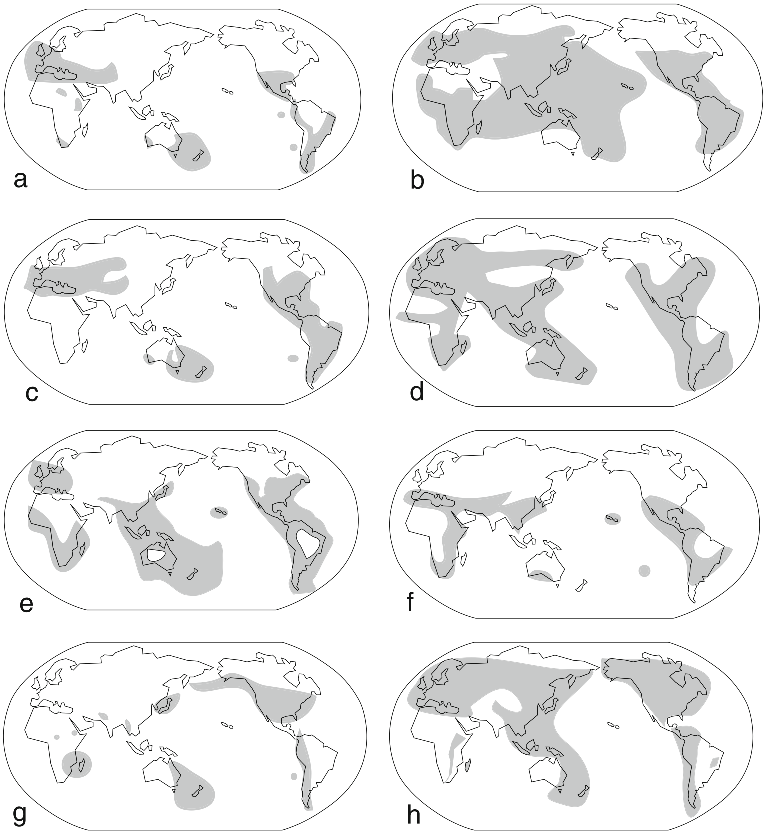

Fig. 3.15 Distribution of several genera exemplifying the cosmopolitan floristic element: **a** *Apium* (Apiaceae); **b** *Bidens* (Asteraceae); **c** *Eryngium* (Apiaceae); **d** *Gnaphalium* (Asteraceae); **e** *Hydrocotyle* (Apiaceae); **f** *Lycium* (Solanaceae); **g** *Mimulus* (Phrymaceae); **h** *Viola* (Violaceae) (sources: Meusel et al. (1978) and Meusel and Jäger (1992))

It numbers 139 genera, some of them occupying the whole country (e.g. *Asplenium, Gnaphalium, Ranunculus, Chenopodium, Silene*), some being restricted to the north (e.g. *Salvia*, *Chloris, Portulaca*), and most being found in central and southern Chile (*Ceratophyllum, Samolus, Aphanes, Geum, Glyceria, Panicum, Hypericum*) (see examples in Fig. 3.16). A few genera are restricted to the Magallanes region (*Huperzia, Landoltia*).

At the moment, the variety of distributions in this element prevents any attempt to classify these genera into different tracks, but this will certainly provide an interesting task for the future.

Fig. 3.16 Representative species of genera pertaining to the *cosmopolitan* element: **a** *Oxalis penicillata*, Portillo; **b** *Salvia paposana*, Paposo; **c** *Viola montagnei*, Laguna Negra; **d** *Euphorbia lactiflua*, Paposo; **e** *Polygala gnidioides*, Concón (photo credits: **a**–**e** A. Moreira-Muñoz)

3.2 To Be or Not To Be Disjunct?

Analysis of disjunct patterns has been one of the main tasks in biogeography since the earlier attempts to unravel biogeographic histories (e.g. Hofsten 1916). Interestingly, disjunctions are often treated as kind of "anomalies" in a supposedly dominant pattern of continuous geographical relationships. In the case of the Chilean vascular flora, it seems that disjunction is a common pattern and rather the rule. Most of the generalized tracks that illustrate main distribution patterns of

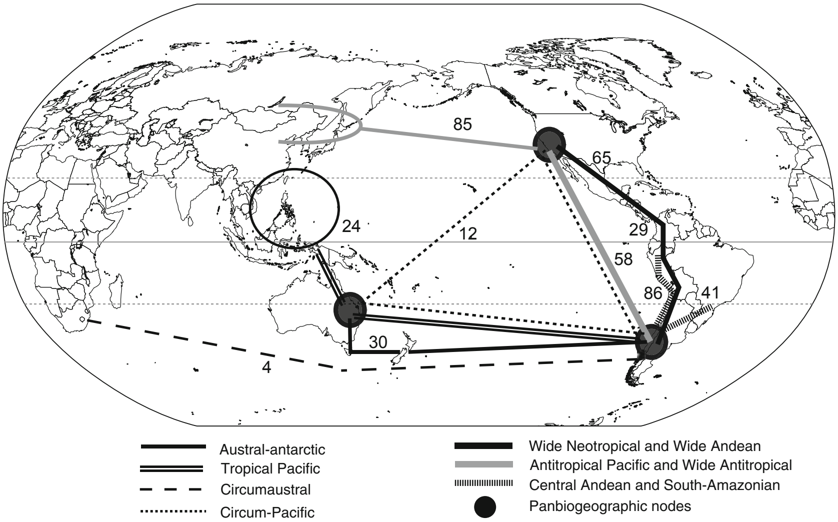

Fig. 3.17 Generalized tracks representing disjunct Chilean plant distributions. The zone of confluence of different tracks can be interpreted as a composite biogeographic zone or a panbiogeographic node (Heads 2004)

the Chilean genera connect territories separated by major physical barriers (oceans, cordilleras) (Fig. 3.17). Only the wide neotropical track (65 genera) and the Andean tracks (Wide Andean and Central Andean = 111 genera) encompass territories on a terrestrial continuum, but many of these genera show indeed a disjunct distribution pattern (e.g. *Ageratina, Bomarea, Dalea*). The South-Amazonian track comprises 39 genera that show a disjunct distribution between southern Chile and south-eastern Brazil (e.g. *Alstroemeria, Azara, Chloraea, Myrceugenia*). Another 85 genera compose a wide antitropical (disjunct) track, and 58 genera comprise a Pacific antitropical track, that connects disjunct genera from Chile/California, and several more reaching Australasia (11) in a circum Pacific track. The australasiatic element is composed of three tracks: an austral-antarctic track (30 genera) a South Pacific tropical track (24), and a circum-austral track (5 genera). Also many of the pantropical (e.g. *Cryptocarya, Cleome, Croton, Cissus, Passiflora*) and (sub)cosmopolitan genera (e.g. *Sanicula, Coriaria*) show a disjunction between their Chilean and their global distribution.

3.2.1 Pacific-Atlantic Disjunctions

Landrum (1981), while analyzing the phylogeny and biogeography of *Myrceugenia*, interpreted the disjunct distribution of this genus and other angiosperms between SE Brazil and central/South Chile as the result of the former existence of a continuous subtropical forest during Oligocene/Miocene times (see Sect. 1.2). According

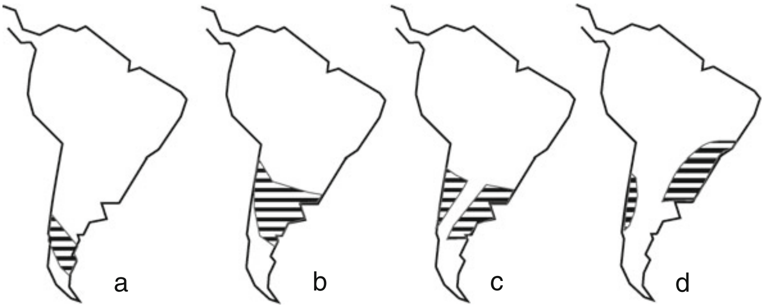

Fig. 3.18 Hypothesized range expansion and posterior fragmentation of the current disjunction in *Myrceugenia* during the Cenozoic: **a** Palaeocene/Eocene; **b** Oligocene; **c** Miocene; **d** current distribution (simplified from Landrum 1981)

to Landrum (1981), oceanic transgressions, the uplift of the Andes and climate changes permitted the migration of this range from the south towards the north into the configuration of the current distribution (Fig. 3.18).

Landrum (1981) noted that many other Chilean genera have similar disjunct distributions on the continent, such as *Araucaria, Bomarea, Crinodendron, Lithrea, Mutisia, Persea, Podocarpus, Perezia, Quillaja,* and *Viviania,* and *Weinmannia*. He interprets this patter as the result of the fragmentation of a continuous Palaeogene/Neogene flora that occupied the whole subtropical belt before and during the emergence of the Andes. The increasing aridity associated to the rise of the Andes since the Miocene onwards seems to be the cause of the "Dry Diagonal" and the origin of the isolation of the southern Chile/Argentina temperate forests (Box 3.1). The hypothesis that the uplift of the Andes fragmented formerly continuous, more mesic to hygric vegetation communities appears already in the earliest plant geographical work of Reiche about the Chilean composites (see Chap. 8).

Stuessy and Taylor (1995) noticed that the uplift of the Andes is commonly treated as a recent geological event, but it is a gradual process that has been active for more than 65 million years from the Palaeogene onwards or even earlier (Riccardi 1988) (Box 1.5). This uplift process seems to be one cause for the high habitat variability (geodiversity), and related high levels of endemism and plant diversity in the Andes (Arroyo et al. 1988; Donato et al. 2003; Mutke and Barthlott 2005). Several recent phylogenetic studies further support a direct association between the diversification of Andean plants (e.g. Hughes and Eastwood 2006; Scherson et al. 2008) and the major episodes of Andean uplift, from the early Miocene (about 20 mya) to the Pliocene (about 3 mya) (Hooghiemstra and van der Hammen 1998) (Box 1.5). The Andean uplift must have had a great influence on climate alterations which directly influenced: (a) adaptive processes, (b) plant migrations, and (c) speciation and extinction rates (Stuessy and Taylor 1995). Vicariant processes also must have been very important in shaping the evolution and distribution of South American plant groups (Landrum 1981) (Sect. 3.2).

Box 3.1 The Andean Dry Diagonal and the Fray Jorge Forest

The “Andean Dry Diagonal” or “Dry Diagonal of South America” is one of the main features of South American geography (De Martonne 1934; Messerli et al. 1998). The core of hyperaridity lies in the Atacama Desert, extending northwards along the Peruvian coast (Fig. 3.19), while semidesertic conditions dominate in Argentinean ecosystems like el Monte and Patagonia (Abraham et al. 2009). The origin of the “Andean Dry Diagonal” is close related to the uplift of the cordillera since the Miocene into the Pliocene, around 17 mya (Box 1.5).

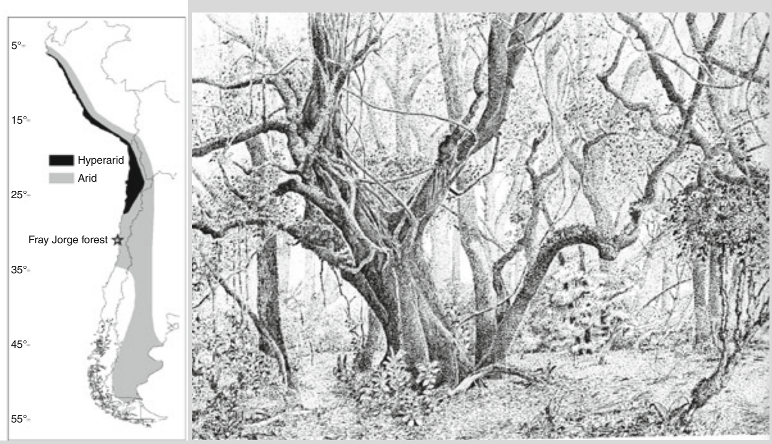

Fig. 3.19 **a** Arid Dry Diagonal (adapted from de Martonne 1934; Houston and Hartley 2003); **b** Fray Jorge Forest (original illustration by E. Sierra in Heusser (1971), by permission of The University of Arizona Press)

During the Pliocene/Pleistocene, the “Dry Diagonal” established under a global and regional cooling associated with the onset of Antarctic glaciation, the development of the Circumantarctic and Humboldt currents and the final Andean uplift (Sect. 1.2). This had at least three main effects on the north/central Chilean ecosystems (Villagrán et al. 2004):

(a) Fragmentation of the subtropical forests of the southern Cone and their restriction to the actual Pacific range (southern Chile/Argentina) and the Atlantic range (southeastern Brazil) (Landrum 1981).
(b) Expansion of the subtropical sclerophyllous forests in central Chile, adapted to a mediterranean climate.

(c) Fragmentation of the Chilean forests at their northern limit (30°S) due to the increase of aridity in the Atacama, and consequently the relict character of the forests which now depend on fog, as in the case of Fray Jorge.

The Fray Jorge Forest (30°40′S) persists today thanks to the capitation of fog water. It is surrounded by an arid territory and has long been of interest to botanists (e.g. Philippi 1884; Muñoz Pizarro and Pisano 1947; Skottsberg 1948; Croizat 1962; Troncoso et al. 1980). This forest is considered as the northernmost advance of a plant community that resembles the southern Valdivian forest. Its main component is the "olivillo" (*Aextoxicon punctatum*), a Chilean/Argentinian endemic that is the sole representative of the Aextoxicaceae, that has its main distribution in southern Chile (Núñez-Avila and Armesto 2006). Other representatives of the southern forests that have disjunct populations in Fray Jorge separated by hundreds of kilometres of the main distribution area to the South are: *Azara microphylla* (Salicaceae), *Lapageria rosea* (Philesiaceae), *Griselinia scandens* (Griseliniaceae), *Mitraria coccinea* and *Sarmienta repens* (Gesneriaceae), *Nertera granadensis* (Rubiaceae), and several species of ferns (e.g. *Hymenophyllum peltatum, Asplenium dareoides, Rumohra adiantiformis*), mosses and liverworts (Villagrán et al. 2004). According to these authors, the forest components of the Fray Jorge flora were already present in the mixed palaeofloras at the beginning of the Cenozoic (Palaeogene). They correspond to tropical and australasiatic lineages that occupied the Gondwana continent prior its fragmentation. They developed under warmer and more humid climatic conditions (Villagrán et al. 2004). The actual floristic characteristics of subtropical forests, affecting Fray Jorge as well as the Central Chilean sclerophyllous forests, established during the Miocene climatic optimum, when the mixed palaeofloras lost part of the australantarctic element and were enriched by new neotropical lineages (Sect. 1.2). At that time the connection with the subtropical forests still existed, under a warmer climate and a constant rainfall regime from the west and the east.

3.2.2 Antitropical (Pacific) Disjunctions

As revised by Wen and Ickert-Bond (2009), researchers have debated the causes of the antitropical (=amphitropical) disjunctions for over a century (e.g. Engler 1882; Bray 1900; Du Rietz 1940; Johnston 1940; Constance 1963; Raven and Axelrod 1974; Hunziker et al. 1972; Solbrig 1972; Werger 1973; Carlquist 1983).

Raven (1963) distinguished three classes of antitropical disjunctions: (a) the bipolar pattern (e.g. *Empetrum, Euphrasia*, see Du Rietz 1940); (b) the pattern encompassing temperate taxa disjunct between North and South America (e.g. *Collomia, Osmorhiza*, *Phacelia*); (c) the pattern showed by desert plants (e.g. *Errazurizia, Larrea, Tiquilia*).

Examples given above are at the genus level, but there are also disjunctions between identical or closely related species such as *Hoffmannseggia glauca* (Simpson et al. 2005), or *Tiquilia nuttallii* (Moore et al. 2006).

Werger (1973) revised the hypotheses that could explain these disjunctions: (a) long-distance dispersal; (b) stepping-stone migration across arid or semi-arid "islands" across the Andes; (c) land-bridges, according to van Steenis (1962) (Chap. 10), including wider coastal areas to the west of the continent; (d) polytopic origin of closely related species due to a widespread ancestor, i.e. parallel evolution of near-identical arid-adapted taxa from widely distributed tropical ancestors (cfr Johnston 1940; Barbour 1969).

Werger's opinion was, taking account of the taxa analysed, that the most plausible hypotheses were the polytopic speciation and the tropical origin of the ancestors of extant taxa, followed by vicariant speciation (Werger 1973, p 16). These conclusions were contrary to the dominant view, since from the 1960s on, most researchers favoured the explanation of long-distance dispersal by birds (Raven 1963; Cruden 1966; Carlquist 1983; 1972; Simpson and Neff 1985). "Small seeds occasionally adhere to birds and exceptionally may not fall off until the bird has reached a favourable habitat on the other side of the tropics. Considering the millions of birds that fly between temperate North and South America every year, some transport might happen at least at the rate postulated for the colonization of Hawaii which lies on no known migration route" (Raven 1963, p 153).

3.3 In the Search for Centres of Origin: Dispersal v/s Vicariance in the Chilean Flora

Linné believed that all species dispersed from Mount Ararat after leaving Noah's arch (Llorente Bousquets et al. 2003). Biogeography surpassed the myth but could not leave the eternal search for centres of origin, a paradigm that gained its strength in Darwin's *The Origin of Species*, and was further developed by the "New York School of biogeography" by renowned researchers such as WD Matthew, GG Simpson, PJ Darlington Jr and GS Myers (Nelson and Ladiges 2001).

Dispersalist biogeography is based on the assumption that taxa originated in relatively small areas (centres of origin) and therefore tries to reconstruct the routes that organisms covered to colonize known past or present ranges. On the other hand, many authors saw problems in the search for the centres of origin and migration routes, like botanist Stanley Cain, who asserted that "... [centres of origin] have been largely accepted without question, despite the lack of substantiating data in some cases, and have been variously and somewhat loosely employed" (Cain 1944, p 185). Croizat called ironically dispersalism "the science of the curious, the mysterious, the improbable" (Croizat 1958).

Only from the 1980s onwards, disjunct distribution patterns on the continent and between continents began to be interpreted as the result of vicariance (e.g. Landrum 1981). This was contemporary to the appearance of a new biogeographic paradigm of *vicariance (cladistic) biogeography* (Nelson and Platnick 1981; Humphries and Parenti 1999) (Box 3.2).

Box 3.2 Vicariance Biogeography

Gareth Nelson and Norman Platnick developed this approach based on the work of León Croizat (Nelson and Platnick 1981), but vicariance as an explanation of disjunct distributions is already found in the early works of von Ihering (1893), in F. Ratzel's biogeography (Ratzel 1901) and in writings from J.D. Hooker (Turrill 1953). In vicariance biogeography distributions of monophyletic groups of taxa over areas are explained by the reconstruction of area cladograms (Fig. 3.20). These area cladograms are hypotheses of historical relationships between areas and are derived from phylogenetic and distributional information of the monophyletic groups concerned. A first-order explanation for correspondence between phylogenetic relationships of taxa and historical relationships among areas is vicariance (Humphries and Parenti 1999). Hovenkamp (1997) even proposed that the object of historical biogeography may be specifically the vicariance events and not necessarily the areas. According to Wiley (1988), vicariance biogeography arose from three events: (1) the emergence of plate tectonics as the major geological paradigm; (2) the emergence of phylogenetic systematics; and (3) the panbiogeography of Croizat that abandoned the centres of origin approach in favor of vicariance explanations. Vicariance biogeography have been also called cladistic biogeography, but Parenti and Ebach (2009) suggests that this last term shall be restricted to "those methods that cpnvert taxon cladograms into areagrams (area cladograms) and that infer biotic area homologs from such areagrams" (Parenti and Ebach 2009, p 121).

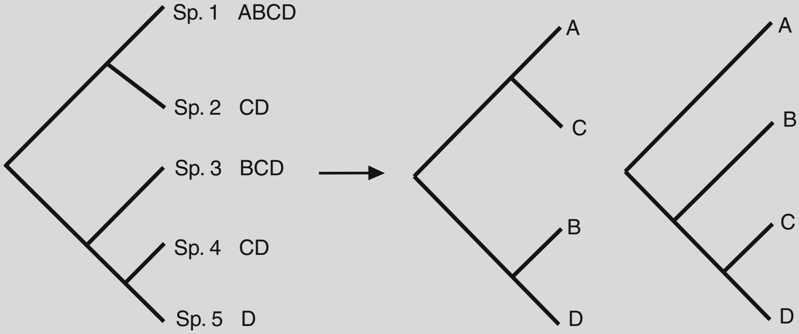

Fig. 3.20 Two possible resolved area cladograms (areagrams) for five hypothetical species distributed in four areas (adapted from Parenti and Ebach 2009)

Nelson and Platnick's approach was much extended during the 1980s by many researchers, announcing a change in the biogeographic paradigm from the Darwinian dispersalist biogeography (Zunino and Zullini 2003).

Vicariance biogeography reached more satisfactory explanations for the disjunct pattern of many traditional studied groups like *Nothofagus* (Humphries 1981) (Chap. 9). With major emphasis on phylogenetic relationships the approach is related to vicariance biogeography (with several divergences) and is called phylogenetic biogeography, as developed by Lars Brundin inspired by Willi Hennig's principles (Williams and Ebach 2008) (Box 10.3). "Taking a survey of the biogeographical literature of the last decades we are faced with a rich flora of concepts like 'means of dispersal', 'spread potential', 'jumps', 'island hopping' 'sweep-stakes', and 'filter bridges', all intermingled in peripheral discussions overlooking the ever present central problem: which is the sister group of the discussed group, and where is it living?" (Brundin 1966, p 5). Several Chilean endemic genera have been investigated in relation to their closest relatives. Renner (2004) proposed that *Peumus* (Monimiacea) diverged from the *Monimia*/*Palmeria* line about 76 mya, by the disruption of a formerly continuous range that stretched from Chile across Antarctica and the Kerguelen plateau to Madagascar (see Sect. 1.2). Another charismatic genus is *Gomortega*: its fossils are only known from the Late Oligocene-Early Miocene (*Gomortegoxylon*, Nishida et al. 1989), but molecular analysis suggests an age of 100 million years for *Gomortega* (Renner 2004) (Fig. 3.21 and Fig. 3.14). Whether the Gomortegaceae was more numerous in the past and suffered from extremely high extinction rates or just had a very slow speciation rate (just one species existing for 100 mya!) is a matter of speculation.

Fig. 3.21 Phylogenetic and geographic relationships of *Gomortega* (according to Renner 2004)

From the Philesiaceae, Vinnersten and Bremer (2001) suggested that the ancestor of *Ripogonum, Lapageria* (Chilean endemic), and *Philesia* (South-temperate) was distributed in South America and New Zealand and possibly also in Australia. The isolation of South America from Australia and New Zealand corresponds to a split off of the South American *Lapageria* and *Philesia* from the Australian–New Zealand *Ripogonum*, estimated at ca 47 mya (Figs. 3.22, 3.11 and 3.14). The same interpretation is possible for the split between Alstroemeriaceae and Luzuriagaceae, so it may be that termination of the Antarctic link during the Eocene resulted in two vicariance events within the Liliales (Vinnersten and Bremer 2001).

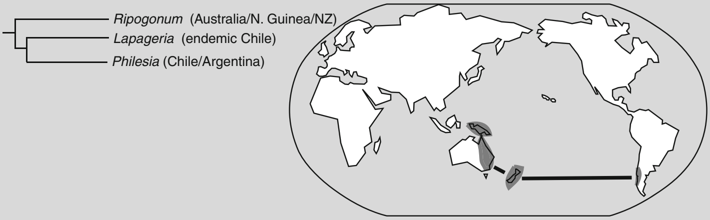

Fig. 3.22 Phylogenetic and geographic relationships of the Philesiaceae (according to Vinnersten and Bremer 2001)

Finally, the southern Andes endemic conifer *Austrocedrus* seems to be related to fossils found in the Early Oligocene of Tasmania (Paull and Hill 2008). The plausible explanation is that the original range was disrupted by one or more vicanriant events with *Austrocedrus chilensis* the sole survivor of the lineage.

3.3.1 Revitalizing Long-Distance Dispersal

Vicariance explanations were not to last, since they remained dominant only until the recent advent of molecular systematic techniques, particularly molecular-based dating of lineage divergences (de Queiroz 2005). In Moore et al.'s (2006) opinion "… using these techniques, much recent scholarship has demonstrated that numerous plant disjunctions are far too young to have resulted from vicariance, leaving transoceanic dispersal as the only plausible alternative… The realization that long-distance dispersal may have been far more frequent than previously supposed has led plant biogeographers using modern molecular tools to reexamine the relative importance of vicariance and dispersal in explaining the classic patterns of worldwide plant disjunction". Moore et al. (2006) consequently found that the disjunct distribution of extant species of *Tiquilia* is the result of at least four long-distance dispersal events from North America to South America (Fig. 3.23a). Many more examples of long-distance dispersal are arising nowadays in systematic papers: applying the same approach, Simpson et al. proposed four long-distance dispersal events in *Hoffmannseggia*, colonizing North America from South America (Fig. 3.23b). The proposed explanatory mechanism is bird dispersal at different times in the late Cenozoic (late Miocene to Pleistocene). Also Meudt and Simpson (2006) proposed that *Ourisia* arose in the Andes of central Chile, then spread to

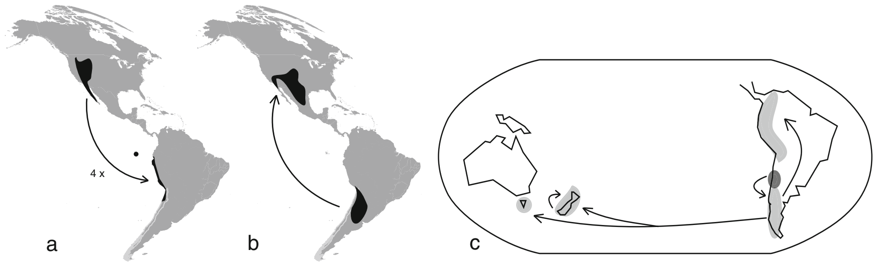

Fig. 3.23 **a** Distribution of *Tiquilia* species, originated by long-distance dispersal (according to Moore et al. (2006)); **b** disjunct populations of *Hoffmannseggia glauca*, originated by a long-distance dispersal event (according to Simpson et al. (2005)); **c** long distance dispersal events that caused the disjunct distribution of *Ourisia* species (according to Meudt and Simpson (2006))

southern Chile and Argentina, then dispersed to the north-central Andes, and finally to Tasmania and New Zealand (Fig. 3.23c).

Also Chung et al. (2005) proposed that the ancestor of *Oreomyrrhis* was distributed in Eurasia and during the late Cenozoic to the Quaternary dispersed to North America and the southern Pacific Rim. For *Osmorhiza* species, Wen et al. (2002) suggested, due to the lack of ITS sequence divergence, recent LDD events via birds from western North America to South America.

Chacón et al. (2006) asserted that the presence of *Oreobolus* in the Hawaiian archipelago can only be explained as a result of LDD from Australasia or Malesia. The arrival of *Oreobolus* in South America was according to these authors a relatively recent event (approximately 5.5 mya) and interpreted therefore as LDD from Australia. The rise of South American species by vicariance after the Gondwanan breakup is discarded, since it would have only been possible through the Antarctic connection, thus much earlier.

Calviño et al. (2008) found that *Eryngium* and its two subgenera originated from western Mediterranean ancestors and that the present-day distribution of the genus is explained by several dispersal events, including a long trans-Pacific dispersal event from Chile to Australia. Kadereit et al. (2008) further found that the *Eryngium* ancestors (tribe Saniculeae) have their origin in southern Africa; from there, the tribe reached western Eurasia; then *Eryngium* entered the New World, and Australia was reached, at its earliest, between 2.6 and 2.2 mya. They described this dispersal pattern as “from south to north and south again”.

Also Tremetsberger et al. (2005) proposed dispersal from Northwest Africa across the Atlantic Ocean for the origin of the South American taxa of *Hypochaeris* (Asteraceae). In the Brassicaceae, Bleeker et al. (2002) suggested that long-distance dispersal via migrating birds explains the antitropical disjunction between South American *Rorippa philippiana* and North American *R. curvisiliqua*. Also for *Lepidium* Mummenhoff et al. (2001) proposed long-distance dispersal from western North America to South America by birds in the Pleistocene. And von Hagen and Kadereit (2001) suggested that *Gentianella* (Gentianaceae) arrived via dispersal from South America into Australia/New Zealand less than 2.7 mya. For *Coprosma* (Rubiaceae, Anthospermeae) Anderson et al. (2001) proposed Africa as the ancestral area, followed by long-distance dispersal into the Pacific; for *Tetrachondra* Wagstaff et al. (2000) suggested LDD between New Zealand – South America; for *Fagonia* (Zygophyllaceae) Beier et al. (2004) proposed dispersal between South America and southern Africa.

But in spite of new molecular tools, not every group has yet allowed researchers to unravel its complicated biogeographic history, and several authors are more cautious: "Given the inherent methodological problems, absolute age of clade divergences, relevant as evidence of long distance dispersal or vicariance, cannot yet be determined with confidence" (Ladiges et al. 2005) (Box 3.3).

Box 3.3 Rocks Around the Clock: The New Paradigm of Molecular Dating

The program of molecular dating of phylogenies has becoming very popular due to the availability of better resolved phylogenies in combination with new methods for estimating divergence times (e.g. Sanderson 1997; Rutschmann 2006; Parker and Markwith 2007). There is also an increasing number of taxonomically identifiable fossils suited for calibration purposes (Gandolfo et al. 2008). In spite of the fact that the datings have given widely different results, more recent studies tend to converge on similar ages (see Box 2.4).

But in spite of Donoghue and Benton's (2007) assertion that "rocks and clocks together are an unbeatable combination", the molecular dating program is not free of problems (Pulquério and Nichols 2007; Heads 2005). Anderson et al. (2005), after discussing the difficulties and uncertainties in obtaining a stem group age for the eudicots, finished their paper asking if the results could not be rather an artifact from constraints or method. Variation in rates of nucleotide substitution along a lineage and between different lineages has demonstrated to be pervasive, therefore the "clock" model of molecular evolution has been changed to the relaxed or "sloppy clock", that tries to address the deviations from the clock-like model (Drummond et al. 2006).

Sanderson and Doyle (2001) pointed out that "non-clocklike behaviour of evolutionary rates might lead to significant deviations among results obtained with different dating methods". Different methods may introduce systematic biases, which are generally hard to detect. Near and Sanderson (2004) suggested that the accurate divergence time estimates might require multiple reliable calibrations, but "Ironically, the systems in which divergence time estimation from sequence data is needed most critically are the ones with few or no good calibrations... Perhaps we should learn to walk in the context of these systems before learning to run in the real world" (Near and Sanderson 2004). Returning to examples mentioned before, many works do not mention the calibration point used for the analysis (e.g. Simpson et al. 2005; Meudt and Simpson 2006).

The mechanisms responsible for long-distance dispersal were experimentally analysed already by Darwin (1859). Ridley (1930) and Carlquist (1983), among others, emphasized the huge possibilities of dispersal in plants related to the immense diversity of seed types. More recently, Muñoz et al. (2004) modelled wind connectivity that could explain floristic similarities in the southern hemisphere, especially for groups known as "good dispersers" (=lichens, mosses, ferns). The authors suggested that this could apply also to angiosperms with tiny seeds, like the orchids, but no empirical observation supports this hypothesis. On the contrary, Van Steenis (1962) rejected long ago this possibility: "Although dispersal of orchids may seem easy by the large amount of dust seed, successful establishment may depend on presence of its mycorrhizal fungus and insects for pollination. That the three of them, fungus spores, seeds, and insects, will travel together over long distances by chance is utterly unlikely". Other genera that superficially appear as good dispersers, like the representatives of the Asteraceae, are not necessarily good dispersers (see Chap. 8).

3.3.2 Relativising Long-Distance Dispersal

Cain already warned us about the error in convenient dispersal stories: "Long-distance dispersal operates for some organisms, and it is especially applicable to littoral species and a portion of the biota of oceanic islands. The hypothesis, however, is much too widely used; in most cases of wide disjunction, a careful investigation shows that the dispersal mechanisms, agents, and establishment requirements of the species rule out this explanation. All too frequently the assumption of long-distance dispersal is merely a careless and easy way out of a difficult problem and it leads to fanciful and even ridiculous conclusions" (Cain 1944, pp 305–306).

But researchers tend to ignore or minimize empirical evidence: "*Hoffmannseggia* fruits and seeds have no obvious adaptations for external animal dispersal and no one has ever recorded their being eaten by birds. Nevertheless, we believe that bird dispersal is the most likely explanation for the repeated pattern of long-distance dispersal from South to North America" (Simpson et al. 2005). The same applies for *Prosopis*: "Although there is no record of *Prosopis* pods being eaten by birds. . . bird dispersal appears to be the most likely explanation for the [antitropical] relationships we have observed" (Bessega et al. 2006).

Taking the dispersalist universe as a framework, Moore et al. (2006) recently avoided mentioning alternative palaeogeographic hypothesis, as listed by Constance (1963), and they ruled out the possibility of ancient vicariance events. These alternative hypotheses are categorized as "grotesque hypotheses that have been proposed to avoid the bugaboo of long-distance dispersal" (Raven 1963, p 153). But whether or not *grotesque* is better than *bugaboo* is just a matter of belief and not a matter of evidence.

Early biogeographers were much more skeptic regarding the real possibility of long-distance dispersal: "If migratory birds really have a high importance in the dispersal of plants, the common floristic pattern would resemble continuous faecal roads, and could be reconstructed as the prehistoric trading routes. But this is not the case…" (von Ihering 1893).

Also the eminent geographer Friedrich Ratzel (1901) wrote down his thoughts about the subject:

"If one inspects the real distribution of organisms, one cannot confirm the effectivity of all the passive means of migration, which gained so much attention since Darwin and Wallace". By the way, he wrote also: "Since lands and oceans have moved uninterrupted and are shifting nowadays under our eyes on the Earth's surface, the 'Lebensraum' for the terrestrial and aquatic organisms likewise changes continuously". Ratzel's opinion is not just anecdotic for biogeographers, since aside from his reputation as a human geographer, he is considered as the founder of the term "biogeography" (Parenti and Ebach 2009, see also Sect. 10.6).

Aditionally, Du Rietz wrote: "My own experience of species differentiation on isolated mountains or mountain chains does not make me inclined to believe that long distance dispersal has played any greater role there than in oceanic islands […] Our present knowledge of bipolar plant distribution and of plant distribution in general does not speak in favour of the assumption that the facts of bipolar distribution could be explained by long distance dispersal" (Du Rietz 1940, pp 239–240). His own experience was greatly influenced by Carl Skottsberg's impressions on oceanic islands such as Juan Fernández (see Chap. 5).

More recently, some authors are appealing to more complex solutions of vicariance and long-distance dispersal events working together: for *Raukaua* (=*Pseudopanax*), Mitchell and Wagstaff (2000) proposed a Gondwanan vicariance between Australasia-South America and long-distance dispersal to Hawaii; for *Laurelia* (Atherospermataceae), Renner et al. (2000) proposed an initial diversification at 100–140 mya, probably in West Gondwana, early entry into Antarctica, and long-distance dispersal to New Zealand and New Caledonia; Wanntorp and Wanntorp (2003) proposed early vicariance followed by recent dispersals in *Gunnera*. For *Caltha* (Ranunculaceae), Schuettpelz and Hoot (2004) proposed a Northern hemisphere origin, followed by dispersal to the Southern Hemisphere (Gondwanaland). For the southern family Proteaceae, Barker et al. (2007) found that four of eight trans-continental disjunctions of sister groups fit vicariance scenarios, and the other half can be only explained by long-distance dispersal. Calibration rests on a few fossils from the subfamily Grevilleoideae. Results provide an age of 118.5 mya for the crown group of the Proteaceae, in agreement with results provided by Anderson et al. (2005). In Barker et al.'s (2007) analysis, all Chilean genera (*Embothrium, Gevuina, Lomatia, Orites*) appear to be congruent with a vicariant history.

Finally, several authors (e.g. Sluys 1994) argued that the contrast of vicariance versus dispersal is an artifice of poorly defined concepts. Williams and Ebach (2008, p 240) called this "another false war". Michaux (2001) suggested instead of this simple contrast, the recognition of five processes that are not logically equivalent as they operate at different time scales: modification, movement, mixing, splitting and juxtaposition.

Modern analytical tools like DIVA-analysis are designed to find the optimal distributions of ancestral species by minimizing the number of dispersal and extinction events (Ronquist 1997; Sanmartín and Ronquist 2004). Applying this approach, Sanmartín et al. (2007) tested the directional dispersal in the Southern Hemisphere. The direction of circumpolar currents predicts predominantly eastward dispersal from New Zealand to South America, but contrary to the expectations, dispersal between New Zealand and South America was more frequently inferred to be westward. The authors concluded that there is still a need of a better understanding of dispersal processes for applying realistic estimates of biogeographical reconstructions (Sanmartín et al. 2007). This better understanding of dispersal processes should not exclude a need for a better understanding of vicariance processes. These last have been frequently oversimplified as a break-up model of several steps, obviating the complex geological and biotic nature of any region composed of geological and biogeographical composite areas (e.g. Heads 1999, 2002, see discussion in Sect. 10.2).

> ...the apparent conflict between those who advocate dispersal and those who advocate vicariance is of little consequence for progress in biogeography. To understand biogeography as a battle for unification between vicariance and dispersal processes is, in short, meaningless. The real task in biogeography is the unification between classification and explanation – a unification that has obsessed biologists since Haeckel and his discussion of chorological processes (Williams and Ebach 2008, p 241).

References

Abraham E, del Valle HF, Roig F, Torres L, Ares JO, Coronato F, Godagnone R (2009) Overview of the geography of the Monte Desert biome (Argentina). J Arid Environ, 73:144–153

Anderson CL, Rova JHE, Andersson L (2001) Molecular phylogeny of the tribe Anthospermeae (Rubiaceae): systematic and biogeographic implications. Aust Syst Bot, 14:231–244

Anderson CL, Bremer K, Friis EM (2005) Dating phylogenetically basal eudicots using rbcL sequences and multiple fossil reference points. Am J Bot, 92:1737–1748

Arroyo MTK, Squeo FA, Armesto JJ, Villagrán C (1988) Effects of aridity on plant diversity in the northern Chilean Andes: results of a natural experiment. Ann Mo Bot Gard, 75:55–78

Barbour M (1969) Patterns of genetic similarity between *Larrea divaricata* of North and South America. Am Midl Nat, 81:54–67

Barker NP, Weston PH, Rutschmann F, Sauquet H (2007) Molecular dating of the "Gondwanan" plant familt Proteaceae is only partially congruent with the timing of the break-up of Gondwana. J Biogeogr, 34:2012–2027

Barlow BA (1981) The Australian flora: its origin and evolution. In: Bureau of Flora and Fauna (ed) Flora of Australia, vol. 1. AGPS, Canberra, pp. 25–75

Beier BA, Nylander JAA, Chase MW, Thulin M (2004) Phylogenetic relationships and biogeography of the desert plant genus *Fagonia* (Zygophyllaceae), inferred by parsimony and Bayesian model averaging. Mol Phylogenet Evol, 33:91–108

Bessega C, Vilardi JC, Saidman BO (2006) Genetic relationships among American species of the genus *Prosopis* (Mimosoideae, Leguminosae) inferred from ITS sequences: evidence for long-distance dispersal. J Biogeogr, 33:1905–1915

Bleeker W, Weber-Sparenberg C, Hurka H (2002) Chloroplast DNA variation and biogeography in the genus *Rorippa* Scop. (Brassicaceae). Plant Biol, 4:104–111

Bray WL (1900) The relations of the North American flora to that of South America. Science, 12:709–716

Brundin L (1966) Transantartic relationships and their significance, as evidenced by chironomid midges. Kungl. Svenska Vetenskapsakademiens Handlingar, 11:1–472

Cain SA (1944) Foundations of plant geography. Harper and Brothers, New York, NY

Calviño CI, Martinez SG, Downie SR (2008) The evolutionary history of *Eryngium* (Apiaceae, Saniculoideae): Rapid radiations, long distance dispersals, and hybridizations. Mol Phylogenet Evol, 46:1129–1150

Carlquist S (1983) Intercontinental dispersal. In: Kubitzki K, (ed) Dispersal and distribution: an international symposium. Sonderbände des Naturwissenschaftlichen Vereins in Hamburg, vol 7. Verlag Paul Parey, Hamburg/Berlin, 37–47

Chacón J, Madriñán S, Chase MW, Bruhl JJ (2006) Molecular phylogenetics of *Oreobolus* (Cyperaceae) and the origin and diversification of the American species. Taxon, 55:359–36

Christ H (1867) Über die Verbreitung der Pflanzen der alpinen Region der europäischen Alpenkette. Denkschr. Schweiz. Nat. Ges. 22

Chung KF, Peng CI, Downie SR, Spalik K, Schaal BA (2005) Molecular systematics of the trans-Pacific alpine genus *Oreomyrrhis* (Apiaceae): phylogenetic affinities and biogeographic implications. Am J Bot, 92:2054–2071

Constance L (1963) Amphitropical relationships in the herbaceous flora of the Pacific Coast of North and South America: a symposium. Introduction and historical review. Q Rev Biol, 38:109–116

Cox CB (1990) New geological theories and old biogeographical problems. J Biogeogr 17(11): 7–130

Craw RC, Grehan JR, Heads MJ (1999) Panbiogeography: tracking the history of life. Oxford Biogeography Series 11. Oxford University Press, New York, NY

Crisp MD, West JG, Linder HP (1999) Biogeography of the terrestrial flora. In: Orchard AE, (ed) Flora of Australia, vol. 1, 2nd edn. Australian Biological Resources Study, Canberra, pp 321–367

Croizat L (1952) Manual of Phytogeography, or an account of plant dispersal throughout the world. Junk, The Hague

Croizat L (1958) Panbiogeography or an introductory synthesis of zoogeography, phytogeography, and geology; with notes on evolution, systematics, ecology, anthropology, etc., 3 vol. Published by the author, Caracas, Venezuela

Croizat L (1962) On the age of Fray Jorge and Talinay in Chile. Rev Univ (Chile), 47:57–61

Cruden RW (1966) Birds as agents of long-distance dispersal for disjunct plant groups of the temperate Western Hemisphere. Evolution, 20:517–532

Darwin C (1859) The origin of species. Oxford World's Classics (1996). Oxford University Press, Cambridge

De Martonne E (1934) The Andes of the North-West Argentine. Geogr J, 84:1–14

de Queiroz A (2005) The resurrection of oceanic dispersal in historical biogeography. Trends Ecol Evol, 20:68–73

Donato M, Posadas P, Miranda-Esquivel DR, Jaureguizar EO, Cladera G (2003) Historical biogeography of the Andean region: evidence from *Listroderina* (Coleoptera: Curculionidae: Rhytirrhinini) in the context of the South American geobiotic scenario. Biol J Linn Soc, 80:339–352

Donoghue PCJ, Benton MJ (2007) Rocks and clocks: calibrating the Tree of Life using fossils and molecules. Trends Ecol Evol, 22:424–431

Drummond AJ, Ho SYW, Phillips MJ, Rambaut A (2006) Relaxed phylogenetics and dating with confidence. PLoS Biol, 4:e88

Du Rietz GE (1940) Problems of bipolar plant distribution. Acta Phytogeogr Suecica, 13:215–282

Engler A (1882) Versuch einer Entwicklungsgeschichte der Pflanzenwelt, insbesondere der Florengebiete seit der Tertiärperiode, Vol. 2. Die Extratropischen Gebiete der Südlichen Hemisphäre und die Tropischen Gebiete. Verlag von W. Engelmann, Leipzig

Gandolfo MA, Nixon KC, Crepet WL (2008) Selection of fossils for calibration of molecular dating models. Ann Mo Bot Gard, 95:34–42

Glasby CJ (2005) Polychaete distribution patterns revisited: an historical explanation. Mar Ecol, 26:235–245

Good R (1947) The geography of the flowering plants. 4th edition 1974. Longman, London

Hannig E, Winkler H, (eds) (1926–1940) Die Pflanzenareale: Sammlung kartographischer Darstellungen von Verbreitungsbezirken der lebenden und fossilen Pflanzen-Familien, -Gattungen und–Arten. Gustav Fischer Verlag, Jena.

Heads M (1999) Vicariance biogeography and terrane tectonics in the South Pacific: analysis of the genus Abrotanella (Compositae). Biol J Linn Soc, 67:391–432

Heads M (2002) Birds of paradise, vicariance biogeography and terrane tectonics in New Guinea. J Biogeogr, 29:261–283

Heads M (2004) What is a node? J Biogeogr, 31:1883–1891

Heads M (2005) Dating nodes on molecular phylogenies: a critique of molecular biogeography. Cladistics, 21:62–78

Heusser CJ (1971) Pollen and Spores of Chile. The University of Arizona Press, Tucson, Arizona

Hinojosa LF (2005) Cambios climáticos y vegetacionales inferidos a partir de paleofloras Cenozoicas del sur de Sudamérica. Rev Geol Chil, 32:95–115

Hofsten N (1916) Zur älteren Geschichte des Diskontinuitätsproblems in der Biogeographie. Zoologische Annalen, 7:197–353

Hooghiemstra H, van der Hammen T (1998) Neogene and Quaternary development of the neotropical rain forest: the forest refugia hypothesis, and a literature overview. Earth Sci Rev, 44:147–183

Houston J, Hartley AJ (2003) The central Andean west-slope rainshadow and its potential contribution to the origin of hyper-aridity in the Atacama Desert. Int J Climatol, 23:1453–1464

Hovenkamp P (1997) Vicariance events, not areas, should be used in biogeographical analysis. Cladistics, 13:67–79

Hughes C, Eastwood R (2006) Island radiation on a continental scale: exceptional rates of plant diversification after uplift of the Andes. Proc Natl Acad Sci Usa, 103:10334–10339

Humphries CJ (1981) Biogeographic methods and the southern beeches. In: Forey PL, (ed) The evolving biosphere. Cambridge University Press, Cambridge, pp 283–297

Humphries CJ, Parenti LR (1999) Cladistic biogeography, 2nd edn. Oxford monographs on biogeography N°2. Clarendon Press, Oxford.

Hunziker JH, Palacios RA, de Valesi AG, Poggio L (1972) Species disjunctions in Larrea: evidence from morphology, cytogenetics, phenolic compounds, and seed albumins. Ann Mo Bot Gard, 59:224–233

Johnston IM (1940) The floristic significance of shrubs common to North and South American deserts. J Arnold Arbor, 21:356–363

Kadereit JW, Repplinger M, Schmalz N, Uhink CH, Worz A (2008) The phylogeny and biogeography of Apiaceae subf. Saniculoideae tribe Saniculeae: from south to north and south again. Taxon, 57:365–382

Katinas L, Morrone JJ, Crisci JV (1999) Track analysis reveals the composite nature of the Andean biota. Aust J Bot, 47:111–130

Katinas L, Crisci JV, Wagner W, Hoch PC (2004) Geographical diversification of tribes Epilobieae, Gongylocarpeae, and Onagreae (Onagraceae) in North America, based on parsimony analysis of endemicity and track compatibility analysis. Ann Mo Bot Gard, 91:159–185

Ladiges PY, Kellermann J, Nelson G, Humphries CJ, Udovicic F (2005) Historical biogeography of Australian Rhamnaceae, tribe Pomaderreae. J Biogeogr, 32:1909–1919

Landrum L (1981) The phylogeny and geography of *Myrceugenia* (Myrtaceae). Brittonia, 33: 105–129

Llorente Bousquets J, Papavero N, Bueno A (2003) Síntesis histórica de la biogeografía. In: Llorente Bousquets J, Morrone JJ, (eds) Introducción a la Biogeografía en Latinoamérica: Teorías, Conceptos, Métodos y Aplicaciones. Las Prensas de Ciencias, Facultad de Ciencias, UNAM, México, pp 1–14

Luna Vega I, Alcántara Ayala O, Morrone JJ, Espinosa Organista D (2000) Track analysis and conservation priorities in the cloud forests of Hidalgo (Mexico). Divers Distrib, 6:137–143

López RP (2003) Phytogeographical relations of the Andean dry valleys of Bolivia. J Biogeogr, 30:1659–1668

Mabberley DJ (1997) The plant-book, 2nd ed. (3rd edn 2008). Cambridge University Press, Cambridge.

Messerli B, Ammann C, Geyh M, Grosjean M, Jenny B, Kammer K, Vuille M (1998) The problem of the "Andean Dry Diagonal": Current precipitation, late Pleistocene snow line, and lake level changes in the Atacama Altiplano (18ºS–28º/29ºS). Bamberger Geogr Schr, 15:17–34

Meudt HM, Simpson BB (2006) The biogeography of the austral, subalpine genus *Ourisia* (Plantaginaceae) based on molecular phylogenetic evidence South American origin and dispersal to New Zealand and Tasmania. Biol J Linn Soc, 87:479–513

Meusel H (1943) Vergleichende Arealkunde. Einführung in die Lehre von der Verbreitung der Gewächse mit besonderer Berücksichtigung der mitteleuropäischen Flora, 2 vols. Verlag Borntraeger, Berlin-Zehlendorf.

Meusel H, Jäger E, (eds) (1992) Vergleichende Chorologie der Zentraleuropäischen Flora, vol. 3. Gustav Fischer Verlag, Jena

Meusel H, Jäger E, Rauschert S, Weinert E, (eds) (1978) Vergleichende Chorologie der Zentraleuropäischen Flora, vol. 2. Gustav Fischer Verlag, Jena

Michaux B (2001) Dispersal versus vicariance, artifice rather than contest. In: Metcalfe I, Smith JMB, et al.(eds) Faunal and floral migrations and evolution in SE Asia-Australasia. AA Balkema Publishers, Lisse, pp 311–318

Mihoc MAK, Morrone JJ, Negritto M, Cavieres LA (2006) Evolución de la serie Microphyllae (*Adesmia*, Fabaceae) en la Cordillera de los Andes: una perspectiva biogeográfica. Rev Chil Hist Nat, 79:389–404

Mitchell AD, Wagstaff SJ (2000) Phylogeny and biogeography of the Chilean Pseudopanax laetevirens. New Zeal J Bot, 38:409–414

Moreira-Muñoz A (2007) Plant geography of Chile: an essay on postmodern biogeography. Doctoral thesis, University Erlangen-Nürnberg, Germany

Moore MJ, Tye A, Jansen RK (2006) Patterns of long-distance dispersal in *Tiquilia* subg. *Tiquilia* (Boraginaceae): implications for the origins of amphitropical disjuncts and Galapagos Islands endemics. Am J Bot, 93:1163–1177

Mummenhoff K, Bruggemann H, Bowman JL (2001) Chloroplast DNA phylogeny and biogeography of *Lepidium* (Brassicaceae). Am J Bot, 88:2051–2063

Muñoz J, Felicísimo AM, Cabezas F, Burgaz AR, Martínez I (2004) Wind as a long-distance dispersal vehicle in the Southern Hemisphere. Science, 304:1144–1147

Muñoz-Schick M, Moreira-Muñoz A, León-Lobos P (2006) Nueva localidad en Chile para *Menodora linoides* Phil. (Oleaceae), especie considerada extinta en el siglo XX. Gayana Bot, 63:175–179

Muñoz Pizarro C, Pisano E (1947) Estudio de la vegetación y flora de los Parques Nacionales Fray Jorge y Talinay. Agric Téc (Chile), 7:71–190

Mutke J, Barthlott W (2005) Patterns of vascular plant diversity at continental to global scales. Biol Skr, 55:521–531

Near TJ, Sanderson MJ (2004) Assessing the quality of molecular divergence time estimates by fossil calibrations and fossil-based model selection. Philos Trans R Soc B Biol Sci, 359: 1477–1483

Nelson EC (1981) Phytogeography of southern Australia. In: Keast A, (ed) Ecological biogeography of Australia. Dr W. Junk, The Hague, pp. 733–759

Nelson G, Platnick N (1981) Systematics and biogeography: Cladistics and vicariance. Columbia University Press, New York, NY

Nelson G, Ladiges PY (2001) Gondwana, vicariance biogeography and the New York School revisited. Aust J Bot, 49:389–409

Nishida M, Nishida H, Ohsawa T (1989) Comparison of the petrified woods from the Cretaceous and Tertiary of Antarctica and Patagonia. Proc NIPR Symp Polar Biol, 2:198–212

Núñez-Avila MC, Armesto JJ (2006) Relict islands of the temperate rainforest tree *Aextoxicon punctatum* (Aextoxicaceae) in semi-arid Chile: genetic diversity and biogeographic history. Aust J Bot, 54:733–743

Parenti LR (2007) Common cause and historical biogeography. In: Ebach MC, Tangney RS, (eds) Biogeography in a changing world. Systematics Association Special Volumes. CRC Press, Boca Raton, FL, pp 61–82

Parenti LR, Ebach MC (2009) Comparative biogeography: discovering and classifying biogeographical patterns of a dynamic earth. University of California Press, San Francisco, CA

Parker K, Markwith S (2007) Expanding biogeographic horizons with genetic approaches. Geogr Compass, 1:246–274

Paull R, Hill RS (2008) Oligocene *Austrocedrus* from Tasmania (Australia): comparisons with *Austrocedrus chilensis*. Int J Plant Sci, 169:315–330

Philippi F (1884) A visit to the northernmost forest of Chile. J Bot, 22:202–211

Pulquério MJF, Nichols RA (2007) Dates from the molecular clock: how wrong can we be? Trends Ecol Evol, 22:180–184

Qian H (1999) Floristic analysis of vascular plant genera of North America north of Mexico: characteristics of phytogeography. J Biogeogr, 26:1307–1321

Qian H, Song J-S, Krestov P, Guo Q, Wu Z, Shen X, Guo X (2003) Large-scale phytogeographical patterns in East Asia in relation to latitudinal and climatic gradients. J Biogeogr, 30:129–141

Ratzel F (1901) Der Lebensraum: eine biogeographische Studie. Laupp'sche Buchhandlung, Tübingen

Raven PH (1963) Amphitropical relationships in the floras of North and South America. Q Rev Biol, 38:151–177

Raven PH (1972) Plant species disjunctions: a summary. Ann Mo Bot Gard, 59:234–246

Raven PH, Axelrod DI (1974) Angiosperm biogeography and past continental movements. Ann Mo Bot Gard, 61:539–673

Reiche C (1905) Monotypische Gattungen der Chilenischen Flora. Verh Dtsch Wiss Vereins Stgo, 5:1–16

Reiche C (1907) Grundzüge der Pflanzenverbreitung in Chile. In: Engler A, Drude O, (eds) Die Vegetation der Erde: Sammlung Pflanzengeographischer Monographien, Vol. VIII. Verlag von V. Engelmann, Leipzig

Renner SS (2004) Variation in diversity among Laurales, early cretaceous to present. Biol Skr, 55:441–458

Renner SS, Murray D, Foreman D (2000) Timing transantarctic disjunctions in the Atherospermataceae (Laurales): evidence from coding and noncoding chloroplast sequences. Syst Biol, 49:579–591

Riccardi AC (1988) The Cretaceous system of southern South America. Geol Soc Am Memoir, 168:1–145

Ridley HN (1930) The dispersal of plants throughout the world. Lovell Reeve & Co, London

Ronquist F (1997) Dispersal-vicariance analysis: a new approach to the quantification of historical biogeography. Syst Biol, 46:193–201

Rothmaler W (1955) Allgemeine Taxonomie und Chorologie der Pflanzen. Grundzüge der speziellen Botanik. Libri Botanici vol. 3, IHW Verlang. Reprint 1992

Rutschmann F (2006) Molecular dating of phylogenetic trees: a brief review of current methods that estimate divergence times. Divers Distrib, 12:35–48

Sanderson MJ (1997) A nonparametric approach to estimating divergence times in the absence of rate constancy. Mol Biol Evol, 14:1218–1231

Sanderson MJ, Doyle JA (2001) Sources of error and confidence intervals in estimating the age of angiosperms from rbcL and 18S rDNA data. Am J Bot, 88:1499–1516

Sanmartín I, Ronquist F (2004) Southern Hemisphere biogeography inferred by event-based models: plant versus animal patterns. Syst Biol, 53:216–243

Sanmartín I, Wanntorp L, Winkworth RC (2007) West Wind Drift revisited: testing for directional dispersal in the Southern Hemisphere using event-based tree fitting. J Biogeogr, 34: 398–416

Scherson RA, Vidal R, Sanderson MJ (2008) Phylogeny, biogeography, and rates of diversification of New World *Astragalus* (Leguminosae) with an emphasis on South American radiations. Am J Bot, 95:1030–1039

Schuettpelz E, Hoot SB (2004) Phylogeny and biogeography of *Caltha* (Ranunculaceae) based on chloroplast and nuclear DNA sequences. Am J Bot, 91:247–253

Simpson BB, Neff JL (1985) Plants, their pollinating bees, and the great American interchange. In: Stehli FG, Webb SD, (eds) The great American biotic interchange. Plenum, New York, NY, pp 427–452

Simpson BB, Tate JA, Weeks A (2005) The biogeography of *Hoffmannseggia* (Leguminosae, Caesalpinioideae, Caesalpinieae): a tale of many travels. J Biogeogr, 32:15–27

Sklenar P, Balslev H (2007) Geographic flora elements in the Ecuadorian superpáramo. Flora, 202:50–61

Skottsberg C (1948) Apuntes sobre la flora y vegetación de Frai Jorge (Coquimbo, Chile). Acta Horti Gotoburgensis, 18:91–184

Sluys R (1994) Explanations for biogeographic tracks across the Pacific Ocean: a challenge for paleogeography and historical biogeography. Prog Phys Geog, 18:42–58

Solbrig OT (1972) New approaches to the study of disjunctions with special emphasis on the American amphitropical desert disjunctions. In: Valentine DH, (ed) Taxonomy, phytogeography and evolution. Academic Press, London, pp 85–100

Stuessy TF, Taylor C (1995) Evolución de la Flora Chilena. In: Marticorena C, Rodríguez R, (eds) Flora de Chile, vol. 1. Universidad de Concepción, Concepción, pp 85–118

Stuessy TF, Tremetsberger K, Müllner AN, Jankowicz J, Guo Y-P, Baeza CM, Samuel RM (2003) The melding of systematics and biogeography through investigations at the populational level: examples from the genus *Hypochaeris* (Asteraceae). Basic Appl Ecol, 4:287–296

Takhtajan A (1986) Floristic regions of the world. Translated by Crovello TJ, edited by Cronquist A from the original Russian edition, Leningrad (1978). University of California. Reprint 1988, B. Singh, M. P. Singh, Dehra Dun, India

Tremetsberger K, Weiss-Schneeweiss H, Stuessy TF, Samuel R, Kadlec G, Ortiz MA, Talavera S (2005) Nuclear ribosomal DNA and karyotypes indicate a NW African origin of South American *Hypochaeris* (Asteraceae, Cichorieae). Mol Phylogenet Evol, 35:102–116

Treviranus GR (1803) Biologie, oder Philosophie der lebenden Natur. Röwer, Göttingen

Troncoso A, Villagrán C, Muñoz-Schick M (1980) Una nueva hipótesis acerca del origen y edad del bosque de Fray Jorge (Coquimbo, Chile). Bol Mus Nac Hist Nat (Chile), 37:117–152

Turrill WB (1953) Pioneer plant geography: the Phytogeographical Researches of Sir Joseph Dalton Hooker. Contributions from the Int. Biohistorical Commission, N°1, The Hague, Netherlands

van Steenis CGGJ (1962) The theory of land bridges in botany, with particular references to tropical plants. Blumea, 11:235–542

Villagrán C, Hinojosa LF (1997) Historia de los bosques del sur de Sudamérica, II: Análisis fitogeográfico. Rev Chil Hist Nat, 70:241–267

Villagrán C, Armesto JJ, Hinojosa LF, Cuvertino J, Pérez C, Medina C (2004) El enigmático origen del bosque relicto de Fray Jorge. In: Squeo FA, Gutiérrez JR, Hernández IR, (eds) Historia Natural del Parque Nacional Fray Jorge. Ediciones Universidad de La Serena, La Serena, pp 3–43

Vinnersten A, Bremer K (2001) Age and biogeography of major clades in Liliales. Am J Bot, 88:1695–1703

von Hagen KB, Kadereit JW (2001) The phylogeny of *Gentianella* (Gentianaceae) and its colonization of the southern hemisphere as revealed by nuclear and chloroplast DNA sequence variation. Org Divers Evol, 1:61–79 von Ihering H (1893) Das neotropische Florengebiet und seine Geschichte. Englers Bot Jahrb, 17:1–54

Wagstaff SJ, Martinsson K, Swenson U (2000) Divergence estimates of Tetrachondra hamiltonii and T. patagonica (Tetrachondraceae) and their implications for austral biogeography. New Zeal J Bot, 38:587–596

Wangerin W (1932) Florenelemente und Arealtypen. Beiträge zur Arealgeographie der deutschen Flora. Beih. Z. Centralbl. (Drude Festschrift), vol 49

Wanntorp L, Wanntorp H-E (2003) The biogeography of Gunnera L.: Vicariance and dispersal. J Biogeog, 30:979–987

Wen J, Ickert-Bond SM (2009) Evolution of the Madrean-Tethyan disjunctions and the North and South American amphitropical disjunctions in plants. J Syst Evol, 47:331–348

Wen J, Lowry PP, Walck JL, Yoo K-O (2002) Phylogenetic and biogeographic diversification in *Osmorhiza* (Apiaceae). Ann Mo Bot Gard, 89:414–428

Werger M (1973) Las disyunciones anfitrópicas en las floras xerofíticas norte y sudamericanas. Darwiniana, 18:9–18

Wielgorskaya T (1995) Dictionary of generic names of seed plants. Columbia University Press, New York, NY

Wiley EO (1988) Vicariance biogeography. Ann Rev Ecol Syst, 19:513–542

Williams DM (2007) Ernst Haeckel and Louis Agassiz: trees that bite and their geographical dimension. In: Ebach MC, Tangney RS, (eds) Biogeography in a changing world. Systematics Association Special Volumes. CRC Press, Boca Raton, FL, pp 1–59

Williams DM, Ebach MC (2008) Foundations of systematics and biogeography. Springer, New York, NY

Wulff EV (1950) An introduction to historical plant geography. The Chronica Botanica Company, Waltham, MA

Zunino M, Zullini A (2003) Biogeografía: la dimensión espacial de la evolución. Fondo de Cultura Económica, México. From the 1995 Italian edition

Chapter 4
Biogeographic Regionalization

Abstract Biogeographic regionalization has been a main task from the beginnings of biogeography with the early works of Gottfried Treviranus, August P. de Candolle, or Frederick Schouw. Regionalization results in a hierarchy encompassing several categories like the realm, the region, the provinces, and so on. Comparison of available regionalization proposals for the Chilean territory is important but challenging, since each author puts the emphasis on a different level in this hierarchy. An independent exercise of regionalization is undertaken by the analysis of the endemic genera with the program NDM/VNDM. This yielded 3 areas of endemism located in Central Chile.

Biogeographic regionalization is tied to the initials of biogeography, beginning with the early works of G. Treviranus, A.P. de Candolle, and J.F. Schouw (Sect. 4.1). Biogeographic regionalization rests upon the chorological tradition (e.g. Huxley et al. 1998, Sect. 3.1), and it is still of crucial importance in modern biogeography (Llorente Bousquets and Morrone 2005; McLaughlin 2007; Mackey et al. 2008; Proches 2008; Escalante 2009).

Biogeograpic regionalization results in a hierarchical system – equivalent to a taxonomic hierarchy – for categorizing geographic areas in terms of their biota (Zunino and Zullini 2003; Escalante 2009). The existence of hierarchical systems is a highly relevant topic in systematics and biogeography, although the nature of such systems is still controversial. While several authors maintain that hierarchies tend to be artificial human constructions (e.g. Grehan 2001), others maintain that they are characteristic of nature's organization (Eldredge 1985; McLaughlin 1992, 1994) (Fig. 4.1). Both visions seem to be complementary: it is a fact that hierarchies are essential for man's understanding of the world: "The assessed patterns of organismal relationship are used to construct hierarchical classifications of coordinate and subordinate groups that are information-rich and have high predictive efficacy; these are the taxonomic hypotheses that change with new information and new modes of analysis" (Stuessy 2006). "The organization of nature is profoundly hierarchical, because from its beginning, interactions between simple elements have continuously created more complex systems, that themselves served as the basis for still more complex systems" (Jagers op Akkerhuis 2008).

A. Moreira-Muñoz, *Plant Geography of Chile*, Plant and Vegetation 5,
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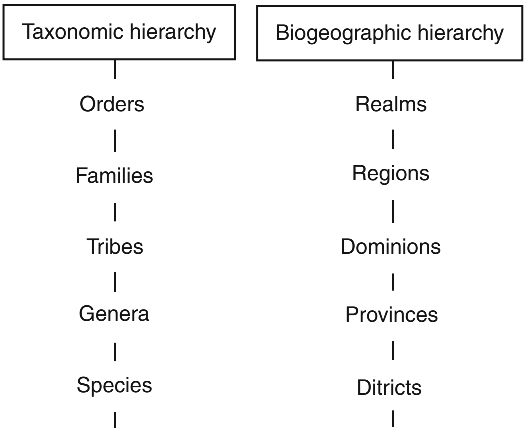

Fig. 4.1 "Natural" hierarchies; entities in the hierarchies are not necessarily equivalent

A regionalization comprises from the general to the particular a hierarchy beginning with the realm (=kingdom), the region, the dominion, and the province (e.g. Engler 1882; Takhtajan 1986; Cabrera and Willink 1973) (Fig. 4.1). There could be also intermediate categories, as subregions or subdominions. The basic unit is the province, although several authors suggest the district (=*Bezirk*) as the finest unit (e.g. Engler 1882). Each of the levels in the biogeographic hierarchy contains the subsequent levels, on the base of the characteristics (taxa) they share; a realm contains various regions, a region contains several dominions, and so on.

4.1 The Chilean Plants in the Global Concert

The Chilean flora appeared as early as the first attempts to geographically classify the global flora. Hereafter a summary of the different ways in which the Chilean flora has been classified is outlined (Table 4.1).

Gottfried R. Treviranus (1776–1837), one of the naturalists who coined the term "biology" (Engels 2005), first intended a global floristic classification, organizing the world flora in 8 principal floras (*Hauptfloren*). In this early classification Chile, (including Magallanes and Tierra del Fuego), and New Zealand composed an Antarctic Flora (*Antarktische Flor*) (Treviranus 1803). Treviranus, based on the early works of JI Molina (1740–1830), J Banks (1743–1820), and G Forster (1754–1794), explicitly recognised the floristic relationship between southernmost South America and Australasia, due to the similarities between New Zealand and Tierra del Fuego. He also noticed the existence of an antitropical floristic element, such as *Pinguicula, Salix* or *Ribes* (Sect. 3.1). He found this relation surprising since at that time the floristic knowledge of Tierra del Fuego was limited to just 40 species (Treviranus 1803, p 132).

Table 4.1 The geographical classification of the Chilean flora in the global context

Author	N° realms	N° regions	Classification of the Chilean Flora
GR Treviranus (1803)	8 *Flor*	–	*Antarktische Flor*
August Pyramus de Candolle (1820)	–	20	*le Chili* and *les terres Magellaniques*
Schouw (1823)	25	–	South of 42° = *Antarktisches Florenreich*; 42°–23° = *Reich der Holzartigen Synanthereen*; North of 23° = *Reich der Cactus und Piper*
Alphonse de Candolle (1835)	–	45	Region 35, *Le Chili*, and region 36, *la Patagonie, la terre de Feu et les iles Malouines (Falkland)*
Grisebach (1872)	–	24	North to 23° = *Tropischen Anden*; 23°–34°= *Chilenisches Übergangsgebiet*; 34°–56°= *Antarktisches Waldgebiet*
Engler (1879–1882)	4	31	*Südamerikanische Florenreich* = to 41°; *Altoceanisches Florenreich* = south from 41°
Drude (1884)	14	55	South of 41° = *Antarktisches Florenreich*; North of 41° = *Andines Florenreich*
Drude (1890)	14	55	*Andines Florenreich* and *Antarktisches Florenreich*
Diels (1908)	6	7	*Antarktisches Florenreich* and *Neotropisches Florenreich*
Christ (1910)	–	12	On the base of fern species, Chile was classified onto an *Andine Flora* and a *Süd Chilenische Flora*, with the limit at around 39°S
Good 1947 (1974)	6	37	Antarctic kingdom, Patagonian region, South of 41°; Neotropical kingdom, Andean region, North of 41°
Mattick (1964)	6	43	South = *Antarktisches Florenreich*; North = *Neotropisches Florenreich*
Takhtajan (1961)	6	37	Antarctic kingdom, Patagonian region, South of 40°; Neotropical kingdom, Andean region, North of 40°
Takhtajan (1986)	6	35	Holantarctic kingdom, Chile-Patagonian region, South of 25° to Antarctic peninsula and Malvinas Islands (Falkland Is.)
Cox (2001)	5	–	South American kingdom
Morrone (2002)	3	12	Austral kingdom, Andean region

Adapted from Moreira-Muñoz (2007).

At that time biogeographic representation by means of biogeographic maps was just at the beginning, and in the hands of Jean B. Lamarck and Augustin-Pyramus de Candolle. In 1805 they published the "first biogeographical map" for the third edition of the *Flore française* (Ebach and Goujet 2006). A-P de Candolle, in his *Géographie botanique*, further classified the world in 20 floristic regions: Chile fitted into two regions, *le Chili* and *les terres Magellaniques* (de Candolle 1820). De Candolle's world classification still lacked a map. Three

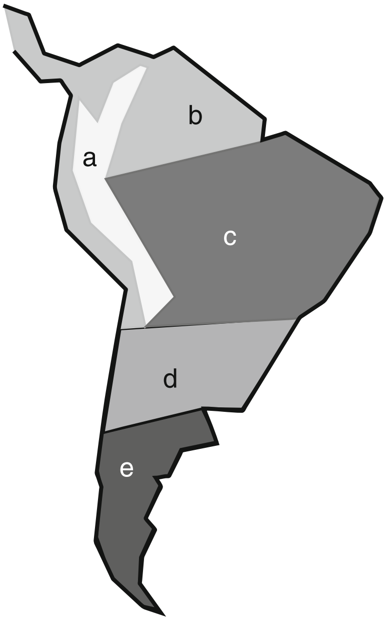

Fig. 4.2 Scheme of Schouw's early classification regarding South America: **a** cinchona realm; **b** *Cactus* and *Piper* realm; **c** palms and Melastomataceae realm; **d** arboreal Compositae realm; **e** Antarctic realm (primarily *Nothofagus*)

years later, the Danish botanist Joakim Frederik Schouw (1789–1852) published the first world map (Schouw 1823; Mennema 1985). Schouw proposed 25 floristic realms (*Florenreiche*). Southern South America was classified into two realms: the *Reich der Holzartigen Synanthereen* (Compositae), and the *Antarktisches Reich*, from 40°S to the South (Fig. 4.2).

Applying the concept of "endemism" as first proposed by A-P de Candolle, Schouw stated explicitly the criteria for classifying and delimiting the floristic realms (Drude 1884, p. 13):

1. half of the known plants have to be native to the territory in question;
2. ¼ of the genera have to be endemic or have their maximal distribution there;
3. a plant realm has to have some endemic families.

De Candolle's son Alphonse de Candolle (1835) critized Schouw's criteria and proposed 45 botanical regions, but for Chile he maintained the division into two regions. But soon de Candolle the younger rejected such schemes of regions and turned to be the first critic of the task of floristic classification: "I thus hold divisions of the sphere by areas, suggested until now, for artificial systems . . . . they just harmed science" (A de Candolle 1855, pp. 1304–1305, as quoted by Nelson 1978). Later he states, with reference to his *Geographie Botanique*: "my work remained completely different from that what my father thought, because the documentation had become more numerous, and my ideas had singularly moved away from those which had reigned in science for twenty years" (A de Candolle Mémoires, p 395, as quoted by Nelson 1978).

Is seems that as botanical information became overwhelming, the task of phytogeographical classification was getting more and more difficult. One of the most important naturalists in this era of growing botanical knowledge was JD Hooker (1817–1911) (Sect. 2.1). Joining James Cook on the *Endeavour*, he much improved the floristic knowledge of the southern hemisphere. Hooker's publications compiled as *The Botany of the Antarctic Voyage…* (Hooker 1844–1860) were, according to Thiselton-Dyer (1909), almost as epoch-making as Darwin's *Origin of species*.

By the second half of the nineteenth century a huge amount of floristic knowledge had accumulated. This knowledge, coupled with the ecological principles developed since A. von Humboldt, permitted August Grisebach (1814–1879) to publish his *Vegetation der Erde*, which related explicitly the plant world with the regional climates (Grisebach 1872). In Grisebach's view, Chile had to be classified into 3 regions (*Gebiete*): 1. a Chilean floristic core, *Chilenisches Übergangsgebiet* (transition zone) from 23° to 34°S, that holds a "unique flora"; 2. an Antarctic region (*Antarktisches Waldgebiet*), ranging from 34° to 56°S, characterized especially by the genus *Nothofagus*; and 3. a tropical Andean flora that ranges from Ecuador to northern Chile (Table 4.1).

Adolf Engler (1844–1930), one of the greatest German botanists, was the first one to try a synthesis of the evolution of the plant world on a global scale (Engler 1879, 1882). He classified the world flora into four realms and 31 regions, dividing each region also into provinces and districts, thus designing a very detailed hierarchical system that turned into the platform for all coming classification systems. Chile was classified into the *Südamerikanische Florenreich* (recognizing the *Nordchilenische Provinz* as the *Chilenische Übergangsgebiet* from Grisebach) and in the *Altoceanisches Florenreich*, South of 36°S. This *Altoceanisches Florenreich* grouped southern Chile together with New Zealand's South Island, the sub-Antarctic islands, most of Australia and the Cape region of South Africa (Table 4.1), (Fig. 4.3). "Engler was surprisingly perceptive in realizing that, scattered over the islands and lands of the southernmost part of the world, lay the remains of a single flora, which he called 'the Ancient Ocean' flora. It was over 80 years before acceptance of the movement and splitting of continents at last explained this very surprising pattern of distribution" (Cox and Moore 2005, p 26).

Later, Engler suggested that *Australe Florenreich* would be a better name as it was characterized by the *Austral-antarktischen Florenelement* (Engler 1899, p 149). He also added a fifth kingdom, the *Ozeanisches Florenreich*, which was composed of the aquatic plants from the vast oceans.

Oscar Drude (1852–1933) worked closely with A. Engler for the publication of the series "Die Vegetation der Erde". Being a student from Grisebach, Drude found several difficulties in synthesizing the floristic knowledge of his predecessors with the growing ecological knowledge systematized by Grisebach (1872). Drude first published his work Die *Florenreiche der Erde* based on a floristic approach (Drude 1884). He defined 14 floristic kingdoms and 55 floristic regions =*Gebiete*. Northern

Fig. 4.3 Floristic realms: **a** according to Engler (1882); **b** Drude (1884)

Chile to 41°S corresponded to the *Andines Florenreich* and southern Chile to the *Antarktisches Florenreich* (Table 4.1) (Fig. 4.3).

Drude's concern about the floristic and ecological differences led him to publish separate maps for a floristic classification and for a vegetation classification (Drude 1887). Three years later he abandoned the floristic classification altogether: "The maps published in the geographical reports of 1884 about my floristic classification show the uncertainty of the boundary lines due to numerous migration routes and directions of dispersal, which overlap from one to the other realm; it is a long

Fig. 4.4 Floristic realms according to Diels (1908)

known fact that each attempt to draw strict floristic boundaries, is itself ruinous" (Drude 1890, p. 329). Drude decided to join the more physiognomic approach from his mentor Grisebach, and he modified the classification on the basis of the new climatological basis provided by Wladimir Köppen (1884). The floristic kingdoms still numbered 14, and South America remained unmodified (Drude 1887).

Ludwig Diels (1874–1945), successor of Engler in Berlin, synthesized Drude's classification into six floristic realms, following the early proposal by Engler (1882) but obviating the oceanic realm (*Ozeanisches Florenreich*), and dividing Engler's *Altoceanisches Florenreich* into an *Antarktis*, an *Australis* and a *Capensis* (Fig. 4.4). Diels (1908) was the first to raise the African Cape region to the category of a realm. He considered the *Australisches Florenreich (Australis)* as comprising only Australia and Tasmania – and considered Malesia and New Zealand as part of the *Paläotropis*. South America and Central America including Mexico and Baja California was part of the *Neotropis*, but southernmost South America retained its designation as a realm, the *Antarktis*. Diels (1908) little book was reprinted five times until 1958, and his realm classification was retained adding only more details at the regional scale by Mattick (1964) and later popular authors like Good (1947) and Takhtajan (1986). Diels' proposal modified by the mentioned authors is still preferred in all modern German phytogeography textbooks (e.g. Richter 1997; Schroeder 1998; Frey and Lösch 2004).

Almost contemporaneous to Diels (1908) is Christ's (1910) specific proposal for the world classification of ferns. As regards this plant group, Chile shared an Andean flora with the other Andean territories, but harboured its own Chilean fern flora west of the Andes and south of 39°S (Christ 1910).

The English botanist Ronald Good (1896–1992) published the first edition of *The Geography of the Flowering Plants* in 1947. The work became one of the most popular books in the field, reaching four editions and two reprints between 1947 and 1974. He followed Diels with the 6 realms, dividing them into 37 regions. Chile south of 41° was classified into the "Antarctic kingdom", and the north as the "Neotropical kingdom". The scheme is very similar to that of Russian botanist

Armen Takhtajan (1910–2009), which became very popular after its translation into English. In a first version he maintained the 6 realms of Diels and the 37 regions of Good (Takhtajan 1961) but in his later proposal he reduced the regions to 35. Diels' scheme of 6 realms stayed unchanged (Takhtajan 1986). In his first classification he considered Central Chile as part of the Neotropical region (Takhtajan 1961), but in his later work he classified all the southern cone South of 25° into the Holantarctic kingdom (Takhtajan 1986).

The basic scheme of 6 floristic realms proposed by Diels (1908) stayed unchanged during the twentieth century. Only more recently Cox (2001) reanalysed both long-standing floristic and faunistic schemes.[1] For the global flora his proposal was a rearrangement of the six former floristic realms into five, more or less consistent with the continental shapes: the Holartic, South American, African, Indo-Pacific, and Australian. This proposal has been disputed by Morrone (2002), and is worth of being revised hereafter.

4.2 The Austral v/s the Neotropical Floristic Realm

> We have known for more than a hundred years that southern South America, Tasmania-Australia, and New Zealand are inhabited by numerous groups of plants and animals which are more closely related to another than to any other group (Brundin 1966, p 8)

As described in Sect. 4.1, the Chilean flora has been alternatively classified under the neotropical and/or the austral floristic realm. We can mention at least three visions that are in conflict:

(a) the older view of Engler (1882), Diels (1908) and Skottsberg (1910), that draw a boundary between the neotropical and the austral kingdoms at around 47°S;
(b) Takhtajan's (1986) later proposal setting this limit at around 23°S;
(c) the more recent proposal of Cox (2001) that aligns all of the South American flora under an "American kingdom".

Regarding the former Antarctic kingdom Cox wrote: "... the consistency of the plant geographical system is better served by transferring some of the regions of the Antarctic Kingdom to the South American Kingdom and the rest to the Australian Kingdom, in each case noting their individual historical and ecological characteristics" (Cox 2001). The author was critical toward Takhtajan's *Holantarctic kingdom* because Takhtajan's *Holantarctic* is based at the family level mainly on American endemic families (e.g. Thyrsopteridaceae, Lactoridaceae, Gomortegaceae, Aextoxicaceae). The dominance of American families seems to give reason to Cox for transferring the areas of their occurrence to the American kingdom.

Cox's vision is contested by Morrone (2002) due to neglecting the austral floristic and faunistic relationships. Morrone (2002) related the classification to the his-

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[1] The faunistic regions date back to Sclater (1858) and Wallace (1876).

tory of these biotas, coming to a scheme of only 3 biotic realms: the Holarctic kingdom, the Tropical kingdom (=East Gondwana), and the Austral kingdom (=West Gondwana). This was Engler's early intention (1879, 1882); in fact the result is remarkably similar to Engler's, but it groups the paleotropis and neotropis into one tropical realm.

Specifically reanalysing floristic relationships, recently Moreira-Muñoz (2007) found support for the existence of an *austral floristic realm*, composed of more than 60 genera and 15 families which uniquely share the southern territories of South America, Australasia and to a minor extent, by the Cape Floristic Region of South Africa (Moreira-Muñoz 2007) (Table 4.2).

Table 4.2 Families composing the Austral floristic realm

Families	Distribution	Genera/species
Araucariaceae	SE Asia, western Pacific, South America (disjunct southern Chile/Argentina and SE Brazil)	3/38
Asteliaceae	New Zealand, Tasmania, SE Australia, New Guinea, Pacific Islands, Hawaii, Chile, Mascarenes	2–4/36
Atherospermataceae	Chile/Argentina, Tasmania, Australia, New Zealand, New Caledonia, New Guinea	6/11
Berberidopsidaceae	Chile, E Australia	1/2
Calceolariaceae	Tropical and W temperate South America, Brazil, New Zealand	2/240–270
Centrolepidaceae	SE Asia, Malesia, New Zealand, southern South America	3/35
Corsiaceae	Southern South America, SE Asia, Papuasia-Australia	3/30
Escalloniaceae	Central and South America, SE and SW Australia, New Zealand, Réunion Is	8/68
Griseliniaceae	New Zealand (2 spp.), Chile (5), one to Argentina and a variety disjunct between Chile/SE Brazil	1/7
Luzuriagaceae	Southern Argentina and Chile, Falkland Islands, New Zealand and Australia (New South Wales to Tasmania)	2/5
Nothofagaceae	New Guinea, New Caledonia, E Australia, New Zealand, South America	1/36
Proteaceae	Australasia, Africa, South America	70/1,000
Restionaceae	Australasia, South Africa, Madagascar, South America	58/520
Stylidiaceae = Donatiaceae	Scattered in South East Asia to Australia and New Zealand, southern South America	6/157

Source: Moreira-Muñoz (2007), by permission of John Wiley and Sons.

4.2.1 *Floristic Elements in the Latitudinal Profile*

Moreira-Muñoz (2007) provided support for the further recognition of an austral and a neotropical floristic realm in South America, but the question of the boundary between both still remains.

After grouping the Chilean plants into seven floristic elements (*Kontingente*), Reiche (1907, p 319) (Table 3.1) proposed that the neotropical and antitropical (Reiche's *Californian*) elements occur in Chile due to a migration route (*Wanderungslinie*) from the north to the south along the Andes down to Magallanes, until this migration was stopped at the border of the "Antarctic realm" (situated sensu Reiche from ~ 40° to the south along the coast).

Schmithüsen (1956) plotted the floristic elements along the latitudinal gradient. He defined therefore eight elements from the northern neotropical to the southernmost evergreen subantarctic forests. He could not define a sharp limit and proposed spatial imbrications of the different elements in Central Chile between 30° and 40°S (Fig. 4.5). Setting sharp limits between floristic/biogeographic units always has been problematic (e.g. Drude 1890, Sect. 4.1), but the analysis of the range extension of taxa has been ever informative in this respect (e.g. Godley 1963; Reiche 1907).

The seven floristic elements distinguished here (Sect. 3.1) contain genera with a diversity of geographic range sizes. In every element, with exception of the endemic element, there are some genera distributed over the whole country, from the southernmost Cabo de Hornos to the northern Parinacota province. Every element also

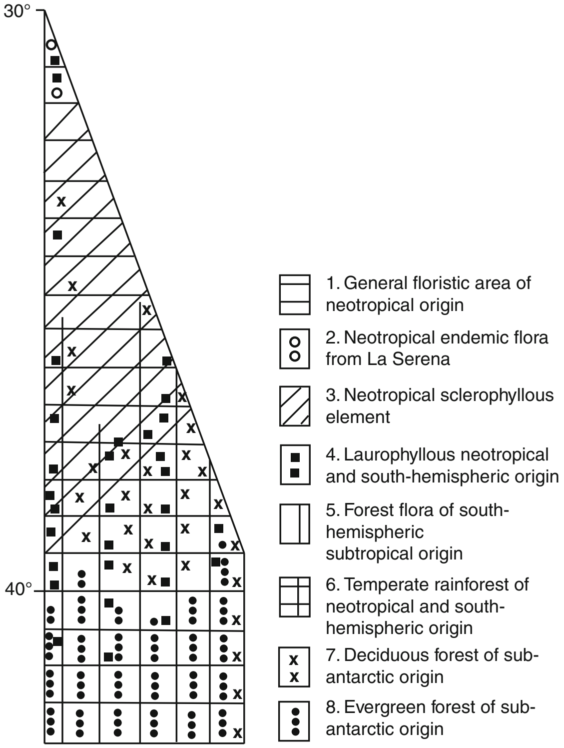

Fig. 4.5 Floristic elements in Central Chile (adapted from Schmithüsen 1956)

Table 4.3 Average of geographic range of floristic elements

Floristic element	Average (°S)
3. Neotropical	29.6
1. Pantropical	32.2
6. Endemic	32.2
4. Antitropical	35.1
7. Cosmopolitan	36.0
2. Australasiatic	41.5
5. South-temperate	42.3

contains a number of genera known for their very restricted range or known only from a couple of localities. One method of assessing the main massing of the genera is to calculate for every element the average distribution of the genera that compose them [northern limit + southern limit/2]. Results are shown in Table 4.3.

The neotropical element has the northernmost average (29.6°S), while the south-temperate element has the southernmost average (42.3°S). The australasiatic element has an average at 41.5°S. The pantropical, antitropical, cosmopolitan and endemic elements show average latitudes between 32° and 36°S. The fact that most elements have their average in Central Chile tends to reinforce the early view of Grisebach (1872), Engler (1882), and Schmithüsen (1956) to consider this region a transition zone with different, converging elements. Central Chile is still considered as a key region for the understanding of the biogeographical history of several South American plant groups, like the Bromeliaceae (Schmidt Jabaily and Sytsma 2010). The southernmost average reached by south-temperate and australasiatic genera show the consistency of the relationship between southern Chile and other austral territories like New Zealand (Moreira-Muñoz 2007).

4.2.2 Similarity Along the Latitudinal Gradient

Since the latitudinal ranges of the genera does not account for possible distribution or collection gaps, four regional floras were selected for a similarity analysis: Antofagasta (ANT), Coquimbo (COQ), Biobío (BIO), and Magallanes (MAG) (Fig. 4.6). The regions included in the analysis have a floristic checklist (Table 4.4), that has been revised and homologized. Regions analysed are dissimilar in area, but some of them harbour similar numbers of native genera (e.g. COQ=457, BIO=465), MAG showing the lowest generic richness: MAG=252.

The Jaccard similarity index was calculated for the data sets (Zunino and Zullini 2003; Cox and Moore 2005; Lomolino et al. 2006). The highest floristic similarity is between COQ and BIO, sharing 323 genera (Table 4.5). The lowest similarity is shown by ANT and MAG, which share 97 genera. There seems to be a relationship between the similarity and the geographic distance, and in Fig. 4.6 both variables are represented, showing this trend of decreasing similarity as the regions are further apart.

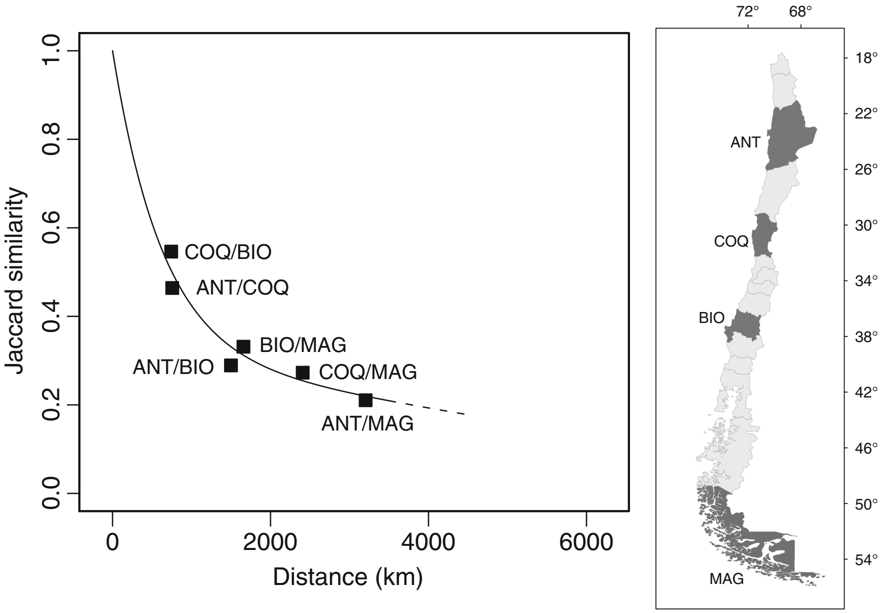

Fig. 4.6 **a** Similarity versus geographic distance between Chilean regions; **b** location of compared regions

Table 4.4 Regions used in the floristic similarity analysis

Abbreviation	Regions	Area (km^2)	N° native vascular plant genera	Source
ANT	Antofagasta	126,049	316	Marticorena et al. (1998)
COQ	Coquimbo	40,580	457	Marticorena et al. (2001)
BIO	Biobío	37,063	465	CONC herbarium, R. Rodríguez pers. comm.
MAG	Magallanes	132,033	252	Henríquez et al. (1995)

Table 4.5 Floristic similarity and geographic distance of different regions in Chile: Antofagasta (ANT), Biobío (BIO), Coquimbo (COQ) and Magallanes (MAG). Geographic distance has been calculated as the latitudinal difference between the respective geographic centroid of each region

Compared regions	Shared genera	Similarity Jaccard	Distance (km)
ANT/COQ	244	0.46	777
ANT/BIO	174	0.29	1,527
ANT/MAG	97	0.21	3,227
COQ/BIO	323	0.54	750
COQ/MAG	150	0.27	2,450
BIO/MAG	178	0.33	1,700

Table 4.6 Floristic elements in each of the compared regions

	Pantropical		Australasiatic		Neotropical		Antitropical		South-temperate		Endemic		Cosmopolitan	
REG	n	%	n	%	n	%	n	%	n	%	n	%	n	%
ANT	28	8.9	8	2.5	115	36.5	45	14.3	17	5.4	15	4.8	82	26.0
COQ	39	8.6	22	4.9	114	25.1	73	16.1	42	9.3	38	8.4	117	25.8
BIO	42	9.1	41	8.9	100	21.6	72	15.6	51	11.0	27	5.8	123	26.6
MAG	11	4.4	38	15.1	29	11.5	44	17.5	42	16.7	1	0.4	84	33.5

These regions have been further compared regarding the floristic elements composing these regional floras. Results indicate a trend along the latitudinal gradient in Chile: the cosmopolitan, antitropical, south-temperate, and australasiatic genera show a proportional increase towards the south, while the proportion of neotropical, pantropical and endemic genera decrease towards the south (Table 4.6, Fig. 4.7). Highly remarkable is the replacement of the neotropical by the australasiatic genera between BIO and MAG (arrow in Fig. 4.7).

The replacement of neotropical genera by australasiatic genera in southernmost Chile (Magallanes) clearly shows the consistency of the inclusion of subantarctic Chile south of 47° in an ***austral floristic realm***, as earlier proposed by Engler (1882), Drude (1884), Reiche (1907, p 282), Diels (1908), and Skottsberg (1916). In Skottsberg's *Plant geographical map of South America south of 41° latitude* (Skottsberg 1910), the author proposed a limit at 47°–48°S, between a more species-rich temperate rainforest to the north, and a "subantarctic" species-poor temperate rainforest to the south. In his more complete account of the southern flora, he explicitly proposed a limit between an "Andean floristic region" and a

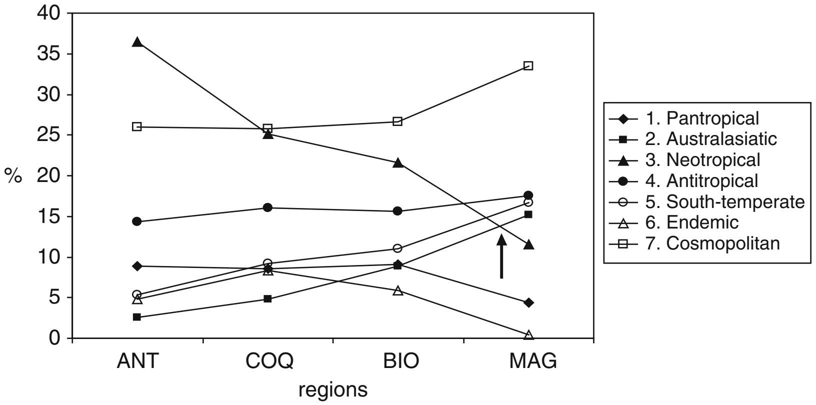

Fig. 4.7 Floristic elements present in four regional floras (percentage). *Arrow* showing relative replacement of neotropical genera by australasiatic ones

"Subantarctic region" from 48°S to the south (including the Falkland [Malvinas] Islands) (Skottsberg 1916, pp 344–345).

4.3 Regions and Provinces

Below the realm level, several schemes have been proposed for the classification of the Chilean territory into regions, subregions and provinces, mostly by means of the distribution of faunal groups (Artigas 1975; Morrone et al. 1997; Hernández et al. 2005; Casagranda et al. 2009).

Biogeographic schemes for Chile based on floristic analysis are sparse. The first plant geographical map for Chile accompanied Reiche's analysis of the distribution of the Compositae (Asteraceae) family (Chap. 8). He defined, based on his experience, ten floristic regions and subregions for the Chilean Compositae (Chap. 8 and Fig. 8.7). On a second map he also proposed possible migration routes for these taxa (Fig. 8.7).

The first attempt towards a synthetical cartography for the Chilean flora is found in the two maps that accompanied Reiche's *Plant geography* (Reiche 1907) at a scale 1:7,500,000 (Fig. 4.8). In the first map Reiche proposed distribution ranges and limits for some key taxa. In the second map he divided the country in several floristic units, integrating floristic and physiognomic knowledge (Fig. 4.8).

Reiche proposed the limit between the Antarctic and Neotropical realms at around 40°S (Table 4.7). Although the resulting picture looks rather simple, this nevertheless is the first attempt of a floristic cartography for Chile. After Reiche, attempts turned into a more physiognomic approach (see Sect. 1.3).

In the search for a synthetic view that integrates floristic and faunistic information, the most long-standing scheme for South America is the one by Cabrera and Willink (1973). They classified Chile into two regions (Neotropical and Antarctic) and dominions (*Andino-Patagónico* and *Subantártico*). They further subdivided these areas in four provinces: *provincia del Desierto, provincia Puneña* (high Andes), *provincia Chilena*, and *provincia Subantártica*. They subdivided the provinces into smaller districts (not mapped). This was a remarkable attempt to integrate historical and ecological information into one classification scheme, although the approach still remained physiognomic rather than floristic/faunistic (see a revision by Ribichich 2002). Also some confusion arose since Cabrera and Willink (1973) translated the traditional concept of the realm as *región biogeográfica* and the traditional concept of the region as *dominio biogeográfico* (Fig. 4.1). Interestingly, their provinces indeed correspond to a third level in a hierarchy, and have been more recently retrieved by Morrone (2001) (Fig. 4.9a).

Morrone (2001) applied individual tracks for the definition of the provinces and emphasises the importance biogeographic homology, i.e. a common evolutionary history in the definition of the provinces. He also argues that one of the main problems is to define the limits between the units. In fact, several authors have focused in the transition zones rather than in the cores of the units (Fig. 4.5) (Ruggiero and Ezcurra 2003; Morrone 2006; see Drude's early concerns in Sect. 4.1).

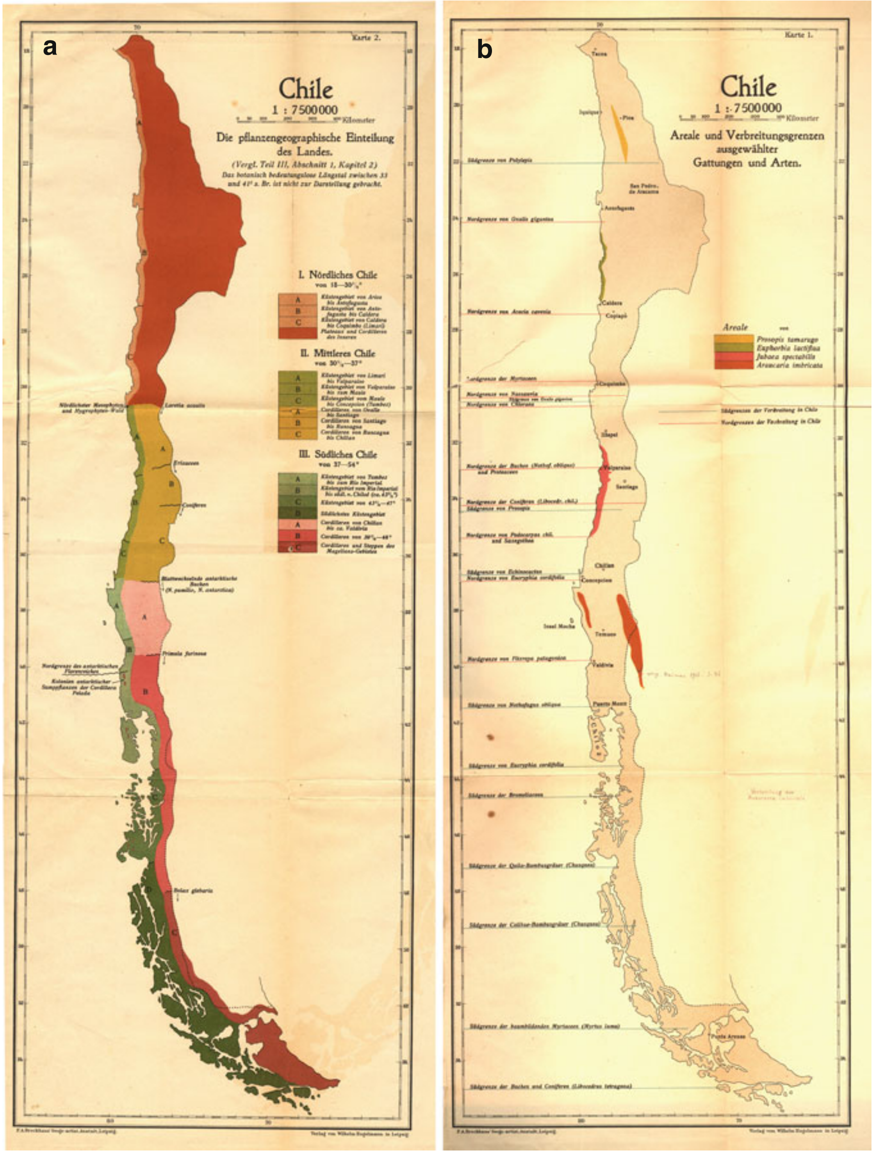

Fig. 4.8 Maps accompanying Reiche's Plant Geography (1907): **a** floristic regions, see Table 4.7; **b** distribution limits for selected taxa

Table 4.7 Floristic units from the "Plant Geography" of Reiche (1907)

Regions and subregions	Extension
I North Chile	18°–30°40′S
(A) Coast Arica to Antofagasta	18°–23°30′S, characteristic *Euphorbia lactiflua*
(B) Coast Antofagasta to Caldera	23°30′–27°S
(C) Coast Caldera to Fray Jorge (río Limarí)	27°–30°40′S, the southern limit is at Fray Jorge, the "northernmost advance of the hygrophilous forest"
(D) Interior Cordilleras	18°–30°40′S
II Central Chile	30°40′S–37°, Río Limarí (Fray Jorge forest) to Concepción
(A) Coast Fray Jorge to Valparaíso	30°40′–33°30′S
(B) Coast Valparaíso to Maule	33°30′–35°S
(C) Maule to Concepción	35°–37°S
(A′) Cordillera Ovalle to Santiago	30°40–33°30′S
(B′) Cordillera Santiago to Rancagua	33°30′–35°
(C′) Cordillera Rancagua to Chillán	35°–37°
III South Chile	37°–54°S
(A) Coast Concepción to Río Imperial	37°–39°S
(B) Coast Río Imperial to Chiloé	39°–43°30′S (At 40°, northern limit of the Antarctic floristic realm)
(C) Coast Chiloé to Taitao	43°30′–47°S
(D) Coast Taitao peninsula to Cabo de Hornos	47°–56°S
(A′) Cordillera Chillán to Panguipulli	37°–39°30′S
(B′) Cordillera Panguipulli to Campo de Hielo Sur	39°30′–48°S
(C′) Campo de Hielo Sur to Magallanes	48°–55°S, Cordillera and Magallanes steppe

4.3.1 Endemism as the Base for Regionalization

Most regionalizations rest upon endemic taxa. Since Augustin Pyramus de Candolle (1820) coined the term, endemism has turned out to be one of the most appealing concepts in historical biogeography. A geographic area that contains two or more non-related endemic taxa is formally defined as an area of endemism, a concept of vital importance in modern historical biogeography (Harold and Mooi 1994; Linder 2001). In the words of Nelson and Platnick (1981) "the most elementary questions of historical biogeography concern areas of endemism and their relationships".

Several methods could be applied nowadays to the problem of regionalization of Chile: methods in common use are Parsimony Analysis of Endemicity (PAE), and the optimality method (NDM/VNDM). Both methods have been widely used in several geographic areas and taxa (Nihei 2006; Escalante 2009).

An exercise is presented here, done with the Chilean endemic plant genera (Sect. 3.1). 65 genera endemic to continental Chile were considered for the analysis, since remaining genera are known from just one or two localities. Several individual distribution maps of endemic genera were presented in Fig. 3.13.

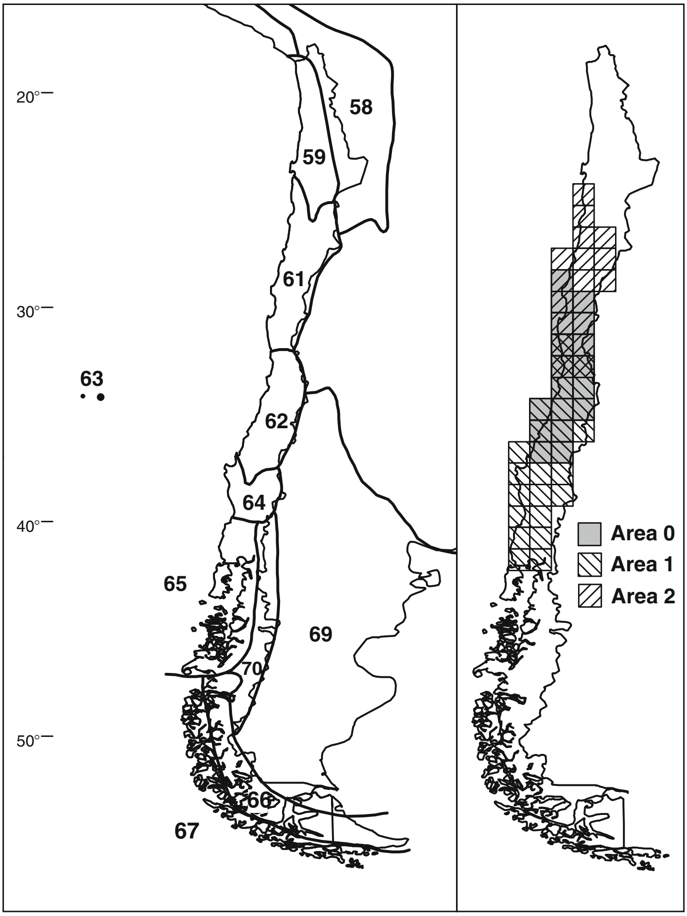

Fig. 4.9 Biogeographic provinces for Chile: **a** according to Morrone (2001): Puna (58), Atacama (59), Coquimbo (61), Santiago (62), Juan Fernández (63), Maule (64), Valdivian Forest (65), Magellanic Forest (66), Magellanic Páramo (67), Central Patagonia (69), Subandean Patagonia (70); **b** according to consensus areas of endemism obtained by NDM/VNDM on the base of the endemic genera

PAE. This method classifies areas using shared taxa using parsimony (Rosen 1988; Nihei 2006). In a PAE cladogram, groups of areas sharing exclusive taxa (based at least on two synapomorphies) are identified as areas of endemism. Since PAE does not perform satisfactorily with fewer characters (taxa) than species (quadrats), it was not applied for the analysis of the endemic genera. It was used for the regionalization of Chilean Cactaceae species (Sect. 7.2).

NDM/VNDM. The optimality algorithm is a biogeographic method to identify areas of endemism that calculates an endemicity index for a set of areas based on the adjustment of the distributions of two or more species (Szumik et al. 2002; Szumik and Goloboff 2004). The algorithm is implemented in the software NDM/VNDM

(Goloboff 2005). Recent results are showing that the use of this algorithm can improve the number of areas of endemism obtained by other methods (Casagranda et al. 2009; Carine et al. 2009; Escalante et al. 2009).

The input for the program NDM is the presence/absence of taxa in grid cells. In this case, 59 quadrats of 1 × 1 degree lat/long cover the area of mainland Chile occupied by endemic genera. Collection localities are entered as xy data. The optimality method was carried out with NDM/VNDM v. 2.6 (Goloboff 2005) with the next options: saving sets with two or more endemic genera, and saving sets with a score above 2.0. The type of swapping was of one cell at a time, with 0% of unique species in overlapping subsets. The search was performed until the number of sets was showed stable in 20 repetitions with different random seeds, using edge proportions. With these parameters, 17 areas of endemism were obtained.

Consensus of 30% of similarity was applied to the obtained sets. With the option "against any of the other areas in the consensus" three consensus areas were obtained, to some extent overlapping. Genera contributing to the final score are those that reach more than 0.5 (Escalante pers. comm., with 1 the highest value possible for a single genus) (Fig. 4.9a and b).

Consensus Area n°0 is built upon eight sets. It is supported by 14 endemic genera reaching a score of 4.3. It includes 18 quadrats in Central Chile between at 28° (coast) and 37°S. Its endemic genera are *Adenopeltis, Avellanita, Epipetrum, Jubaea, Miersia, Moscharia, Ochagavia, Placea, Pleocarphus, Speea, Tecophilaea, Tetilla, Traubia* and *Trevoa*. The consensus includes two genera with scores below 0.5 (*Cyssatobryon* and *Neoporteria*).

Consensus Area n°1 was obtained from two sets, supported by the presence of five endemic genera and a score of 3.71. It includes 26 quadrats in Central-South Chile between 31° (coast) and 42°S. Its endemic genera are *Acrisione, Fascicularia, Gymnachne, Lapageria* and *Vestia*. The consensus includes three genera with scores below 0.5 (*Francoa, Peumus* and *Nothanthera*).

Consensus Area n°2 is built by seven sets, formed by 10 endemic genera and a score of 3.52. It includes 18 quadrats in North-Central Chile between 24° and 33°S. Its endemic genera are *Bakerolimon, Balsamocarpon, Bridgesia, Copiapoa, Dinemagonum, Eriosyce, Leontochir, Phrodus, Pintoa* and *Thelocephala*. The consensus includes one genus with a score below 0.5 (*Microphyes*).

Comparing the areas of endemism recognized by NDM with previous biogeographic schemes, it appears noteworthy that Area 2 is perfectly coincident with Morrone's (2001) *provincia de Coquimbo* and to some extent with the *distrito Coquimbano* from Cabrera and Willink (1973).[2] On the contrary, Area 1 encloses part of Morrone's (2001) *provincia de Coquimbo*, the *provincia de Santiago* and *provincia del Maule*, and the northern part of the *provincia del Bosque Valdiviano*. The northern limit of NDM's Area 1 is coincident with the location of the Fray Jorge forest, a long recognized northern advance of the Valdivian forest (Box 3.1). The Río Limarí and Fray Jorge forest was already proposed by Reiche as the limit between

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[2] Compared with the description in Cabrera and Willink's text, not the map!

the floristic regions of North Chile and Central Chile (Table 4.7). Finally, NDM's Area 0 encompasses most genera strictly endemic (14) to Central Chile between 28° and 37°. This area is highly coincident, especially in its southern limit, with the region of Central Chile from Reiche (1907).

The three consensus areas can be interpreted as having each an evolutionary history. It is interesting that consensus area 0 has a degree of overlap with the one to the north (Area 2) and the one to the south (Area 1), showing even a range of overlap between the three from 31° (coast) to 33°S. This range can be interpreted as a panbiogeographic node, i.e. an area where different evolutionary lines coincide (Heads 2004). Indeed, at 33°S, La Campana National Park has been long recognized as a mosaic of elements of Neotropical and Gondwanic origin (Luebert et al. 2002), showing also the extant northern distribution limit of the genus *Nothofagus* in the Southern Cone of America (Chap. 9).

The results of this exercise further show that the units of a biogeographic regionalization rarely have sharp limits and, on the contrary, tend to superpose in the form of transition areas. Still, results seem to be highly dependent on the grid size, the origin assigned to the grid, the data base strength, the number of species analysed and the search parameters (Carine et al. 2009). More exercises on this topic have been done with the Chilean Cactaceae and Asteraceae in Chaps. 7 and 8.

Finally, the naming of biogeographic units resulting from a regionalization is not a trivial thing, and a formal system has been recently proposed by Ebach et al. (2008) as an International Code of Area Nomenclature, ICAN. Further developments in this field of research should take account of this systematization proposal of the Systematic and Evolutionary Biogeographical Association, SEBA (http://www.uac.pt/~seba/).

References

Artigas J (1975) Introducción al estudio por computación de las areas zoogeográficas de Chile continental basado en la distribución de 903 especies terrestres. Gayana (Chile) 4:1–25

Brundin L (1966) Transantarctic relationships and their significance, as evidenced by chironomid midges: with a monograph of the subfamilies Podonominae and Aphroteniinae and the austral Heptagyiae. K Sven Vetenskapsakad Handl 11:1–472

Cabrera AL, Willink A (1973) Biogeografía de América Latina. Monografía 13. Serie de Biología. (2nd Revised edn 1980). Secretaría General de la Organización de los Estados Americanos, Washington, DC

Carine MA, Humphries CJ, Guma R, Reyes-Betancort JA, Santos Guerra A (2009) Area and algorithms: evaluating numerical approaches for the delimitation of areas of endemism in the Cabary Islands archipelago. J Biogeogr 36:593–611

Casagranda MD, Roig-Juñent S, Szumik C (2009) Endemismo a diferentes escalas espaciales: un ejemplo con Carabidae (Coleóptera: Insecta) de América del Sur austral. Rev Chil Hist Nat 82:17–42

Christ H (1910) Die Geographie der Farne. Gustav Fischer Verlag, Jena

Cox CB (2001) The biogeographic regions reconsidered. J Biogeogr 28:511–523

Cox CB, Moore PD (2005) Biogeography: an ecological and evolutionary approach, 7th edn. Blackwell Publishing, Oxford de Candolle A (1835) Introduction à l'étude de la Botanique I, II. Librairie Encyclopédique de Roret, Paris

de Candolle A (1855) Géographie botanique raisonnée, 2. vol. Paris

de Candolle, A-P (1820) Geographie botanique. In: Dictionnaire des sciences naturelles, XVIII. Flevrault, Strasbourg, pp 359–422

Diels L (1908) Pflanzengeographie. Göschen'sche Verlagshandlung, Leipzig

Drude O (1884) Die Florenreiche der Erde: Darstellung der gegenwärtigen Verbreitung sverhältnisse der Pflanzen: Ein Beitrag zur vergleichenden Erdkunde. Ergänzungsheft N° 74, Petermanns Mitteilungen, Gotha, Justus Perthes

Drude O (1887) Atlas der Pflanzenverbreitung. Berghaus" Physikalischer Atlas, Abteilung V, Gotha, Justus Perthes

Drude O (1890) Handbuch der pflanzengeographie. Bibliothek Geographischer Handbücher (ed. by F Ratzel). Verlag J. Engelhorn, Stuttgart

Ebach MC, Goujet DF (2006) The first biogeographical map. J Biogeogr 33:761–769

Ebach MC, Morrone JJ, Parenti LR, Viloria AL (2008) International code of area nomenclature. J Biogeogr 35:1153–1157

Eldredge N (1985) Unfinished synthesis: biological hierarchies and modern evolutionary thought. Oxford University Press, New York, NY

Engels E-M (2005) Ethik in den biowissenschaften. In: Maring M, (ed) Ethisch-Philosophisches Grundlagenstudium 2. Ein Projektbuch. Münster, LIT Verlag, pp. 135–166

Engler A (1879) Versuch einer Entwicklungsgeschichte der Pflanzenwelt, insbesondere der Florengebiete seit der Tertiärperiode. Vol 1. Die Extratropischen Gebiete der Nördlichen Hemisphäre. Verlag von W. Engelmann, Leipzig.

Engler A (1882) Versuch einer Entwicklungsgeschichte der Pflanzenwelt, insbesondere der Florengebiete seit der Tertiärperiode. Vol. 2. Die Extratropischen Gebiete der Südlichen Hemisphäre und die Tropischen Gebiete. Verlag von W. Engelmann, Leipzig.

Engler A (1899) Die Entwickelung der Pflanzengeographie in den letzten hundert Jahren und weitere Aufgaben derselben. (ed by Gesellschaft für Erdkunde zu Berlin) pp 1–247

Escalante T (2009) Un ensayo sobre regionalización biogeográfica. Rev Mex Biodivers 80: 551–560

Escalante T, Szumik C, Morrone JJ (2009) Areas of endemism of Mexican mammals: reanalysis applying the optimality criterion. Biol J Linn Soc 98:468–478

Frey W, Lösch R (2004) Lehrbuch der Geobotanik, 2nd edn. Elsevier-Spektrum Akad. Verlag, Munich

Godley EJ (1963) Contributions to the plant geography of southern Chile. Rev Univ (Chile) 48:31–39

Goloboff P (2005) NDM/VNDM ver. 2.6. Programs for identification of areas of endemism. http://www.zmuc.dk/public/phylogeny/endemism

Good R (1947) The geography of the flowering plants. 4th edition 1974. Longman, London

Grehan JR (2001) Panbiogeography from tracks to ocean basins: evolving perspectives. J Biogeogr 28:413–429

Grisebach A (1872) Die vegetation der Erde nach ihrer klimatischen Anordnung: ein Abriss der vergleichenden Geographie der Pflanzen, 2 vols, 1st edn. Engelmann Verlag, Leipzig. (2d revised ed. 1884)

Harold AS, Mooi RD (1994) Areas of endemism – definition and recognition criteria. Syst Biol 43:261–266

Heads M (2004) What is a node? J Biogeogr 31:1883–1891

Henríquez JM, Pisano E, Marticorena C (1995) Catálogo de la flora vascular de Magallanes (XII Región), Chile. An Inst Pat Ser Cs Nat (Chile) 23:5–30

Hernández CE, Moreno RA, Rozbaczylo N (2005) Biogeographical patterns and Rapoport's rule in southeastern Pacific benthic polychaetes of the Chilean coast. Ecography 28:363–373

Huxley CR, Lock JM, Cutler DF, (eds) (1998) Chorology, taxonomy and ecology of the floras of Africa and Madagascar. Royal Botanic Gardens, Kew

Jagers op Akkerhuis GAJM (2008) Analysing hierarchy in the organization of biological and physical systems. Biol Rev 83:1–12

Köppen W (1884) Die Wärmezonen der Erde, nach der Dauer der heissen, gemässigten and kaltern Zeit and nach der Wirkung der Wärme auf die organische Welt betrachtet. Meteor Z 1:215–226

Linder HP (2001) On areas of endemism, with an example from the African Restionaceae. Syst Biol 50:892–912

Llorente Bousquets J, Morrone JJ, (eds) (2005) Regionalización biogeográfica en Iberoamérica y tópicos afines. Las Prensas de Ciencias, Facultad de Ciencias, UNAM, México DF

Lomolino MV, Riddle BR, Brown JH (2006) Biogeography, 3rd edn. Sinauer Associates, Sunderland, MA

Luebert F, Muñoz-Schick M, Moreira-Muñoz A (2002) Vegetación y Flora de La Campana. In: Elórtegui S, Moreira-Muñoz A, (eds) Parque Nacional La Campana: origen de una Reserva de la Biosfera en Chile Central. Taller La Era, Santiago

Mackey B, Berry S, Brown T (2008) Reconciling approaches to biogeographical regionalization: a systematic and generic framework examined with a case study of the Australian continent. J Biogeogr 35:213–229

Marticorena C, Matthei O, Rodríguez R, Arroyo MTK, Muñoz-Schick M, Squeo FA, Arancio G (1998) Catálogo de la Flora Vascular de la Segunda Región (Región de Antofagasta), Chile. Gayana Bot 55:23–83

Marticorena C, Squeo FA, Arancio G, Muñoz-Schick M (2001) Catálogo de la flora vascular de la IV Región de Coquimbo. In: Squeo FA, Arancio G, Gutiérrez JR, (eds) Libro Rojo de la Flora Nativa y de los Sitios Prioritarios para su Conservación: Región de Coquimbo. Ediciones Universidad de La Serena, La Serena, pp 105–142

Mattick F (1964) Übersicht über die Florenreiche und Florengebiete der Erde. In: Melchior H, (ed) A. Engler's Syllabus der Pflanzenfamilien, vol. 2, 12th edn. Angiospermen, Gerbrüder Borntraeger, Berlin, pp 626–629

McLaughlin SP (1992) Are floristic areas hierarchically arrange? J Biogeogr 19:21–32

McLaughlin SP (1994) Floristic plant geography: the classification of floristic areas and floristic elements. Prog Phys Geogr 18:185–208

McLaughlin SP (2007) Tundra to tropics: the floristic plant geography of North America. Sida Bot Misc 30:1–58. Botanical Research Institute of Texas

Mennema J (1985) The first plant distribution map. Taxon 34:115–117

Moreira-Muñoz A (2007) The Austral floristic realm revisited. J Biogeogr 34:1649–1660

Morrone JJ (2001) Biogeografía de América Latina y el Caribe. Manuales y Tesis SEA 3, Zaragoza

Morrone JJ (2002) Biogeographical regions under track and cladistic scrutiny. A comment on CB Cox (2001). J Biogeogr 29:149–152

Morrone JJ (2006) Biogeographic areas and transition zones of Latin America and the Caribbean Islands based on panbiogeographic and cladistic analyses of the entomofauna. Annu Rev Entomol 51:467–494

Morrone JJ, Katinas L, Crisci JV (1997) A cladistic biogeographic analysis of Central Chile. J Comp Biol 2:25–42

Nelson G (1978) From Candolle to Croizat: comments on the history of biogeography. J Hist Biol 11:289–305

Nelson G, Platnick N (1981) Systematics and biogeography: Cladistics and vicariance. Columbia University Press, New York, NY

Nihei SS (2006) Misconceptions about parsimony analysis of endemicity. J Biogeogr 33:2099–2106

Proches S (2008) Three ways to split a continent. J Biogeogr 35:195–196

Reiche C (1907) Grundzüge der Pflanzenverbreitung in Chile. In: Engler A, Drude O, (eds) Die Vegetation der Erde: Sammlung Pflanzengeographischer Monographien, vol. VIII. Verlag von V. Engelmann, Leipzig

Ribichich AM (2002) El modelo clásico de la fitogeografía de Argentina: un análisis crítico. Interciencia 27:669–675

Richter M (1997) Allgemeine Pflanzengeographie. Teubner Studienbücher der Geographie, Stuttgart

Rosen BR (1988) From fossils to earth history: applied historical biogeography. In: Myers AA, Giller PS, (eds) Analytical biogeography. Chapman and Hall, London, pp 437–481

Ruggiero A, Ezcurra C (2003) Regiones y transiciones biogeográficas: complementariedad de los análisis en biogeografía histórica y ecológica. In: Morrone JJ, Llorente J, (eds) Una perspectiva latinoamericana de la biogeografía. Las Prensas de Ciencias, UNAM, Mexico DF, pp 141–154

Schmidt Jabaily R, Sytsma KJ (2010) Phylogenetics of *Puya* (Bromeliaceae): placement, major lineages, and evolution of Chilean species. Am J Bot 97:337–356

Schmithüsen J (1956) Die räumliche Ordnung der chilenischen Vegetation. Bonn Geogr Abh 17:1–86

Schouw JF (1823) Grundzüge einer allgemeinen Pflanzengeographie (+ Atlas). Reimer, Berlin

Schroeder F-G (1998) Lehrbuch der Pflanzengeographie. Quelle and Meyer, Wiesbaden

Sclater PL (1858) On the general geographical distribution of the members of the class Aves. Zool J Linn Soc 2:130–145

Skottsberg C (1910) Botanische Ergebnisse der schwedischen Expedition nach Patagonien unde dem Feuerlande 1907–1909. I. Übersicht über die wichtigsten Pflanzenformationen Südamerikas S von 41°, ihre geographische Verbreitung und Beziehungen zum Klima. K Sven Vetenskapakad Handl 46:1–28

Skottsberg C (1916) Botanische Ergebnisse der schwedischen Expedition nach Patagonien und dem Feuerlande 1907–1909. V. Die Vegetationsverhältnisse längs der Cordillera de los Andes südlich von 41 Grad südlicher Breite. K Sven Vetenskapsakad Handl 56:1–366. Stockholm, Almqvist and Wiksell

Stuessy TF (2006) Principles and practice of plant taxonomy. In: Leadlay E, Jury S, (eds) Taxonomy and plant conservation. Cambridge University Press, Cambridge, pp 31–44

Szumik CA, Cuezzo F, Goloboff P, Chalup AE (2002) An optimality criterion to determine areas of endemism. Syst Biol 51:806–816

Szumik C, Goloboff P (2004) Areas of endemism: an improved optimality criterion. Syst Biol 53:968–977

Takhtajan A (1961) The origin of angiospermous plants, 2nd edn. original Russian edition, Gos. izd. Vysšaja Škola, Moscow

Takhtajan A (1986) Floristic regions of the world. University of California (translated from the original Russian edition 1978, Leningrad). Reprint (1988), B Singh, MP Singh, Dehra Dun, India

Thiselton-Dyer WT (1909) Geographical distribution of plants. In: Seward AC (ed) Darwin and modern science. Cambridge University Press, Cambridge, pp 298–318

Treviranus GR (1803) Biologie, oder Philosophie der lebenden Natur. Röwer, Göttingen

Wallace AR (1876) The geographical distribution of animals. Macmillan and Co, London

Zunino M, Zullini A (2003) Biogeografía: la dimensión espacial de la evolución. Fondo de Cultura Económica, México. From the 1995 Italian edition

Part III
Islands Biogeography

Chapter 5
Pacific Offshore Chile

Abstract The study of island biotas has been one of the most productive issues in biogeography. Indeed, one of the most interesting and challenging aspects of Chilean plant geography correspond to the Pacific islands offshore the American continent. This applies especially for the Juan Fernández and the Islas Desventuradas archipelagos that are analyzed regarding their geographical relationships. The flora of Juan Fernández is especially attractive for biogeography due to the presence of many locally endemic taxa, and a primitive endemic family: the Lactoridaceae, represented by the only species *Lactoris fernandeziana*. Finally, the threatened status of most of the Fernandezian flora is discussed with attention for the possibilities of conservation and restoration.

The Pacific islands offshore the continent have been called “the portion of Chile that is not in America”[1] (Fig. 1.1). These are three separate clusters of islands that are emerged seamounts on the Nazca Plate, formed by intraplate volcanoes that occur along linear chains (Stern et al. 2007). The volcanic origin of these islands is most evident in Rapa Nui, which harbors three coalescent volcanic centres (Rano-Kau, Poike, and Maunga Terewaka), plus ca 70 secondary eruptive centres (IGM 2005).

5.1 Rapa Nui

Rapa Nui (= Isla de Pascua, Easter Island) (27°05′S, 109°20′W, 160 km^2) (Fig. 5.1) is known all over the world due to its peculiar culture and the *moai* sculptures. Considered the most isolated inhabited island on the planet, it lies 3,760 km away from the South American continent, and 3,800 km from Tahiti. It occurs at the western edge of a chain of volcanic seamounts that also includes Isla Salas y Gómez (26°27′S, 105°28 W) (see Fig. 1.1). In spite of the geographical isolation, Rapa Nui has a long history of human occupation. The timing of the agricultural colonization of Rapa Nui has been dated at ca 1200 AD, and was accompanied by rapid deforestation, probably exacerbated by the primeval fires (Mann et al. 2008). Bork

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[1] Balcells (2005) called it “el Chile que no está en América”.

A. Moreira-Muñoz, *Plant Geography of Chile*, Plant and Vegetation 5,
DOI 10.1007/978-90-481-8748-5_5,

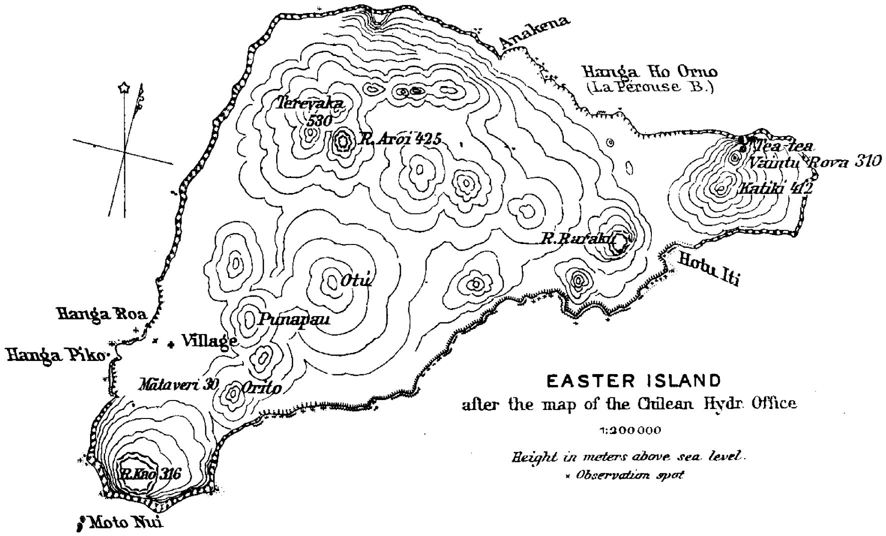


Fig. 5.1 Rapa Nui (Easter Island) after Skottsberg (1920–1956)

(2006) proposed, on the base of soil analysis, that the extinct palm *Paschalococos disperta*, once occupied the whole island. The isolated system was not able to support the human impact and the community collapsed (Bologna and Flores 2008). Only recent decades have seen a rebirth of the community promoted by the national and international interest on the ancient culture (Arancibia 2009).

From a botanical point of view, Isla de Pascua is the poorest of the Chilean Pacific islands, showing only a 7.7 % of specific endemism (Marticorena 1990). There are anyhow some interesting native genera and families (mostly ferns) not present in continental Chile, such as *Davallia, Psilotum, Vittaria, Doodia* (Chap. 2). These are pantropical genera, widely distributed on the Pacific Islands.

The long history of occupation by Polynesian folks has left a landscape and a floristic poverty that seems to be very far from the original one (prior to the arrival of man) (Zizka 1991; Bork 2006). Based on the works of Fuentes (1913) (Fig. 5.2) and Skottsberg (1920–1956), more recently revised by Marticorena (1990) and Zizka (1991), a checklist with a total of 29 native genera pertaining to 20 families was compiled (Table 5.1). A synopsis of the native flora is very difficult: several taxa are treated as either native or alien by different authors (or idiochores v/s anthropochores sensu Zizka 1991).

Several taxa that appeared with a question mark in Zizka's revision and are considered as introduced by Marticorena (1990) have been left out from the analysis (e.g. *Caesalpinia, Calystegia*), while some listed by Marticorena as aliens have been retained due to the reasons given by Zizka, such as *Triumfetta* (Malvaceae), or *Kyllinga* (Cyperaceae). The best represented family is the Poaceae, with 5 genera. The resulting phytogeographic analysis shows a clear predominance of pantropical (41%) and cosmopolitan genera (49%), with little presence of australasiatic (7%)

RESEÑA BOTÁNICA
SOBRE
LA ISLA DE PASCUA
Segun la Espedicion Meteorolójica de 1911 a bordo
de la Corbeta Baquedano
por
FRANCISCO FUENTES
Botánico del Museo Nacional

Santiago de Chile
IMPRENTA UNIVERSITARIA
BANDERA 130
1913

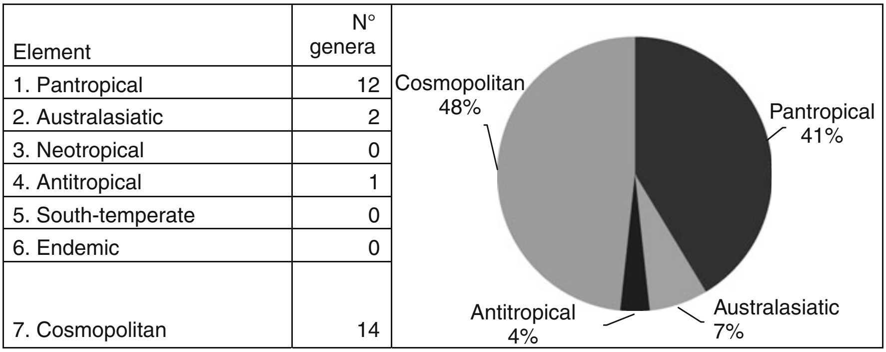
Fig. 5.2 Aspects of the botany of Isla de Pascua: **a** cover of the early review by F. Fuentes (1913); **b** *Doodia paschalis*; **c** *Sophora toromiro*; **d** *Axonopus paschalis* (SGO collections)

(*Doodia*, *Rytidosperma*) and one antitropical genus (*Agrostis*) (Fig. 5.3). The extinct palm *Paschalococos disperta*, known only from subfossil endocarps, is possible related to *Jubaea chilensis* from the continent.

The natural history of the island was discussed by Skottsberg (1920–1956). He emphasized the floristic relationships with the palaeotropics, and remarked that the flora is so depauperate due to human influence, that it does not allow any further biogeographical conclusions regarding the origins of the island flora. Today the island's flora is dominated by alien species, but the presence of several endemic taxa like

Table 5.1 List of native plant genera and species of Rapa Nui

Groups	Family	Genus	N° species	Floristic element
Ferns	Aspleniaceae	*Asplenium*	2	7
	Blechnaceae	*Doodia*	1	2
	Davalliaceae	*Davallia*	1	1
	Dennstaedtiaceae	*Microlepia*	1	1
	Dryopteridaceae	*Diplazium*	1	7
		Dryopteris	1	7
		Polystichum	1	7
	Lomariopsidaceae	*Elaphoglossum*	1	1
	Ophiglossaceae	*Ophioglossum*	2	7
	Polypodiaceae	*Microsorum*	1	1
	Psilotaceae	*Psilotum*	1	1
	Thelypteridaceae	*Thelypteris*	2	1
	Vittariaceae	*Vittaria*	1	1
Dicots	Apiaceae	*Apium*	1	7
	Convolvulaceae	*Ipomoea*	1	1
	Fabaceae	*Sophora*	1	7
	Malvaceae	*Triumfetta*	1	1
	Samolaceae	*Samolus*	1	7
	Solanaceae	*Lycium*	1	7
		Solanum	1	7
Monocots	Cyperaceae	*Kyllinga*	1	1
		Pycreus	1	1
		Scirpus	1	7
	Juncaceae	*Juncus*	1	7
	Poaceae	*Agrostis*	1	4
		Axonopus	1	1
		Paspalum	1	7
		Rytidosperma	1	2
		Stipa	1	7



Element	N° genera
1. Pantropical	12
2. Australasiatic	2
3. Neotropical	0
4. Antitropical	1
5. South-temperate	0
6. Endemic	0
7. Cosmopolitan	14

Fig. 5.3 Floristic elements of Rapa Nui

“toromiro” (*Sophora toromiro*) and especially its archaeological and cultural richness, justify its status as a National Park since 1935 and the declaration as UNESCO World Heritage Centre since 1995.

5.2 Islas Desventuradas

This relatively small volcanic archipelago is located approximately 850 km off the Chilean coast (see Fig 1.1). The Desventuradas archipelago (i.e. “unfortunate islands”) consists of two main islands: Isla San Félix (26°17′S, 80°05′W) and Isla San Ambrosio (26°21′S, 79°53′W) (Fig. 5.4); plus several rocks and stacks: Islote Gonzalez and Roca Catedral. Together, the Desventuradas Islands have a surface area of only 10.3 km^2. The topography is very rugged, with peak elevations of 193 m asl on Isla San Félix, and 479 m asl on Isla San Ambrosio.

In spite of the relative sparse flora, these little islands have attracted naturalists due to their isolation and the presence of several interesting endemic taxa. Botanical descriptions of the islands’ flora have been given by Philippi (1870, 1875), Johnston (1935), Skottsberg (1937, 1951, 1963), Gunckel (1951), and Kuschel (1962). More recent treatments are authored by Marticorena (1990) and Hoffmann and Teillier (1991). According to these authors, the vascular flora of the islands consists of 13 families, 18 genera and 25 native species, including several endemic genera: *Lycapsus* and *Thamnoseris* (Asteraceae), *Nesocaryum* (Boraginaceae), and *Sanctambrosia* (Caryophyllaceae). Teillier and Taylor (1997) add one native genus to the list, *Maireana* (Amaranthaceae), with one species formerly known only from Australia. Based on the works of these authors, a checklist with a total of 19 native genera pertaining to 13 families was compiled (Table 5.2). The best represented family is the Amaranthaceae (4 genera formerly classified under the Chenopodiaceae).

The floristic element that dominates in the islands is the cosmopolitan element (52%), but the endemic element is also noteworthy, reaching a 21% (Fig. 5.5). This

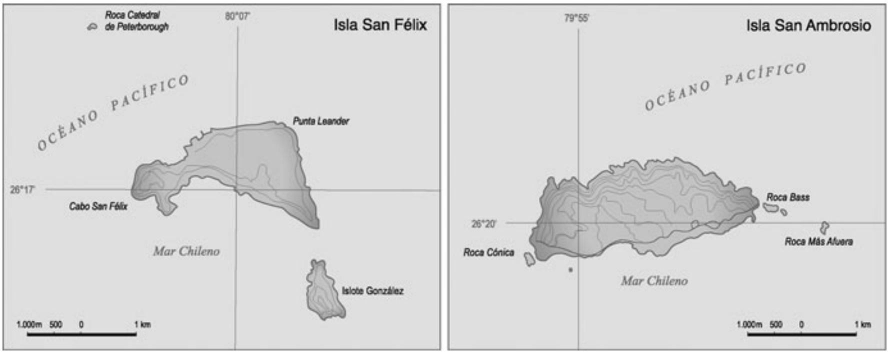


Fig. 5.4 Islas Desventuradas: San Félix and San Ambrosio (reproduced with permission of the Geographical Military Institute (IGM), Chile)

Table 5.2 List of native plant genera and species of Islas Desventuradas. Taxa endemic to the archipelago in bold

Groups	Family	Genus	N° SP	Floristic element
Dicots	Aizoaceae	*Tetragonia*	1	4
	Amaranthaceae	*Atriplex*	2	7
		Chenopodium	1	7
		Maireana	1	2
		Suaeda	2	7
	Asteraceae	***Lycapsus***	1	6
		Thamnoseris	1	6
	Boraginaceae	***Nesocaryum***	1	6
	Brassicaceae	*Lepidium*	1	7
	Caryophyllaceae	***Sanctambrosia***	1	6
		Spergularia	1	7
	Cucurbitaceae	*Sicyos*	1	4
	Frankeniaceae	*Frankenia*	1	7
	Malvaceae	*Cristaria*	2	3
		Fuertesimalva	1	3
	Plantaginaceae/ Veronicac.	*Plantago*	1	7
	Solanaceae	*Solanum*	1	7
	Urticaceae	*Parietaria*	1	7
Monocots	Poaceae	*Eragrostis*	1	7

percentage is higher than the one for the continental flora or Juan Fernández at the genus level. Furthermore, Marticorena (1990) reports a level of endemism of 60.6% at the species level, the highest for a Chilean region.

The natural history of the archipelago has been analysed by Skottsberg (1937), who argued that the Desventuradas flora shows a continental character rather than an oceanic one. The existence of four endemic angiosperm genera and 20 endemic species reinforces the view of an old floristic history not in accordance with relatively recent migration events (discussion in Sect. 5.3). This view can be challenged by the recent report of the genus *Maireana*, formerly known only from Australia

Element	N° genera
1. Pantropical	0
2. Australasiatic	1
3. Neotropical	2
4. Antitropical	2
5. South-temperate	0
6. Endemic	4
7. Cosmopolitan	10

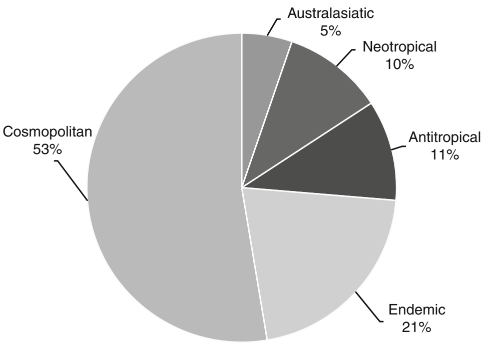


Fig. 5.5 Floristic elements of Desventuradas Islands

and hypothesized as the result of a recent long-distance dispersal event (Teillier and Taylor 1997). The contemporary discovery of the genus on the coast of the Atacama region (Marticorena 1997) tends to support this hypothesis, since it is unlikely that such a shrub stayed unnoticed till the present. This could be one of the few worldwide contemporaneous evidences for the effective operation of long-distance dispersal (see Chap. 3).

5.3 Juan Fernández Archipelago

A prominent feature on the Nazca Plate is the Juan Fernández hot spot chain (see Fig. 1.1). The Juan Fernández Ridge is a topographic swell crested by a series of disconnected, large seamounts that first collided with the Chile margin in the north at about 22 mya (Early Miocene) (Yáñez et al. 2001). The ridge has moved progressively southwards to the current collision point located at roughly 32°–33°S. Today the hot spot chain has two principal islands located between 667 and 850 km from the continent (see Fig. 1.1):

- Alejandro Selkirk Island (33°46′ S, 80°47′ W) (also known as Isla Masafuera), 850 km from the American continent. Its highest elevation is Cerro Los Inocentes (1,380 m asl) (Fig. 5.6a).
- Robinson Crusoe Island, (33°38′ S, 78°51′ W) (also known as Isla Masatierra), located at around 667 km from the continent. Its highest peak is Cerro El Yunque (915 m asl). Close to Robinson Crusoe there are two islets: Islote Juanango, and Santa Clara, this latter located at 1 km southwest of Robinson Crusoe (Fig. 5.6b).

The archipelago is worldwide known as having been the scenario for the real history that inspired the novel of Robinson Crusoe. The island Masafuera was renamed in honour of the Scottish seaman Alejandro Selkirk, who survived 4 years and 4 months on Masatierra. Since its official discovery in 1574 by the pilot Juan Fernández, Masatierra was an obligate anchor place for seamen and buccaneers after trespassing Cape Horn, i.e. lost treasure histories are symptomatic on the archipelago. But several botanists have long stated that the real treasure of this archipelago lies in its unique plant world.

5.3.1 The Unique Plant World of Juan Fernández

The flora of the archipelago has been long a subject of interest for botanists (Gay 1832; Philippi 1856; Johow 1896 (Fig. 5.7), Skottsberg 1920–1956; Muñoz Pizarro 1969, Stuessy et al. 1984a, 1998b; Marticorena et al. 1998; Danton et al. 2000; Danton and Perrier 2003). The native vascular flora comprises 203 species, 110 genera, and 55 families (Marticorena et al. 1998; Danton and Perrier 2006). The best represented family are the Poaceae (10 genera) and the Asteraceae (9 genera). The Fernandezian flora harbours two endemic families (Lactoridaceae and

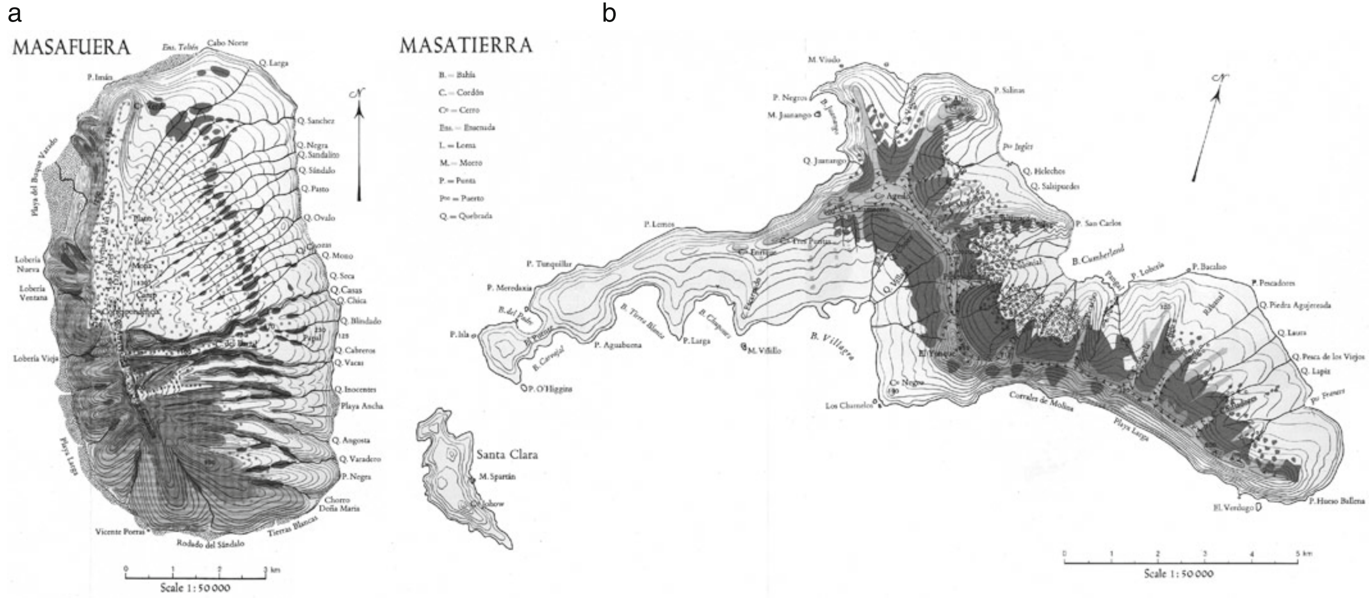


Fig. 5.6 Juan Fernández archipelago: **a** Isla Alejandro Selkirk (Masafuera); **b** Isla Robinson Crusoe (Masatierra) (from Skottsberg (1920–1956))

ESTUDIOS
SOBRE LA
Flora de las Islas de Juan Fernandez
POR EL DOCTOR
FEDERICO JOHOW
Profesor Real Prusiano
Miembro docente i honorario de la Universidad i profesor de los Institutos Pedagójico i Nacional de Chile

CON UNA INTRODUCCION
SOBRE LAS CONDICIONES JEOGRÁFICAS I JEOLÓJICAS DEL ARCHIPIÉLAGO
escrita por el doctor don ROBERTO PÖHLMANN, Injeniero de la Direccion de Obras Públicas.

OBRA ILUSTRADA
CON 2 MAPAS, 8 GRABADOS I 18 LÁMINAS
hechos parte segun dibujos de don BERNARDO KRÜSSEL, profesor de la Escuela Normal de Preceptores, i parte segun vistas fotográficas tomadas por el doctor don CÁRLOS SCHÖNLEIN, ex-profesor de la Escuela de Medicina.

EDICION HECHA A ESPENSAS DEL GOBIERNO

SANTIAGO DE CHILE
IMPRENTA CERVANTES
78, CALLE DE LA BANDERA, 78
1896

Juania australis, la chonta.

Fig. 5.7 **a** cover of Johow's work; **b** illustration of (*Juania australis*) from the *Flora de las Islas de Juan Fernández*

Thyrsopteridaceae) (see Sect. 2.2), 12 strictly endemic genera (plus 2 genera that are endemic to continental Chile and the islands: *Ochagavia* and *Notanthera*) (Table 5.3), and 132 endemic species (Marticorena et al. 1998) (Figs. 5.9 and 5.10).

The analysis of the floristic elements of the flora of Juan Fernández shows that 14% are neotropical genera and 11% are australasiatic genera. Most important is the cosmopolitan element (28%), with a somewhat smaller contribution of the pantropical (17%), the endemic (14%) and the antitropical elements (12%) (Fig. 5.8).

Floristic Element	N° genera
1. Pantropical	19
2. Australasiatic	12
3. Neotropical	16
4. Antitropical	13
5. South-temperate	5
6. Endemic	15
7. Cosmopolitan	30

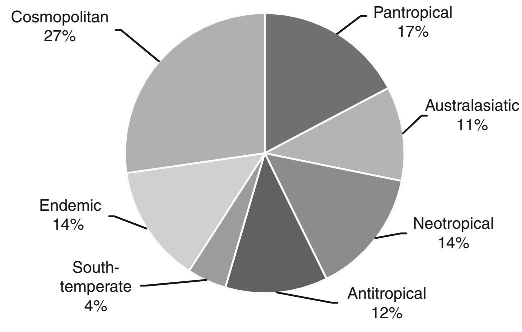


Fig. 5.8 Floristic elements of Juan Fernández

Table 5.3 List of native plant genera and species of Juan Fernández Islands. Taxa endemic to the archipelago in bold

Groups	Family	Genus	N° SP	Floristic element
Ferns	Aspleniaceae	*Asplenium*	4	7
	Blechnaceae	*Blechnum*	7	7
	Dennstaedtiaceae	*Histiopteris*	1	1
		Hypolepis	1	1
	Dicksoniaceae	*Dicksonia*	2	2
		Lophosoria	1	3
	Dryopteridaceae	*Elaphoglossum*	1	1
		Megalastrum	1	1
		Polystichum	1	7
		Rumohra	1	2
	Gleicheniaceae	*Sticherus*	3	1
	Hymenophyllaceae	*Hymenoglossum*	1	6
		Hymenophyllum	10	7
		Serpyllopsis	1	5
		Trichomanes	3	1
	Lycopodiaceae	*Lycopodium*	2	7
	Ophioglossaceae	*Ophioglossum*	1	7
	Polypodiaceae	*Grammitis*	1	1
		Pleopeltis	2	1
		Synammia	1	5
	Pteridaceae	*Adiantum*	1	7
		Notholaena	1	1
		Pteris	3	7
	Tectarinaceae	*Arthropteris*	1	2
	Thyrsopteridaceae	***Thyrsopteris***	1	6
	Woodsiaceae	*Cystopteris*	1	4
Dicots	Amaranthaceae	*Chenopodium*	3	7
		Sarcocornia	1	7
	Apiaceae	*Apium*	2	7
		Centella	1	1
		Eryngium	4	7
	Asteraceae	*Abrotanella*	1	2
		Centaurodendron	2	6
		Dendroseris	11	6
		Erigeron	5	4
		Gamochaeta	1	3
		Lagenophora	1	2
		Robinsonia	8	6
		Taraxacum	2	4
		Yunquea	1	6
	Berberidaceae	*Berberis*	2	4
	Boraginaceae	***Selkirkia***	1	6
	Brassicaceae	*Cardamine*	3	4
	Campanulaceae	*Lobelia*	1	1
		Wahlenbergia	5	4
	Caryophyllaceae	*Spergularia*	2	7
	Convolvulaceae	*Calystegia*	1	7
		Dichondra	1	1

Table 5.3 (continued)

Groups	Family	Genus	N° SP	Floristic element
	Ericaceae	*Empetrum*	1	4
		Gaultheria	1	4
	Escalloniaceae	*Escallonia*	1	3
	Euphorbiaceae	*Dysopsis*	1	3
	Fabaceae	*Sophora*	2	7
	Gunneraceae	*Gunnera*	4	1
	Haloragaceae	*Haloragis*	2	2
	Lactoridaceae	***Lactoris***	1	6
	Lamiaceae	*Cuminia*	1	6
	Loranthaceae	*Notanthera*	1	6
	Myrtaceae	*Myrceugenia*	2	3
		Myrteola	1	3
		Ugni	1	3
	Orobanchaceae	*Euphrasia*	1	4
	Phrymaceae	*Mimulus*	1	7
	Piperaceae	*Peperomia*	4	1
	Ranunculaceae	*Ranunculus*	1	7
	Rhamnaceae	*Colletia*	1	3
	Rosaceae	*Acaena*	1	4
		Margyracaena	1	6
		Margyricarpus	1	3
		Rubus	1	7
	Rubiaceae	*Coprosma*	2	2
		Galium	1	7
		Oldenlandia	1	1
		Nertera	1	2
	Rutaceae	*Fagara*	2	1
	Salicaceae	*Azara*	1	3
	Santalaceae	*Santalum*	1	2
	Solanaceae	*Nicotiana*	1	1
		Solanum	2	7
	Urticaceae	*Boehmeria*	1	1
		Parietaria	1	7
		Urtica	3	7
	Verbenaceae	*Rhaphithamnus*	1	5
	Plantaginaceae/ Veronicac.	*Plantago*	3	7
	Winteraceae	*Drimys*	1	3
Monocots	Arecaceae	***Juania***	1	6
	Bromeliaceae	*Greigia*	1	3
		Ochagavia	1	6
	Cyperaceae	*Carex*	2	7
		Cyperus	2	7
		Eleocharis	1	7
		Machaerina	1	1
		Oreobolus	1	2
		Scirpus	2	7
		Uncinia	4	2

Table 5.3 (continued)

Groups	Family	Genus	N° SP	Floristic element
	Iridaceae	*Herbertia*	1	3
		Libertia	1	2
	Juncaceae	*Juncus*	5	7
		Luzula	1	7
	Orchidaceae	*Gavilea*	1	5
	Poaceae	*Agrostis*	1	4
		Bromus	1	4
		Chusquea	1	3
		Danthonia	2	4
		Leptophyllochloa	1	5
		Megalachne	2	6
		Nassella	2	3
		Piptochaetium	1	3
		Podophorus	1	6
		Trisetum	1	7

Fig. 5.9 Juan Fernández ferns: **a** *Arthropteris altescandens*; **b** *Dicksonia berteroana*; **c** *Thyrsopteris elegans* (photo credits: **a**–**c** S. Elórtegui Francioli)

Fig. 5.10 Juan Fernández angiosperms: **a** *Lactoris fernandeziana*; **b** *Sophora fernandeziana*; **c** *Rhaphithamnus venustus*; **d** *Escallonia callcottiae*; **e** *Gunnera peltata* (photo credits: **a**–**e** S. Elórtegui Francioli)

5.3.2 Floristic Similarity of Juan Fernández

Including Juan Fernández (JF) into the similarity analysis done between Chilean regions (Sect. 4.2) results in a closer floristic relationship between JF/MAG than between JF and the other Chilean regions (Table 5.4, Fig. 5.11). JF shares more native genera with BIO (81) but Jaccard's similarity is higher between JF/MAG, taking account of the much richer generic flora of BIO as compared to MAG or JF.

In Fig. 5.11, geographic distance is plotted against Jaccard's distance. Two expected trends are recovered, one for the continental regions, and the decreasing similarity between JF and each of the continental regions according to their geo-

Table 5.4 Floristic similarity between regions including Juan Fernández

Compared regions	Similarity Jaccard	Distance (km)	Shared genera
ANT/COQ	0.46	777	244
ANT/BIO	0.29	1,527	174
ANT/MAG	0.21	3,227	97
COQ/BIO	0.54	750	323
COQ/MAG	0.27	2,450	150
BIO/MAG	0.33	1,700	178
JF/MAG	*0.18*	2,261	56
JF/BIO	0.16	792	81
JF/COQ	0.12	895	64
JF/ANT	0.08	1,439	33

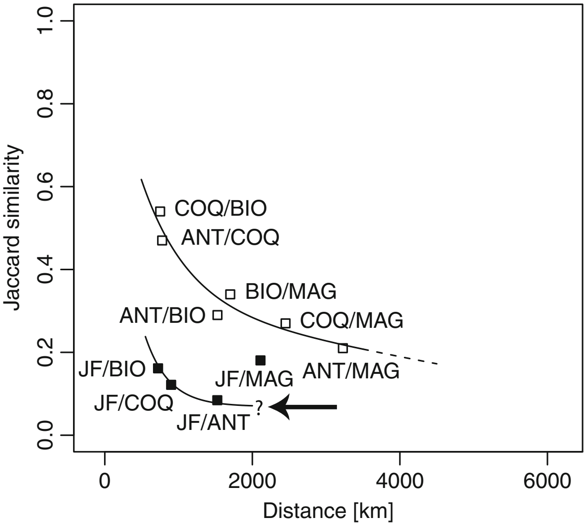


Fig. 5.11 Floristic similarity between different regions in Chile: Antofagasta (ANT), Biobío (BIO), Coquimbo (COQ) and Magallanes (MAG). Jaccard similarity is plotted against geographical distance within Chile (*white squares*), and between Juan Fernández and Chilean continental regions (*black squares*). The *lines* represent trends as exponential curves. The relation JF/MAG is considered as an outlier. The *arrow* and *question mark* show the possible position of the relation JF/MAG following the trend (see discussion in the text)

graphic distances. But the relationship MAG/JF is noteworthy and escapes from this trend (outlier). According to geographic distance, these two regions should have a much lower similarity (see arrow). This closer floristic relationship between MAG and JF appeals to two different explanations:

(a) The Magallanes biota had once a more northward distribution, till central Chile, and from there it reached the islands via long-distance dispersal. The presence of south-temperate elements in the Fray Jorge fog forest at 30°40′ long has been suggested as evidence of the more widespread occurrence of temperate forests during the Cenozoic (Box 3.1). But the remnants of these forests are still represented along the coast of BIO and there is no apparent reason why the relation BIO/JF stays within the trend of the similarity/distance curve, contrary to MAG/JF.

(b) An alternative explanation for the floristic similarity between JF and MAG is a direct connection of the two land masses. This explanation is contrary to current geological scenarios, since the islands seem to be geologically too young for this type of explanation. The islands are located on top of the Juan Fernández ridge, which controls the tectonic and geological evolution of the southern Andes at 33°–34°S since the Tertiary (Yáñez et al. 2002). The seafloor age assigned by Müller et al. (1997) to the seafloor offshore Chile between 18° and 40°S, based on magnetic anomalies and relative plate reconstructions, ranges from 20 to 48 mya. Juan Fernández rests on seafloor dated at around 20–33 mya.

Several early geologists believed in a former land west of South America occupying the whole Pacific (Burckhardt 1902; Beloussov 1968), or at least a portion of it as a *Transandiner Kontinent* close to the South American coast (Illies 1967; Cañas 1966). Brüggen (1950, p 59) proposed the name *Tierra de Juan Fernández* for this larger continental land mass west of current South America. Miller (1970) analysed different possibilities for the disappearance of this land and concluded that the *Ozeanisierung* of the *Juan Fernández Land* occurred in the Late Cenozoic, and that this land was not at all at the same location of today's Juan Fernández archipelago (Miller 1970, p 934). Based on the floristic similarities as analysed in the present work, this land should have existed much more to the South. To fit in the trend line of the similarity/distance relation shown by other Chilean regions, the Juan Fernández islands (*Juan Fernández Land*) could be located at the same longitude (80°W), but at 48°S instead of 33°, i.e. 15 degrees latitude or around 1,650 km towards the South. (Fig. 5.12, see also Sect. 10.4).

Biogeographic connections between Juan Fernández, Magallanes and the Falkland (Malvinas) Islands have been also identified by Morrone (1992), as a generalized track composed by plants as well as insects, Crustaceans, and Oligochaeta.

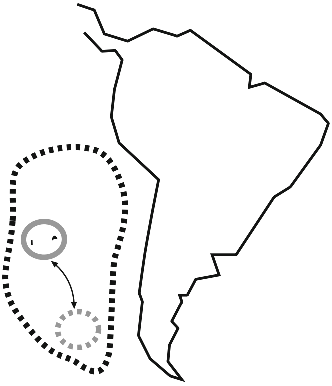


Fig. 5.12 Hypothetical closer geographic position of Juan Fernández to southern South America (Magallanes), according to floristic similarity in Fig. 5.11 (*grey dotted line*); and possible position of the *Juan Fernández Land* or the Pacifica continent, according to Dickins et al. (1992) (*black dotted line*)

5.3.3 Origins of the Fernandezian Flora

The origin of the Fernandezian flora has been the subject of considerable study and debate (e.g. Skottsberg 1925, 1936, 1956; van Balgooy 1971). Traditionally the origin of an island flora has been explained in direct relationship with its nearest continental mass by means of long-distance dispersal (e.g. Carlquist 1974). Oceanic islands are often explained as geologically new territories and Juan Fernández is not an exception: Masatierra has been dated at ca. 4 mya, Masafuera at 1–2 mya, and Isla Santa Clara at 5.8 mya (Stuessy et al. 1984b). The islands are supposed to be the products of isolated intraplate volcanism associated with the volcanic hotspot (Stern et al. 2007). The relative young age of the archipelago seems to leave no doubt for a recent origin of its flora, as revised by Bernardello et al. (2006).

But the high level of endemism, the variety of floristic relationships and the limited methods of dispersal put some unresolved questions on this theme. Bernardello et al. (2006) report that 80% of the island's species have dry fruits, and fleshy fruits are comparatively uncommon, challenging the supposed ability for long-distance dispersal by birds. In fact, the dispersal syndrome that prevails in the flora is autochory (i.e. autonomous passive dispersal). Bernardello et al. (2006) therefore suggest that the principal dispersal processes are anemochorous dispersal (air flotation) and epizoochory (carried by birds attached to their feathers). But since the extant bird fauna is scarce, the real opportunities for dispersal are relatively few.

This was early recognized by Skottsberg (1925, 1956) and he therefore suggested that the origin of the island flora should be found in alternative palaeoscenarios. Skottsberg revised and discussed all available evidence in floristic and faunistic elements, in geotectonics of the Pacific, and in the continental Cenozoic flora and came to the conclusion that the Fernandezian flora is not of an oceanic but of a continental nature. This is in conflict with the early classification of Wallace (1880) that considered all oceanic islands as having an oceanic biota (see also Cowie and Holland 2006). Skottsberg proposed a "tentative sketch" on the history of the Fernandezian flora that is in concordance with Brüggen's *Tierra de Juan Fernández*, an old submerged landmass west of today's South America that could have been the source for the unique Fernandezian flora (Brüggen 1950; Skottsberg 1956, p 394) (Fig. 5.12).

Skottsberg's critical vision has been systematically oversimplified by modern authors, while emphasizing that he noted the close relationship with the American flora (e.g. Crawford et al. 1990; Bernardello et al. 2006). Skottsberg certainly recognized the floristic relationship between the islands and the American continent, but he also noted the closest relationship with the western Pacific and especially with Australasia. Indeed, several genera not found in continental Chile show a wider distribution in Australasia, such as *Coprosma* (Rubiaceae), *Arthropteris* (Tectarinaceae) (Fig. 5.9), *Haloragis* (Haloragaceae) or *Santalum* (Santalaceae).

"In traditional dispersalist interpretations of oceanic island biotas, a volcanic island just 'pops up' and its location is not considered relevant. Islands are assumed to be populated from the nearest mainland and endemism is explained by isolation from the mainland However, since volcanism recurs in certain areas, volcanic islands might instead ‘inherit’ flora and fauna from prior volcanic islands in the same region” (Heads 2009, p 236). Heads (2009) exemplifies his proposal with *Fitchia* (Asteraceae) a small tree endemic to montane forests in SE Polynesia. The genus has “presumably survived as a metapopulation on the volcanic islands and atolls which have come and gone around the Cook Islands/Tokelau and other localities in SE Polynesia. Its ancestors may date back to the origin of the Pacific plate and the Cretaceous plateaus” (Heads 2009, p 236). A similar history can be hypothesized for the small trees *Robinsonia, Dendroseris, Yunquea,* endemic to Juan Fernández, and *Thamnoseris* and *Lycapsus* endemic to the Desventuradas Islands. These Asteraceous genera could be the remnants of a more “ancient Asteraceous world” related to the origins of the Pacific plate.

The sole presence of the endemic family Lactoridaceae with its single species puts a big question mark on the supposed oceanic character of the Fernandezian flora. *Lactoris* has been the subject of many studies because of its systematic placement among basal angiosperms (e.g. Stuessy et al. 1998a; González and Rudall 2001). The cladistic analysis by Lammers et al. (1986) suggests that the Lactoridaceae diverged sometime prior to the Maastrichtian (69 mya). This has been corroborated recently by the analysis of Wikström et al. (2001): *Lactoris* appears as a very ancient taxon at the base of the angiosperm phylogenetic tree: the split between *Lactoris* and *Aristolochia* has been dated at around 85 mya.

In Lammers et al. (1986) opinion “it seems unlikely that the Lactoridaceae evolved autochthonously in the Juan Fernandez Islands. A more plausible hypothesis is that the plants on Masatierra are relicts of a once more extensive continental distribution in South America and possibly other portions of the Southern Hemisphere, perhaps originating from the western Gondwanaland flora”. Indeed, microfossils related to *Lactoris* (Fig. 5.13) and referred to the fossil genus *Lactoripollenites* have been found in South Africa and Australia (Macphail et al. 1999), thus suggesting that the Lactoridaceae were widespread across the Southern Hemisphere during the Late Cretaceous (Lammers et al. 1986). “Differences between *Lactoripollenites* and *Lactoris* pollen imply that these represent different clades within the Lactoridaceae or that the former evolved into the latter genus elsewhere in the Southwest Pacific region prior to its migration onto Masatierra in the Plio-Pleistocene” (Macphail et al. 1999).

Recently, a new fossil find of lactoridaceous tetrads from the early Miocene of eastern Patagonia has been reported by Gamerro and Barreda (2008). These authors compiled all the fossil evidence for the Lactoridaceae concluding that it probably has a South African origin, with the oldest records in the Cretaceous (Turonian–Campanian), reaching its widest palaeogeographical distribution (Australia, India, Antarctica, and North and South America) by the Maastrichtian. According to this new finding “the family may have migrated into South America, either via Africa (through the Atlantic Ocean) or Antarctica, by the Maastrichtian, growing in eastern Patagonia up to the early Miocene. Arid conditions established in this region by the middle–late Miocene onwards would have determined the restriction of forests to the western lands. The Lactoridaceae may have followed a similar migration pattern towards the Pacific coast of South America” (Gamerro and Barreda 2008). The

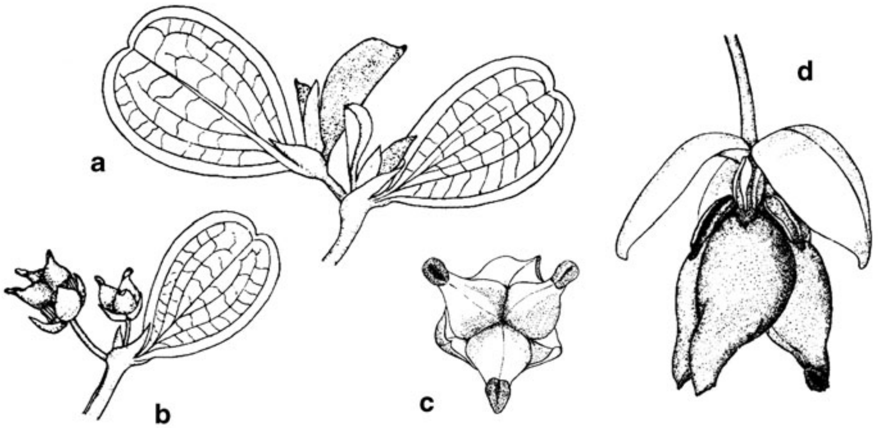


Fig. 5.13 *Lactoris fernandeziana*, as illustrated in Skottsberg (1920–1956): **a** top of branch in August; **b** terminal inflorescence; **c** female flower; **d** hermaphrodite flower. See also Fig. 5.10

last part of its history is already known: "The shifting of Lactoridaceae towards Masatierra Island would have occurred during the last 4 my by long-distance dispersal events (perhaps by birds)" (Gamerro and Barreda 2008).

Crawford et al. (2001) also suggested that the species or its ancestors could have reached Masatierra by means of long-distance dispersal, but may have been carried by the wind, due to its small seeds. However, the authors recognized that "the plants occur primarily in the forest understory, which would seemingly minimize the effectiveness of wind as a means of long-distance dispersal" (Crawford et al. 2001, p 189).

Other endemic taxa might be also the remnants of older groups that have evolved in a completely different palaeogeographic scenario. As an example, the fern species *Thyrsopteris elegans* is the sole representative of the Thyrsopteridaceae (Smith et al. 2006) (Sect. 2.2). This fern is clearly related to the tree ferns, but of uncertain position within the group (Korall et al. 2006). Fossil representatives of the genus (or related taxa) are widespread; its distributional restriction to Juan Fernández is obviously a relict situation (Kramer and Green 1990). Also the shrubby Fernandezian *Wahlenbergia* species, together with the species from New Zealand and St. Helena, are considered as the more basal members of the wahlenbergioid group, suggesting a Gondwanic origin (Eddie et al. 2003).

The splitting between *Drimys confertifolia* from the continental sister species (clade *D. andina* + *D. winteri*), has been dated at 9–10.8 mya by the phylogenetic analyses from Marquínez et al. (2009). These authors are well aware of the fact that this age notably predates the formation of the Juan Fernández islands.

Stuessy et al. (1984b) knew the earlier view from Brüggen (1950) and Skottsberg (1956), but they gave much value to the Potassium-Argon dating. Thus, most of the papers dealing with the evolution of the Fernandezian flora in the last two decades start from the 4 mya date. The dating of Santa Clara puts another question on the problem, since this little islet seems to be almost two million years (5.8 +-2.1 mya)

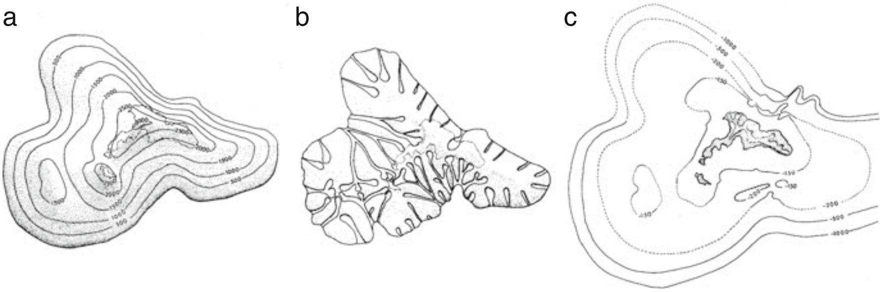


Fig. 5.14 Reconstruction of the geomorphological history of Masatierra + Santa Clara: **a** putative emerged shape of the islands at 4 mya; **b** erosional patterns showing amphitheater valleys; **c** present configuration showing bathymetric contours (adapted from Stuessy et al. 1984a)

older than Robinson Crusoe. Stuessy et al. (1984b), in spite of their high confidence in the dating, do not rule out other models of Pacific aseismic ridges (e.g. Nur and Ben-Avraham 1981). Also, Stuessy et al. (1984a) recognized that the islands could have been much more extended and may have been rapidly eroded during the last 4 million years (Fig. 5.14). All Chilean Pacific islands show indeed advanced erosion stages, related to volcanic sector-collapse processes (Araya-Vergara and Vieira 2005; Stern et al. 2007).

Thus, advancing definitive conclusions on this topic can be very risky; biogeographical islands' enigmas are not exclusive to Juan Fernández: the moss species *Hedenasiastrum percurrens*, which is endemic to the Madeiran archipelago, most probably diverged about 40 mya. But the emergence of Madeira has been dated at only 5.2 mya (Aigoin et al. 2009).

5.3.4 Conservation of Juan Fernández Plants

The archipelago is one of the most dramatically threatened territories worldwide (Stuessy et al. 1998c), an actual tendency on oceanic islands (Sax and Gaines 2008). The combined introduction of browsing animals and highly invading continental plants place the fernandezian native flora at a competitive disadvantage (Dirnböck et al. 2003). Today at least 75% of the endemic flora is highly threatened (Swenson et al. 1997; Cuevas and van Leersum 2001). Danton and Perrier (2005, 2006) listed eight species that went extinct (EX) in historical times, mostly during the last decades: *Podophorus bromoides, Santalum fernandezianum, Chenopodium nesodendron, Empetrum rubrum, Eryngium sarcophyllum, Notanthera heterophylla, Robinsonia berteroi,* and *R. macrocephala*. Applying IUCN criteria, the authors further classified one more species as "Extinct in the wild" (*Margyracaena skottsbergii*, still conserved ex-situ at the National Botanical Garden in Viña del Mar). Another 28 species were classified as "Critically endangered" (CR), 79 as "Endangered" (EN), and 65 as "Vulnerable" (VU). Finally, 32 species were classified as "Least Concern" (LC) or "Data Deficient" (DD). That means that from the

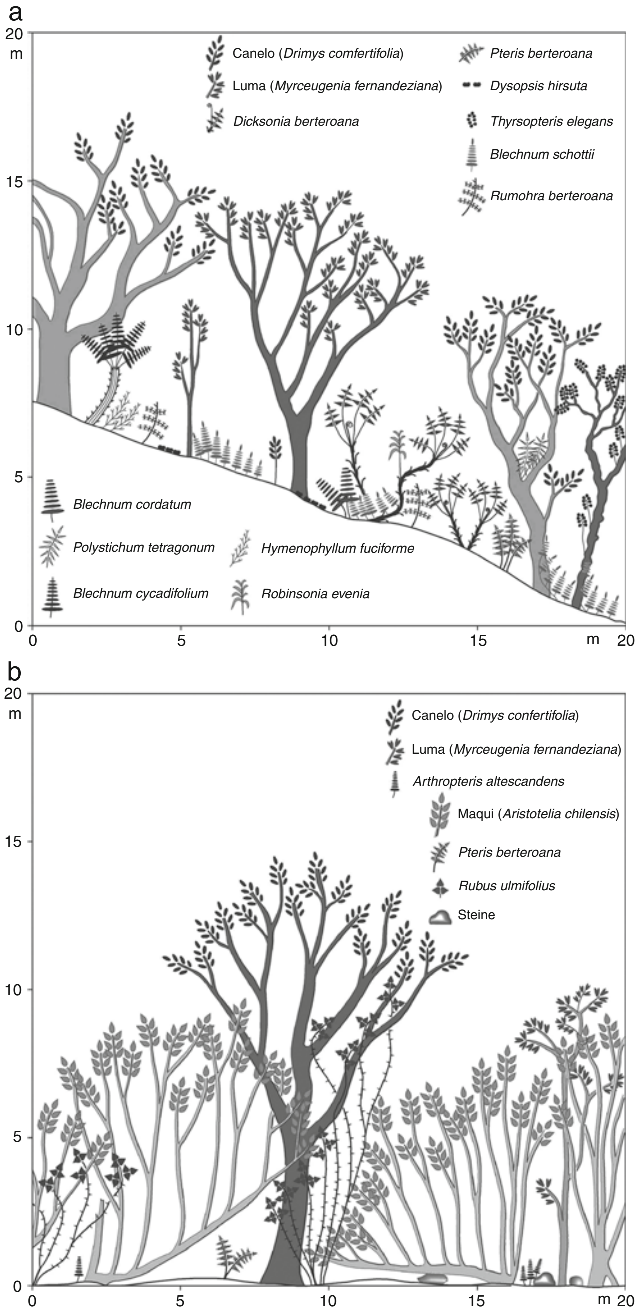


Fig. 5.15 Natural v/s invaded vegetation stands in Masatierra: **a** lower montane forest near Plazoleta del Yunque; **b** native *Drimys confertifolia* and *Myrceugenia fernandeziana* oppressed by the continental aliens *Aristotelia chilensis* and *Rubus ulmifolius* (original illustrations by Rudi Rössler (Erlangen University) based on schemes by Prof. Michael Richter, December 2005)

213 native species evaluated, nine are already extinct in the archipelago and 172 (80%)! are critically endangered to vulnerable.

The native flora is being directly attacked by invading animals (e.g. rabbits, rats) and plants, and the alien flora is continuously expanding: Johow (1896) listed 95 introduced species, whereas Marticorena et al. (1998) listed a total of 212 naturalized species in the archipelago (against 211 native). This number is increasingly growing, and species that are presently considered naturalized and cultivated (potentially invaders), bring the number at 503 species (Danton and Perrier 2006). That means that the alien flora is already double as large as the native flora!

There have been continuous efforts to eradicate the plant and animal pests (rabbits, goats, rats), but they still do not show much success (Cuevas and van Leersum 2001). Even after cattle exclusion, vegetation recovery seems to be very slow (Cuevas and Le Quesne 2006). Presently the high number of alien species does not seem to be the worst problem: most effective invaders are several continental natives like "maqui" (*Aristotelia chilensis*) and "murtilla" (*Ugni molinae*), plus the European weed "zarzamora" (*Rubus ulmifolius*) (Fig. 5.15b). These three alien species are virtually replacing the native vegetation on Masatierra. Modelling the invasion's extent for these highly invasive species since their introduction 80 years ago, suggests that 50% of the remaining montane forest could be totally replaced in just another 80 years… (Greimler et al. 2002; Dirnböck et al. 2003).

Even of the iconic plant *Lactoris fernandeziana*, the last survey could find no more than 1,000 plants (Ricci 2001). Conservation efforts in situ as well as ex situ at the National Botanical Garden in Viña del Mar continue, but most botanists are pragmatically pessimistic about the future of this unique flora, if definite actions are not taken. The great botanist Carl Skottsberg was very impressed to see the last exemplar of the species *Santalum fernandezianum* (Box 5.1, Fig. 5.16)

Box 5.1 Skottsberg's Impressions on the Encounter with the Last Exemplar of the Extinct *Santalum fernandezianum*

"The discovery of the sandal-wood, famous since the days of Solomon, on Juan Fernández most surely attracted notice. We have no reports of it previous to 1624, when, according to Burney, L'Heremite reported sandal-trees in great number. According to another authority ships used to visit the place as early as 1664 to bring the valuable wood to the coast, where it was highly appreciated. One did not think of preserving anything; a hundred years later it was hardly possible to find a living tree, and in the beginning of last century it was regarded as extinct. No botanist had ever seen the leaves or flowers. Suddenly F. Philippi in Santiago got some fresh twigs brought to him in 1888; he found them to belong to the genus *Santalum*; the species being new, it received the name of *S. fernandezianum*. The general interest in the tree was increased, but nobody told where the branches came from; a living tree was still unknown. Only in 1892 did Johow get news of one; a colonist had found it in Puerto Inglés, high up in the valley. He was the first botanist who saw this plant. It is easily understood that I was anxious to become the second. How many people had looked for other specimens! All their efforts were fruitless; as far as we knew Johow's tree was the very last. If it were still there! The man who brought Johow to the spot still lived, and after we had explained our purely scientific interest he promised to send his son with us. It would have been more than uncertain for us alone to look for a single tree in a valley clad with virgin forest. [. . .] We walked up the valley and made an ascent of the western side; the place is so steep that one is forced to grasp the trees and shrubs to get a foothold. Our guide stopped, looked round for a minute, down a few hundred yards, and we had reached our destination. The last sandal-tree. Absolutely the last descendant of *Santalum fernandezianum*. It is so queer to stand at the death-bed of a species; probably we were the last scientists who saw it living. We look at the old tree with a religious respect, touch the stem and the firm, dark green leaves – it is not only an individual, it is a species that is dying. It cannot last very long. There is only one little branch left fresh and green; the others are dead. We cut a piece to get specimens of the peculiar red, strongly scented wood. A photo was taken, I made some observations on the place, and we said goodbye. Should I happen to go there once more I shall not see the sandal-tree; it will be dead and its body cut up into precious pieces – curiosities taken away by every stranger" (Skottsberg 1911).

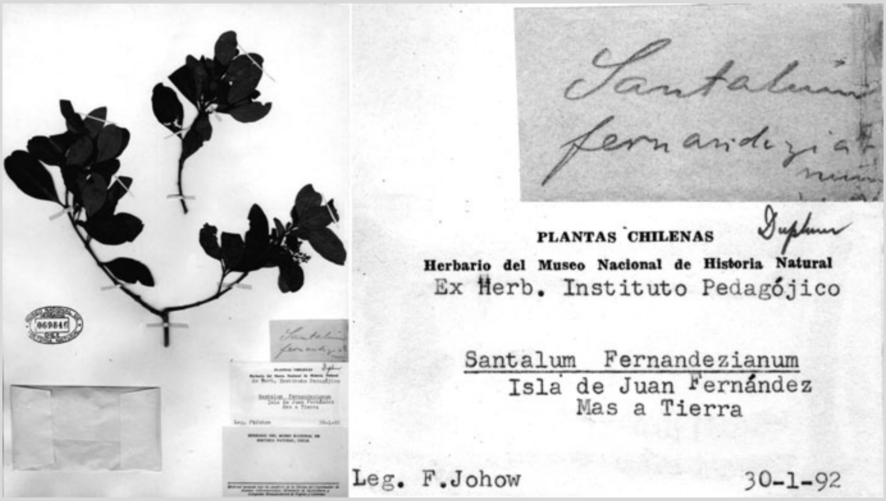


Fig. 5.16 Herbarium exemplar of *Santalum fernandezianum from SGO*

Fig. 5.17 Juan Fernández landscapes: **a** view towards the west from Mirador de Selkirk; **b** Puerto Inglés; **c** volcanic scarps seen from the sea; **d** intensive erosion towards Puerto Francés (photo credits: (**a**–**d**) S. Elórtegui Francioli)

With the support of several botanists like Carl Skottsberg and the Chilean state, Juan Fernández has the status of a National Park since 1935, and it has been declared also as a Biosphere Reserve in 1977 (see Sect. 6.1). These formal protection statuses so far did not succeed to prevent the extinction process that is currently affecting the Fernandezian flora. There is still much work to be done on the control of pests and invasive species, in erosion control and ecological restoration. Encouraged staff and personal efforts done for decades by the personal from CONAF (Corporación Nacional Forestal) could not stop the threats. Personal engagement exists, but it must be supported by national and international investment in conservation and restoration. If international conservation agencies are looking for highly threatened territories to invest their efforts, here we have a territory that has too long been waiting for a coordinated action to definitely stop the natural depletion and floral extinctions. "If we do not stop the invaders now, the saddest aspects of Robinson Crusoe's parable will succeed: nature will have been definitely subjugated by man, transforming a marvelous floristic and evolutionary space into a human-induced desert" (Danton and Perrier 2006, p 420) (Fig. 5.17).

References

Aigoin DA, Devos N, Huttunen S, Ignatov MS, Gonzalez-Mancebo JM, Vanderpoorten A (2009) And if Engler was not completely wrong? Evidence for multiple evolutionary origins in the moss flora of Macaronesia. Evolution 63:3248–3257

Arancibia V, (ed) (2009) Rapa Nui: iorana te ma'ohi: dilemas estratégicos. Eds. Universidad Católica de Chile, Santiago

Araya-Vergara JF, Vieira R (2005) Formas costeras y submarinas de destrucción en los sistemas volcánicos San Félix y Robinson Crusoe, Pacífico Suroriental. Ciencia y Tecnología del Mar 28:5–23

Balcells I (2005) El Chile que no está en América. In: Badal G, Balcells F, Montanari M, et al. (eds) Chile: País Oceánico (2nd edn). Ocho Libros Editores, Santiago, pp 96–97

Beloussov VV (1968) Some general aspects of development of the Tectonosphere. Rep. 28. Int Geol Congr 1:9–17

Bernardello G, Anderson GJ, Stuessy TF, Crawford DJ (2006) The angiosperm flora of the Archipelago Juan Fernández (Chile): origin and dispersal. Can J Bot 84:1266–1281

Bologna M, Flores JC (2008) A simple mathematical model of society collapse applied to Easter Island. EPL 81: 48006 (4 pp) doi: 10.1209/0295–5075/81/48006

Bork H-R (2006) Landschaften der Erde unter dem Einfluss des Menschen. Wissenschaftliche Buchgesellschaft (WGB), Darmstadt

Brüggen J (1950) Fundamentos de la Geología de Chile. Instituto Geográfico Militar, Santiago

Burckhardt C (1902) Traces géologiques d'un ancient continent Pacifique. Rev. Mus. La Plata 10:179–192

Cañas J (1966) Tectónica y sedimentación de la Formación Los Molles, Prov. de Aconcagua. Comun. Escuela De Geol. (Santiago) 11:22

Carlquist S (1974) Island biology. Columbia University Press, New York, NY

Cowie RH, Holland BS (2006) Dispersal is fundamental to biogeography and the evolution of biodiversity on oceanic islands. J Biogeogr 33:193–198

Crawford DJ, Stuessy TF, Lammers TG, Silva M, Pacheco P (1990) Allozyme variation and evolutionary relationships among three species of *Wahlenbergia* (Campanulaceae) in the Juan Fernandez Islands. Bot Gaz 151:119–124

Crawford D, Tago-Nakazawa M, Stuessy TF, Anderson GJ, Bernardello G, Ruiz E, Jensen RJ, Baeza CM, Wolfe AD, Silva M (2001) Intersimple sequence repeat (ISSR) variation in *Lactoris fernandeziana* (Lactoridaceae), a rare endemic of the Juan Fernández Archipelago, Chile. Plant Spec Biol 16:185–192

Cuevas JG, Le Quesne C (2006) Low vegetation recovery after short-term cattle exclusion on Robinson Crusoe Island. Plant Ecol 183:105–124

Cuevas JG, van Leersum G (2001) Proyecto conservación, restauración y desarrollo de las islas Juan Fernández, Chile. Rev Chil Hist Nat 74:899–910

Danton P, Breteau E, Baffray M (2000) Les îles de Robinson: Trésor vivant des mers du Sud, entre légende et réalité. Ed. Nathan.

Danton P, Perrier C (2003) Liste de la flore vasculaire de l'île Robinson Crusoe, archipel Juan Fernández, Chili. J Bot Soc Bot France 24:67–78

Danton P, Perrier C (2005) Notes sur la disparition d'une espèce emblématique: *Robinsonia berteroi* (DC.) Sanders, Stuessy & Martic. (Asteraceae), dans l'île Robinson Crusoe, archipel Juan Fernández (Chili). J Bot Soc Bot France 31:3–8

Danton P, Perrier C (2006) Nouveau catalogue de la flore vasculaire de l'archipel Juan Fernández (Chili). Acta Bot Gall 153:399–587

Dickins JM, Choi DR, Yeates AT (1992) Past distribution of oceans and continents. In: Chatterjee S, Hotton N III, (eds) New concepts in global tectonics. Texas Tech. University Press, Lubbock, TX, pp. 193–199

Dirnböck T, Greimler J, Lopez P, Stuessy TF (2003) Predicting future threats to the native vegetation of Robinson Crusoe Island, Juan Fernandez Archipelago, Chile. Conserv Biol 17:1650–1659

Eddie WMM, Shulkina T, Gaskin J, Haberle RC, Jansen RK (2003) Phylogeny of Campanulaceae s. str. inferred from ITS sequences of nuclear ribosomal DNA. Ann Mo Bot Gard 90: 554–575

Fuentes F (1913) Reseña botánica sobre la Isla de Pascua. Bol Mus Nac Hist Nat 5:320–337

Gamerro JC, Barreda V (2008) New fossil record of lactoridaceae in southern South America: a palaeobiogeographical approach. Bot J Linn Soc 158:41–50

Gay C (1832) La Isla de Juan Fernández. Reprint 1974. Mus Nac Hist Nat (Santiago) Ser Educativa 9:5–16

González F, Rudall PJ (2001) The questionable affinities of *Lactoris*: evidence from branching pattern, inflorescence morphology and stipule development. Am J Bot 88: 2143–2150

Greimler J, López P, Stuessy TF, Dirnböck T (2002) The vegetation of Robinson Crusoe Island (Isla Masatierra), Juan Fernández Archipelago, Chile. Pac Sci 56:263–284

Gunckel H (1951) Algunas plantas vasculares de la Isla de San Ambrosio. Rev Univ (Santiago) 36:291–314

Heads M (2009) Globally basal centres of endemism: the Tasman-Coral Sea region (south-west Pacific), Latin America and Madagascar/South Africa. Biol J Linn Soc 96:222–245

Hoffmann AJ, Teillier S (1991) La flora de la Isla San Félix (Archipiélago de las Desventuradas, Chile). Gayana Bot 48:89–99

IGM (2005) Atlas de Chile. Instituto Geográfico Militar, Santiago

Illies H (1967) Randpazifische Tektonik und Vulkanismus im südlichen Chile. Geol Rundsch 57:81–101

Johnston IM (1935) The flora of San Félix Island. J Arnold Arbor 16:440–447

Johow F (1896) Estudios sobre la flora de las Islas de Juan Fernández. Imprenta Cervantes, Santiago

Korall P, Pryer KA, Metzgar JS, Schneider H, Conant DS (2006) Tree ferns: monophyletic groups and their relationships as revealed by four protein-coding plastid loci. Mol Phylogenet Evol 39:830–845

Kramer KU, Green PS (1990) Pteridophytes and gymnosperms. In: Kubitzki K, (ed) The families and genera of vascular plants, vol 1. Springer, Berlin

Kuschel G (1962) Zur Naturgeschichte der Insel San Ambrosio (Islas Desventuradas, Chile). 1. Reisebericht, geographische Verhältnisse und Pfalzenverbreitung. Arkiv Bot 4:413–419

Lammers TG, Stuessy TF, Silva M (1986) Systematic relationships of the *Lactoridaceae*, an endemic family of the Juan Fernandez Islands, Chile. Plant Syst Evol 152:243–266

Macphail MK, Partridge AD, Truswell EM (1999) Fossil pollen records of the problematical primitive angiosperm family *Lactoridaceae* in Australia. Plant Syst Evol 214:199–210

Mann D, James E, Chase J, Beck W, Reanier R, Mass M, Finney B, Loret J (2008) Drought, vegetation change, and human history on Rapa Nui (Isla de Pascua, Easter Island). Quat Res 69:16–28

Marquínez X, Lohmann LG, Faria Salatino ML, Salatino A, González F (2009) Generic relationships and dating of lineages in Winteraceae based on nuclear (ITS) and plastid (*rp*S16 and *psb*A-*trn*H) sequence data. Mol Phylogenet Evol 53:435–449

Marticorena C (1990) Contribución a la estadística de la flora vascular de Chile. Gayana Bot 47: 85–113

Marticorena C (1997) La presencia de *Maireana brevifolia* (R.Br.) Paul G. Wilson (Chenopodiaceae), en Chile continental. Gayana Bot 54:193–194

Marticorena C, Stuessy TF, Baeza CM (1998) Catalogue of the vascular flora of the Robinson Crusoe or Juan Fernández Islands, Chile. Gayana Bot 55:187–211

Miller H (1970) Das problem des hypothetischen „Pazifischen Kontinentes“ gesehen von der chilenischen Pazifikküste. Int J Earth Sci 59:927–938

Morrone JJ (1992) Revisión sistemática, análisis cladístico y biogeografía histórica de los géneros *Falklandius* Enderlein y *Lanteriella* gen. Nov. (Coleoptera: Curculionidae). Acta Entomol Chil 17:157–174

Müller RD, Roest WR, Royer J-Y, Gahagan LM, Sclater JG (1997) Digital isochrones of the world’s ocean floor. J Geophys Res 102:3211–3214

Muñoz Pizarro C (1969) El Archipiélago de Juan Fernández y la conservación de sus recursos naturales renovables. Reprint 1974. Mus Nac Hist Nat (Santiago) Ser Educativa 9:17–47

Nur A, Ben-Avraham Z (1981) Volcanic gaps and the consumption of aseismic ridges in South America. In: Kulm LVD, Dymond J, Dasch EJ et al. (eds) Nazca Plate: Crustal Formation and Andean Convergence. Geol Soc Am Mem 154:729–740

Philippi RA (1856) Observaciones sobre la flora de Juan Fernández. An Univ Chile 13:157–169

Philippi RA (1870) Vegetation der Inseln San Ambrosio und S. Felix. Bot. Zeitung (Berlin) 28:496–502

Philippi F (1875) La flora de las islas San Ambrosio i San Félix. An Univ Chile 47:185–194

Ricci M (2001) Evaluation of conservation status of *Lactoris fernandeziana* Philippi (Lactoridaceae) in Chile. Biodivers Conserv 10:2129–2138

Sax DF, Gaines SD (2008) Species invasions and extinction: the future of native biodiversity on islands. Proc Natl Acad Sci Usa 105:11490–11497

Skottsberg C (1911) The wilds of Patagonia: a narrative of the Swedish expedition to Patagonia, Tierra del Fuego and the Falkland Islands in 1907–1909. Macmillan, Edward Arnold, NY, Londres

Skottsberg C, (ed) (1920–1956) Natural history of Juan Fernandez and Easter Island, 3 vol. Almqvist & Wiksell, Uppsala

Skottsberg C (1925) Juan Fernandez and Hawaii. A phytogeographical discussion. Bernice P. Bishop Mus. Spec. Publ. 16:1–47

Skottsberg C (1936) La población botánica y zoológica de las islas chilenas del Pacífico. Imprenta Universitaria, Santiago. Translated by G. Looser from the French original: Berland L, Berlioz J, Bryan EH et al. (eds) Le peuplement des îles pacifiques du Chili. Contribution à l’étude du peuplement zoologique et botanique des îles du Pacifique (1934), Société de Biogéographie, Paris, pp 271–280

Skottsberg C (1937) Die flora der Desventuradas-Inseln (San Félix und San Ambrosio) nach Sammlungen F. Johows Göteborgs Kungl Vetensk. -Vitterh -Samh. Handl. ser 5 B 5:1–88

Skottsberg C (1951) Weitere Beiträge zur Flora der Insel San Ambrosio. Arkiv Bot 2:12

Skottsberg C (1956) Derivation of the flora and fauna of Juan Fernandez and Easter Island. In: Skottsberg C, (ed) The natural history of the Juan Fernandez and Easter Islands, vol 1 (Botany). Almqvist & Wiksell, Uppsala, pp 193–405

Skottsberg C (1963) Zur Naturgeschichte Der Inseln San Ambrosio (Islas Desventuradas, Chile) 2. Blütenpflanzen. Arkiv Bot 4:464–490

Smith AR, Pryer KM, Schuettpelz E, Korall P, Schneider H, Wolf PG (2006) A classification for extant ferns. Taxon 55:705–731

Stern C, Moreno H, López-Escobar L, Clavero J, Lara LE, Naranjo JA, Parada MA, Skewes MA (2007) Chilean volcanoes. In: Moreno T, Gibson W, (eds) The geology of Chile. The Geological Society of London, London, pp 147–178

Stuessy TF, Sanders RW, Silva M (1984a) Phytogeography and evolution of the flora of the Juan Fernández Islands: a progress report. In: Redovsky FJ, Raven PH, Sohmer SH, (eds) Biogeography of the Tropical Pacific. Assoc Syst Coll and B.P. Bishop Museum, Lawrence, KS, pp 55–69

Stuessy TF, Foland KA, Sutter JF, Sanders RW, Silva M (1984b) Botanical and geological significance of Potassium-Argon dates from the Juan Fernandez Islands. Science 225:49–51

Stuessy TF, Crawford DJ, Anderson GJ, Jenner RJ (1998a) Systematics, biogeography and conservation of Lactoridaceae. Perspect Plant Evol Syst 1–2:267–290

Stuessy TF, Crawford DJ, Marticorena C, Silva M (1998b) Isolating mechanisms and modes of speciation in endemic angiosperms of the Juan Fernández Islands. In: Stuessy TF, Ono M, (eds) Evolution and speciation of island plants. Cambridge University Press, Cambridge, pp 79–95

Stuessy TF, Swenson U, Marticorena C, Matthei O, Crawford DJ (1998c) Loss of plant diversity and extinction on Robinson Crusoe Islands, Chile. In: Peng CI, Lowry PP (eds) Rare, threatened and endangered floras of Asia and the Pacific Rim. Acad Sin Monogr 16:243–257

Swenson U, Stuessy TF, Baeza M, Crawford DJ (1997) New and historical plant introductions, and potential pests in the Juan Fernández Islands, Chile. Pac Sci 51:23–253

Teillier S, Taylor C (1997) *Maireana* Moq., un nuevo género para Chile (Islas Desventuradas). Gayana Bot 54:15–17

van Balgooy MMJ (1971) Plant-geography of the pacific. Blumea 6(Suppl):1–22

Wallace AR (1880) Island life (or The phenomena and causes of insular faunas and floras: including a revision and attempted solution of the problem of geological climates). Macmillan, London

Wikström N, Savolainen V, Chase MW (2001) Evolution of the angiosperms: calibrating the family tree. Proc R Soc Lond B 268:2211–2220

Yáñez GA, Cembrano J, Pardo M, Ranero C, Selles D (2002) The challenger-Juan Fernández-Maipo major tectonic transition of the Nazca-Andean subduction system at 33–34°S: geodynamic evidence and implications. J South Am Earth Sci 15:23–38

Yáñez GA, Ranero CR, von Huene R, Díaz J (2001) Magnetic anomaly interpretation across the southern central Andes (32°–34°S): the role of the Juan Fernández Ridge in the late Tertiary evolution of the margin. J Geophys Res Solid Earth 106:6325–6345

Zizka G (1991) Flowering plants of Easter Island. Palmarum Hortus Francofurt 3:1–108

Chapter 6

Islands on the Continent: Conservation Biogeography in Changing Ecosystems

Abstract Conservation biogeography meets many challenges around the world associated with increasing human pressure on ecosystems and processes like global change. Threats as well as conservation opportunities are differentially distributed over the Chilean territory, and are here explored in relation to modern approaches such as systematic conservation planning.

During the seventies researchers found that concepts theoretical and empirical concepts developed under the mainframe of island biogeography, as extinction and colonization, could be adapted to the analysis of other isolated territories on the mainland like mountains, deserts, water pods, or forest fragments surrounded by the human-altered matrix (MacArthur and Wilson 1967; Marzluff 2005; Whittaker et al. 2008). In practice, concepts of island biogeography have been increasingly applied in conservation planning and the design of reserves networks (Wilson and Willis 1975; Shafer 1990; Pisano 1996; Lomolino et al. 2006). The explicit link between conservation and biogeography has been systematized as a new scientific field, namely "conservation biogeography" (Whittaker et al. 2005).

6.1 Fragmentation v/s Conservation on Chilean Landscapes

Chile has a long history of landscape modification and forests substitution, since the native people inhabiting the land, through the Spanish conquerors' settlement and the successive waves of European immigration (Lauer 1961; Golte 1973). The country's rapid economic development during the last decades of the twentieth century has only increased the expansion of the cultural landscape and the urban limits (Pauchard et al. 2006). Dramatic is the widespread substitution of sclerophyllous and deciduous forests in Central Chile by exotic plantations and agriculture (Torres-Mura et al. 2008), and the progressive fragmentation, by logging and clearance, of

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the southern temperate forests (Grez et al. 2006; Echeverría et al. 2006) (Figs. 6.1 and 6.2).

The impacts of human activities already affect most ecosystems, from the northern "bofedales" (cushion bogs) and tamarugales through the mediterranean matorral to the coastal southern forests (Hoffmann 1998; Smith-Ramírez 2004; Torres-Mura et al. 2008) (see Sect. 1.3). Activities that have a big impact on Chilean ecosystems are related to all industrial sectors from forestry to mining, including agriculture and even non-regulated tourism. Fires are not a natural aspect of the Chilean territory, but induced by *colonos* affected ca 3 million hectares in the north patagonian forests between the 1936 and 1956 (Quintanilla 2008) and continue affecting thousands of hectares yearly in Mediterranean Chile (Quintanilla and Castro 1998). Mining is the main economic activity of the country, and the environmental impacts of the industry are huge, especially in the North where the sparse water resource has been constantly captured by the mining projects in detriment of the fragile Andean ecosystems and indigenous communities (see also Sect. 7.3). Mining projects are even affecting other physical features like glaciers and rock glaciers (Brenning 2008).

Calls for a reduction of the effects of human impact on Chilean ecosystems were already made by Gay (1838), Albert (1903), Garaventa (1936), Elizalde-McClure (1970), Cunill (1970), and Muñoz Pizarro (1973), among others. Federico Albert was the principal promoter of the forest and conservation legislation (Camus 2006). Carl Skottsberg was one of the promoters of the creation of Juan Fernández National Park (Chap. 5). Agustín Garaventa was the promoter of the creation of iconic La Campana National Park (Garaventa 1964). Carlos Muñoz Pizarro (Chap. 2) provided the first national list of conservation priority sites (1969), and the first national account of endangered plant species (1973). Following scientific recommendations, the reaction of the state was a strong impulse towards the creation of protected areas during the 1960s and 1970s according to the "pristine" or "wilderness" concept (Pauchard and Villarroel 2002) (Box 6.1).

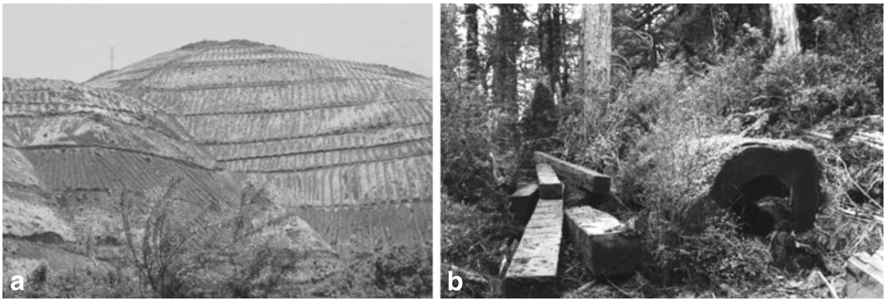

Fig. 6.1 Examples of human impacts on native ecosystems: **a** substitution of matorral for plantations; **b** exploitation of alerce (*Fitzroya cupressoides*) inside the temperate forest (photos by A. Moreira-Muñoz)

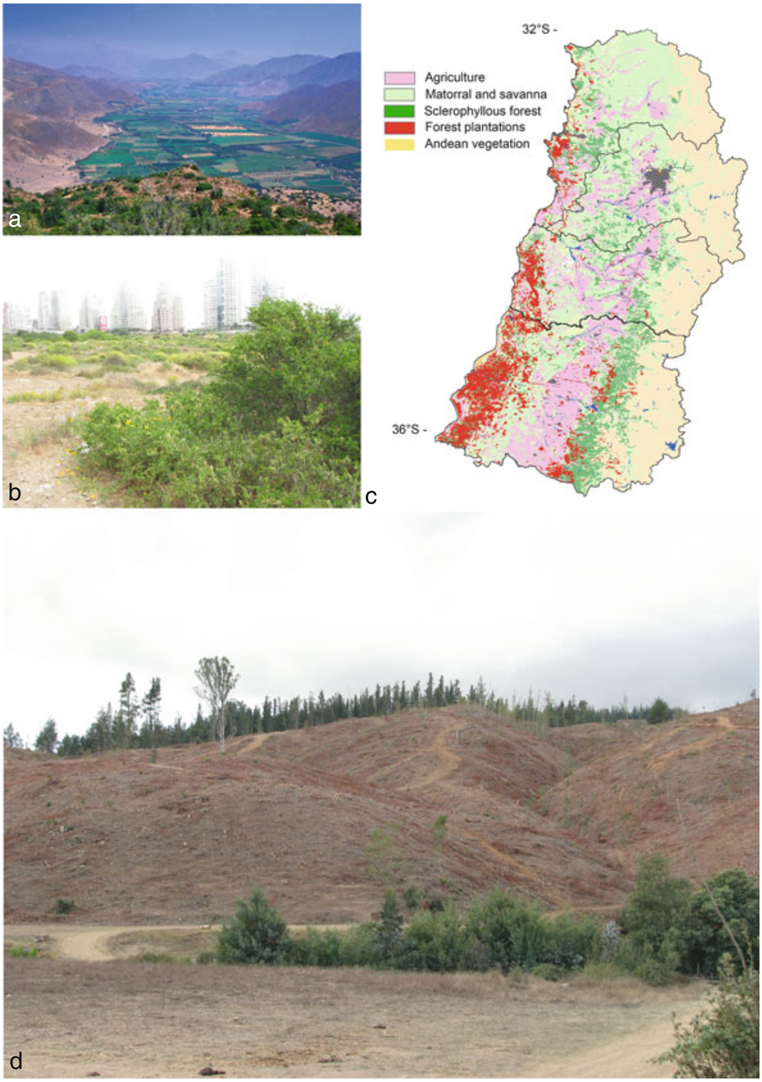

Fig. 6.2 Cultural landscapes: **a** intensively cultivated Central Depression, Río Aconcagua; **b** advancement of the city upon natural ecosystems as the case of Concón palaeodunes; **c** map of Central Chile showing remnants of native vegetation and cultural land uses; **d** intensive substitution of natural vegetation for *Pinus* plantations, Maule region (photo/maps credits: **a**, **b**, **d** A. Moreira-Muñoz; **c** National Vegetation Survey (1997) CONAF/CONAMA/BIRF)

Box 6.1 The First Protected Area and the Evolution of the SNASPE

The first Chilean protected area was created in 1907, namely the Malleco National Forest Reserve established in southern Chile (Cabeza 1988). In 1925 the first National Park, Benjamín Vicuña Mackennna, was created and a few years later its limits were modified. The first protected area which still exists is Vicente Pérez Rosales National Park, designed in 1926 (Fig. 6.3).

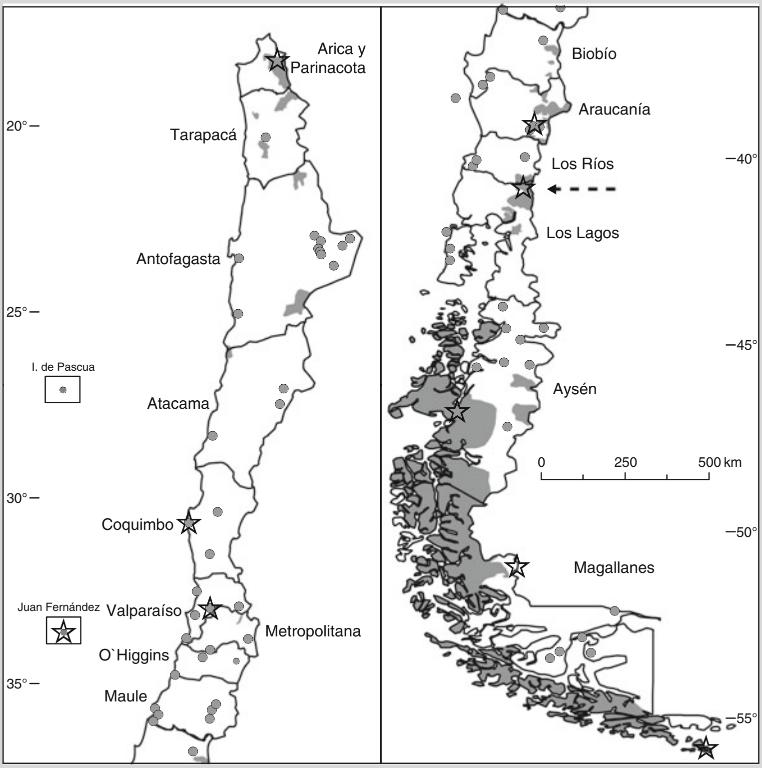

Fig. 6.3 Distribution of protected areas in Chilean administrative regions: *arrow* shows the location of Vicente Pérez Rosales National Park; *dots* represent reduced areas; *stars* show the presence of Biosphere Reserves

The creation of protected areas in the early 1900s was more a response to the interest of visionary naturalists acting against deforestation, rather than a national conservation policy (Pauchard and Villarroel 2002). During the 1960s and 1970s the protected surface grew exponentially, especially in southern Chile, and this was more related to aesthetic considerations and the low value of the land than to "biodiversity", a concept that at that time still did not existed. Only in 1984 the "Sistema Nacional de Áreas Silvestres Protegidas del Estado" (SNASPE) was officially created. The SNASPE adopted the framework of the 1978 IUCN protected area categories to comply with international agreements. Four categories of protected areas were defined: Virgin Region Reserves (with no unit in Chile), National Parks, Natural Monuments, and National Reserves. The management of the system was assigned to the "Corporación Nacional Forestal" (CONAF), a private corporation dependent of the Agriculture Ministry.

At present (December 2009) the system is composed of 97 units occupying more than 14 million ha, or 19% of the national territory (Fig. 6.3) This includes 33 National Parks, 49 National Reserves, and 15 Natural Monuments.

The 19% of national protected territory is a good proportion at global standards. Nevertheless, the system shows a weakness as it is not representative: most of the protected areas are located in the south, and the Central Chilean ecosystems are absolutely underrepresented (Mardones and Henríquez 1996; Luebert and Becerra 1998; Luebert and Pliscoff 2006). This last assessment shows that the protected areas system still does not protect 25 of 127 ecosystems, and 47 of the 127 ecosystems have less than 10% of their remnant surface under protection (Luebert and Pliscoff 2006). The ecosystem conservation approach is still under development in Chile, since most conservation efforts have been concentrated on several iconic target faunal or floral species, like alerce (*Fitzroya cupressoides*).

Efforts to improve the representativeness of the system include the recognition of priority sites at the national and regional levels, coupled with species red lists (Benoit 1989; Muñoz-Schick et al. 1996; Squeo et al. 2001, 2008; Serey et al. 2007; CONAMA 2008), but the real incorporation of new units is a slow process. A newer system should incorporate, under different protocols of use and management, natural sanctuaries, private parks, and other categories. Complementary to the in-situ conservation are efforts catalogued as ex-situ, like the National Botanic Garden (www.jardin-botanico.cl), the Metropolitan Botanic Garden "Chagual" (www.chagual.cl) and the Millennium Seedbank with its centre located in Vicuña, Coquimbo region (León-Lobos et al. 2003).

6.2 Global Change Biogeography: A Science of Uncertainties . . . and Possibilities

Range shifts of species promoted by global change have enormous implications for biodiversity planning and management (Root et al. 2007). This means but working within scenarios of crescent uncertainty (Regan et al. 2005; Pearson et al. 2006;

Guilhaumon et al. 2008; McDonald-Madden et al. 2008). "Our uncertainty regarding the consequences of losing species can seem overwhelming, even paralyzing" (Kareiva and Levin 2003, p. 345). This might not be stimulating thoughts for planners and decision-makers, and serve to maintain skepticism towards global change. Alternatively, these people need certainties in order to act, and therefore they need to tergiversate scientific models into "realities" (Lehmkuhl 2008; Egner 2008). "While the climate skeptics have sought to refute climate change science by exposing the socially negotiated assumptions and uncertainties of the climate models, advocates of greenhouse gases reduction have responded by denying them altogether. Neither response is very helpful. What is needed instead is a more reflexive understanding of science as a social practice" (Demeritt 2001, p. 329).

In this sense, conservation biogeography seeks a better understanding of the impacts of global change on ecosystems and species. Species range dynamics have long been of crucial interest for ecologists and biogeographers as illustrated by the classical example from Peters and Lovejoy (1992) (Fig. 6.4).

Ecological responses to recent climate change are already evident (Channell and Lomolino 2000; Walther et al. 2002; Araújo et al. 2004). Global climate change has already begun affecting species' geographic ranges by means of poleward shifts in range limits correlated with a warming climate and changes in precipitation, and phenological changes portend poleward shifts (Parmesan and Yohe 2003; Parmesan 2007). Upslope shifts in range boundaries along temperate elevational gradients also have been documented (Wilson et al. 2007; Lenoir et al. 2008). Even in tropical lowland areas, biotas may face a level of contraction due to global warming (Colwell et al. 2008).

The effects of global change on Chilean geosystems are increasingly attracting attention and research (e.g. Andrade and Peña 1993; Lauenroth et al. 2004). Widespread retreat of glaciers in the Central Andes during the nineteenth and twentieth century has been extensively documented (Rivera et al. 2006; Le Quesne et al. 2009) (Fig. 6.5). Scenarios of increasing temperatures and decreasing precipitation, spatially differentiated, predict important effects on the Chilean ecosystems (see Arroyo et al. 1993; DGF 2006; Searle and Rovira 2008).

To improve biodiversity conservation across the landscape, a possibility is to abandon the "wilderness ideal" (Jax and Rozzi 2004) and move towards a more

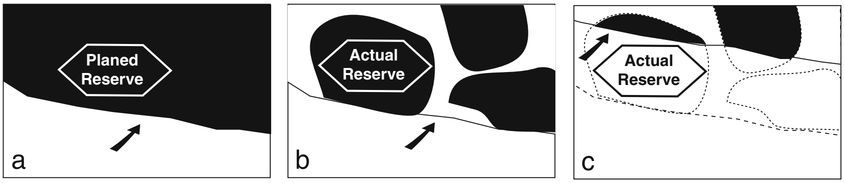

Fig. 6.4 **a** represents a reserve created today for the conservation of a targeted endangered taxon (*black area*). **b** It is very plausible that in several decades the geographic range of this species will move (*arrow*) in response to anthropogenic pressure and climate changes. **c** The core of the distribution area would rapidly disappear and the species would be *left* at the edge. The reserve, at least for the conservation of this taxon, has become useless (redrawn from Peters and Lovejoy (1992))

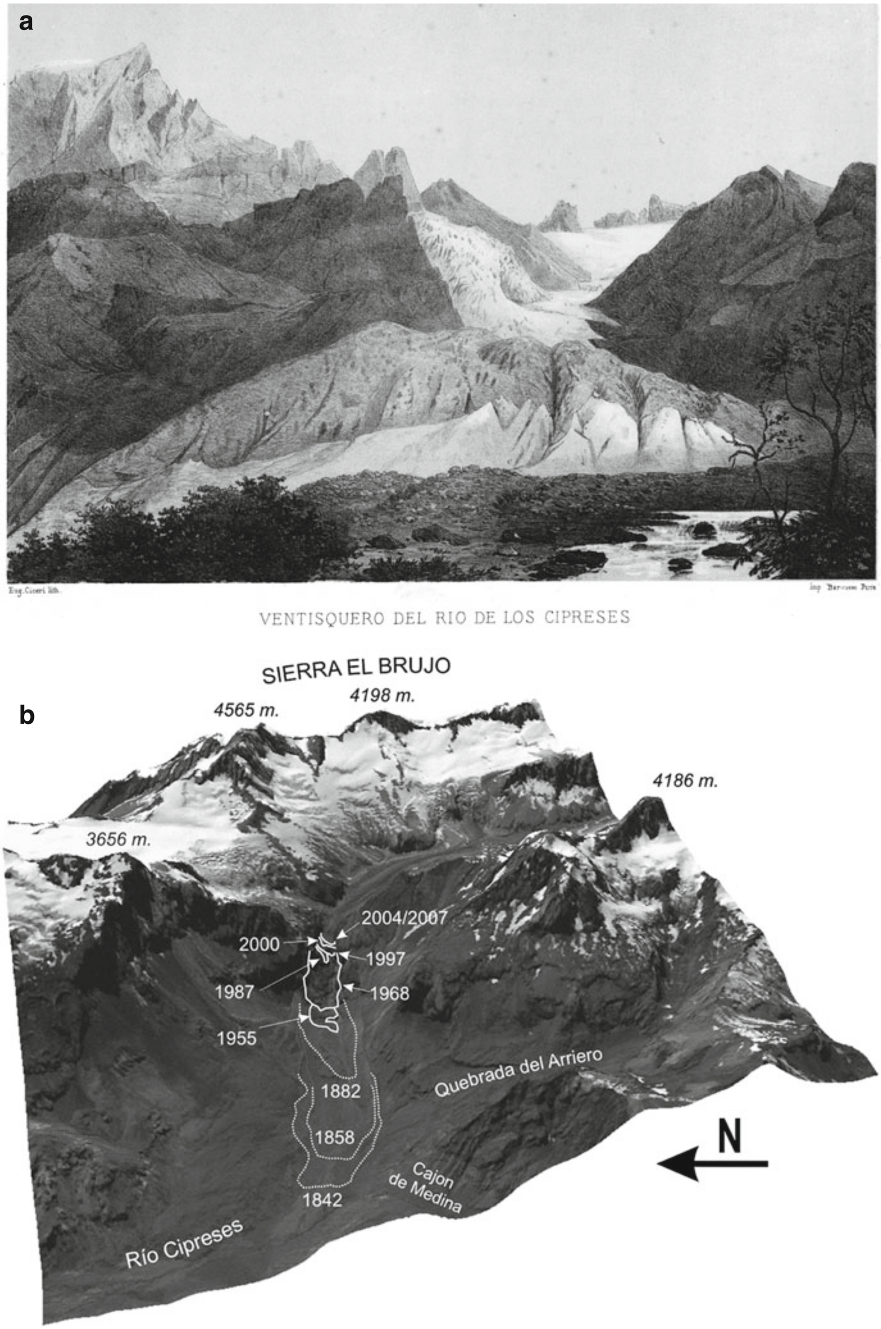

Fig. 6.5 Glaciar retreat in Cajón de Cipreses (35ºS) from 1840 to the present; **a** illustration from Pissis' Atlas (1975) (Chap. 2); **b** glacier retreat as shown in an aerial photograph (from Le Quesne et al. 2009, by permission of Elsevier)

realistic one, in which human activities are incorporated into conservation objectives in vast territories, i.e. a model of conservation "in the real world" (Prendergast et al. 1999; Moreira-Muñoz 2005; Branquart et al. 2008). This is certainly a very compelling option for a rapidly urbanizing country like Chile. The actual tendency runs towards a new protected areas systems (a kind of SNASPE 2.0) that explicitly incorporated Natural Sanctuaries, RAMSAR-sites, marine reserves (Rovira et al. 2008), and privately protected areas into a new spatially and operationally integrated system. This should include peri-urban parks at the edge of the city (Elórtegui 2005) and novel concepts like *geoparks* (Castro and Zúñiga 2007) that follow new international standards of protected areas systems (e.g. Boitani et al. 2008).

In the same direction is the reconsideration of the old but always valid *biosphere reserve model*: "Biosphere reserves celebrate the cultural relationship between people and places" (Berghofer et al. 2008) and are indeed the best suited places for promoting the environmental education of the community (Fraser and Jamieson 2003). The spatial arrangement of transition zones, buffers and corridors has to be realized with the participation of local stakeholders in a joint process with the scientific community, as in the case of La Campana-Peñuelas Biosphere Reserve (Elórtegui and Moreira-Muñoz 2002). This implies the rescue of ancient local knowledge, which opens a better opportunity for learning, communication, and acting. Indeed, the association with indigenous and rural communities towards common conservation goals is one of the biggest challenges for the protected areas system in Chile (see Oltremari and Jackson 2006; Castro and Romo 2008).

Biosphere reserves in Chile are still lacking support to cover the multiple challenges that includes this nomination, but a slow but constant local impulse is generating management plants (e.g. for La Campana) and the creation of new reserves, like *Cabo de Hornos* (Rozzi et al. 2004) and *Bosques Templados*, this latter in a bi-national effort with Argentina. Currently there are nine reserves in Chile on the more diverse ecosystems (Fig. 6.3).

The biosphere reserves concept is an attempt to integrate the protected areas with the surrounding human matrix, trying to couple biodiversity conservation with human interests (Naughton-Treves et al. 2005). Therefore, conservation planning problems can be formulated as optimization problems (Sarkar et al. 2006; Margules and Sarkar 2007) (Box 6.2).

Box 6.2 Systematic Conservation Planning and Priority Site Selection

Different algorithms have been developed in the search for the "best" solution for conservation, and planning tools are typically used to satisfy this while dealing with multiple criteria (Sarkar et al. 2006). This approach got the name of "systematic conservation planning", defined as a structured approach with feedback and reiteration at any stage (Margules and Sarkar 2007). These stages include engagement of stakeholders, choices about biodiversity measurements, GIS mapping, setting of surrogates, the application of complementarity as a main concept for the identification of new conservation areas, and monitoring management actions, among others (Margules and Pressey 2000). A key concept is complementarity: the marginal contribution of an area to represent the full set of attributes defined as biodiversity surrogates (Margules and Sarkar 2007).

Conservation biogeography is specifically focusing on inter-related factors like scale dependency (both spatial and temporal), and inadequacies in taxonomic and distributional data (the so-called Linnean and Wallacean shortfalls): the Linnean shortfall means the lack of appropriate knowledge on the taxonomy of the species; and the Wallaceaen shortfall, approaching the lack of adequate knowledge on the distribution of the species (Whittaker et al. 2005). As expressed by Myers and Giller (1988): "Knowledge of the distribution of most organisms is weak, as is knowledge of the faunas and floras of many regions of the globe. In this respect, current biogeographic hypotheses are built around very incomplete basic data and we are perhaps trying to run before we can walk" (Myers and Giller 1988, p. 21)

The systematic conservation planning approach has been recently applied in Chile by Ramírez de Arellano (2007) and Tognelli et al. (2009). As an example from Central Chile, currently protected areas and priority sites have been assessed by a set of surrogates related to available biological information at the regional scale (Fig. 6.6). The map shows some of the cartographic results expressed as complementary sites composing a regional connected reserves network, concentrated towards the coastal Cordillera, which harbours most of endemics and taxa with restricted ranges.

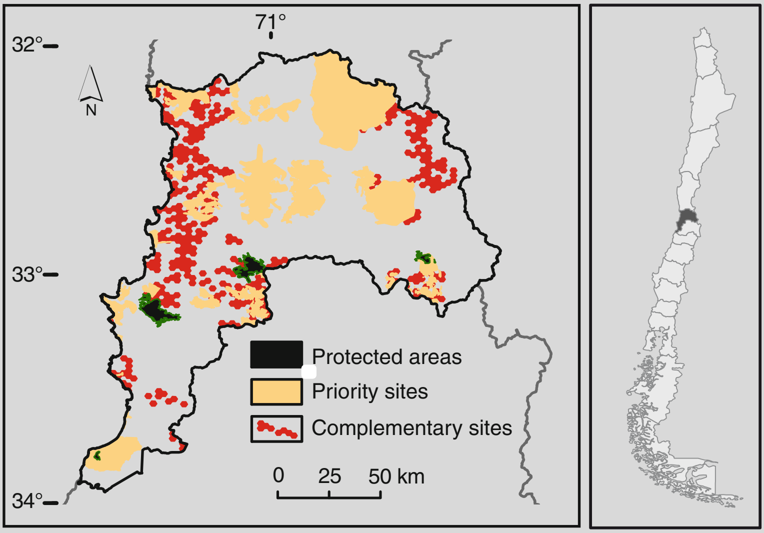

Fig. 6.6 Proposal of a network of reserves for the conservation of the vascular flora of the Valparaíso region (Morales and Moreira-Muñoz 2009)

Cartographic proposals are highly dependent on available biological data: most models rely on species richness, but there are other aspects to be considered like "phylogenetic diversity" (Rodrigues and Gaston 2002; Forest et al. 2007). Specific assessment for southern South America showed that Central Chile is one of the highest priority areas for conservation (Posadas et al. 2001). Also Heads (2009) emphasized the importance of South American basal angiosperm groups like *Lactoris, Gomortega, Berberidopsis*, and *Aextoxicon*, as components of one of the "globally basal centres of endemism". All these relevant species are in serious danger of extinction due to human activities (Hechenleitner et al. 2005; Alarcón et al. 2007), together with other iconic species like *Nothofagus alessandrii* (Bustamante and Castor 1998; Olivares et al. 2005), *Nothofagus glauca* (Burgos et al. 2008), *Fitzroya cupressoides*, *Pitavia punctata* or *Legrandia concinna* (Altamirano et al. 2007).

References

Alarcón D, Smith-Ramírez C, Hechenleitner P, Oliva M, Pinto M (2007) Nuevas poblaciones de la enredadera *Berberidopsis corallina* Hook. F. en la Región del Bío Bío, Chile. Ubicación, hábitat y grado de conservación. Gayana Bot 64:216–229

Albert F (1903) Informe de Federico Albert sobre sus estudios en las provincias de Malleco, Cautín y Valdivia. Memoria del Ministerio de Industria y Obras Públicas, Santiago

Altamirano A, Echeverría C, Lara A (2007) Effect of forest fragmentation on vegetation structure of *Legrandia concinna* (Myrtaceae) threatened populations in south-central Chile. Rev Chil Hist Nat 80:27–42

Andrade B, Peña H (1993) Chilean geomorphology and hydrology: response to global change. In: Mooney HA, Fuentes ER, Kronberg BI, (eds) Earth system responses to global change: contrast between North and South America. Academic Press, New York, NY, pp 101–114

Araújo MB, Cabeza M, Thuiller W, Hannah L, Williams PH (2004) Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. Glob Change Biol 10:1618–1626

Arroyo MTK, Armesto JJ, Squeo FA, Gutiérrez J (1993) Global change: Flora and Vegetation of Chile. In: Mooney HA, Fuentes ER, Kronberg BI, (eds) Earth system responses to global change: contrast between North and South America. Academic Press, New York, NY, pp 239–263

Benoit I, (ed) (1989) Libro Rojo de la Flora Terrestre de Chile. Ministerio de Agricultura, Corporación Nacional Forestal, Santiago

Berghofer U, Rozzi R, Jax K (2008) Local versus global knowledge: diverse perspectives on nature in the Cape Horn Biosphere Reserve. Environ Ethics 30:273–294

Boitani L, Cowling RM, Dublin HT, Mace GM, Parrish J, Possingham HP, Pressey RL, Rondinini C, Wilson KA (2008) Change the IUCN protected area categories to reflect biodiversity outcomes. PLoS Biol 6:e66. doi:10.1371/journal.pbio.0060066

Branquart E, Verheyen K, Latham J (2008) Selection criteria of protected forest areas in Europe: the theory and the real world. Biol Conserv 141:2795–2806

Brenning A (2008) The impact of mining on rock glaciers and glaciers: examples from Central Chile. In: Orlove BS, Wiegandt E, Luckman B, (eds) Darkening peaks: glacier retreat, science, and society. University of California Press, Berkeley, CA, pp 196–205

Burgos A, Grez AA, Bustamante RO (2008) Seed production, pre-dispersal seed predation and germination of *Nothofagus glauca* (Nothofagaceae) in a temperate fragmented forest in Chile. For Ecol Manag 255:1226–1233

Bustamante RO, Castor C (1998) The decline of an endangered temperate ecosystem: the ruil (*Nothofagus alessandrii*) forest in central Chile. Biodivers Conserv 7:1607–1626

Cabeza A (1988) Aspectos históricos de la legislación forestal vinculada a la conservación, la evolución de las áreas silvestres protegidas de la zona de Villarrica y la creación del primer Parque Nacional en Chile. Documento de Trabajo No. 101, CONAF, Santiago

Camus P (2006) Ambiente, bosques y gestión forestal en Chile. 1541–2005. Colección Sociedad y Cultura, Central de Investigaciones Diego Barros Arana, LOM ediciones, Santiago

Castro C, Zúñiga A (2007) Geomorfología del AMCP – MU Isla Grande Atacama. Instituto de Geografía, Pontificia Universidad Católica de Chile, Santiago

Castro V, Romo M (2008) Tradiciones Culturales y Biodiversidad. In: CONAMA (ed) Biodiversidad de Chile: patrimonio y desafíos, 2nd edn. CONAMA, Santiago, pp 468–493

Channell R, Lomolino MV (2000) Trajectories to extinction: spatial dynamics of the contraction of geographical ranges. J Biogeogr 27:169–179

Colwell RK, Brehm G, Cardelus CL, Gilman AC, Longino JT (2008) Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. Science 322:258–261

CONAMA (2008) Biodiversidad de Chile: Patrimonio y Desafíos. 2nd edn. Comisión Nacional de Medio Ambiente, Chile. www.conama.cl

Cunill P (1970) Factores en la destrucción del paisaje chileno: recolección caza y tala coloniales. Inf Geogr 20:235–264

Demeritt D (2001) The construction of global warming and the politics of science. Ann Assoc Am Geogr 91:307–337

DGF (2006) Estudio de la Variabilidad Climática en Chile para el siglo XXI: Informe Final. Departamento de Geofísica, Facultad de Ciencias Físicas y Matemáticas, Universidad de Chile, CONAMA, Santiago

Echeverría C, Coomes D, Salas J, Rey-Benayas JM, Lara A, Newton AC (2006) Rapid deforestation and fragmentation of Chilean Temperate Forests. Biol Conserv 130:481–494

Egner H (2008) See what you can't see – on "truth" and the credibility of science in the climate discourse. GAIA 17:337–338

Elizalde-McClure R (1970) La sobrevivencia de Chile. Editorial Universitaria, Santiago

Elórtegui S, (ed) (2005) Las Dunas de Concón: El desafío de los espacios silvestres urbanos. Taller La Era, Valparaíso

Elórtegui S, Moreira-Muñoz A, (eds) (2002) Parque Nacional la campana: Origen de una reserva de la Biósfera en Chile Central. Taller la Era, Santiago

Forest F, Grenyer R, Rouget M, Jonathan Davies T, Cowling RM, Faith DP et al. (2007) Preserving the evolutionary potential of floras in biodiversity hotspots. Nature 445:757–760

Fraser R, Jamieson G (2003) Community environmental education: challenges within the Biosphere Reserve Concept. Prospects 33:293–302

Garaventa A (1936) La deforestación en la zona de Chile central y su importancia. Rev Univ 21:131–135

Garaventa A (1964) Importancia e interés botánico que presenta la vegetación del cerro La Campana. Bol Inf Soc Cient de Valparaíso 23:2

Gay C (1838) Sobre las causas de la disminución de los montes de la provincia de Coquimbo. In: Squeo FA, Arancio G, Gutiérrez JR, (eds) Libro Rojo de la Flora Nativa y de los Sitios Prioritarios para su Conservación: Región de Coquimbo (2001). Ediciones Universidad de La Serena, La Serena, pp 281–286

Golte W (1973) Das südchilenische Seengebiet: Besiedlung und wirtschaftliche Erschliessung seit dem 18. Jahrhundert. Bonn Geogr Abh 47:1–183. + Figs

Grez A, Simonetti J, Bustamante RO (2006) Biodiversidad en Ambientes Fragmentados de Chile: Patrones y Procesos a Diferentes Escalas. Editorial Universitaria, Santiago

Guilhaumon F, Gimenez O, Gaston KJ, Mouillot D (2008) Taxonomic and regional uncertainty in species-area relationships and the identification of richness hotspots. Proc Natl Acad Sci USA 105:15458–15463

Heads M (2009) Globally basal centres of endemism: the Tasman-Coral Sea Region (south-west Pacific), Latin America and Madagascar/South Africa. Biol J Linn Soc 96:222–245

Hechenleitner P, Gardner MF, Thomas PI, Echeverría C, Escobar B, Brownless P, Martínez C (2005) Plantas Amenazadas del Centro-Sur de Chile: Distribución, Conservación y Propagación. Universidad Austral de Chile y Real Jardín Botánico de Edimburgo, Valdivia

Hoffmann AE, (ed) (1998) La Tragedia del Bosque Chileno. Defensores del Bosque Chileno, Ocho Libros Editores, Santiago

Jax K, Rozzi R (2004) Ecological theory and values in the determination of conservation goals: examples from temperate regions of Germany, United States of America, and Chile. Rev Chil Hist Nat 77:349–366

Kareiva P, Levin SA, (eds) (2003) The importance of species: perspectives on expendability and triage. Princeton University Press, Princeton, NJ

Lauenroth WK, Epstein HE, Paruelo JM, Burke IC, Aguiar MR, Sala OE (2004) Potential effects of climate change on the temperate zones of North and South America. Rev Chil Hist Nat 77:439–453

Lauer W (1961) Wandlungen im Landschaftsbild des Südchilenischen Seengebietes seit Ende der spanischen Kolonialzeit. Schr Geogr Inst Univ Kiel 20:227–276

Le Quesne C, Acuña C, Boninsegna JA, Rivera A, Barichivich J (2009) Long-term glacier variations in the Central Andes of Argentina and Chile, inferred from historical records and tree-ring reconstructed precipitation. Paleogeogr Paleoclim Paleoecol. doi:10.1016/j.palaeo.200801.039

Lehmkuhl M (2008) Neither coincidence nor success: how to interpret the current debate about climate change. GAIA 17:9–11

Lenoir J, Gégout JC, Marquet PA, de Ruffray P, Brisse H (2008) A significant upward shift in plant species optimum elevation during the 20th century. Science 320:1768–1771

León-Lobos P, Way M, Pritchard H, Moreira-Muñoz A, León M, Casado F (2003) Conservación ex situ de la Flora de Chile en banco de semillas. Chloris chilensis 6. http://www.chlorischile.cl

Lomolino MV, Riddle BR, Brown JH (2006) Biogeography. Sinauer Associates, Sunderland, MA

Luebert F, Becerra P (1998) Representatividad vegetacional del Sistema Nacional de Áreas Silvestres Protegidas del Estado (SNASPE) en Chile. Ambiente y Desarrollo 14:62–69

Luebert F, Pliscoff P (2006) Sinopsis bioclimática y vegetacional de Chile. Editorial Universitaria, Santiago

MacArthur RH, Wilson EO (1967) The theory of island biogeography. Princeton University Press, New York, NY

Mardones G, Henríquez C (1996) Áreas Silvestres Protegidas de Chile. Serie de Monografías, Doc. de trabajo N° 1. CODEFF, Santiago

Margules CR, Pressey RL (2000) Systematic conservation planning. Nature 405:243–253

Margules CR, Sarkar S (2007) Systematic conservation planning. Cambridge University Press, Cambridge

Marzluff JM (2005) Island biogeography for an urbanizing world: how extinction and colonization may determine biological diversity in human-dominated landscapes. Urban Ecosyst 8:157–177

McDonald-Madden E, Baxter PWJ, Possingham HP (2008) Making robust decisions for conservation with restricted money and knowledge. J Appl Ecol 45:1630–1638

Morales V, Moreira-Muñoz A (2009) GIS and systematic conservation planning in Chile, abstracts, international cartography conference, Santiago, Chile, Nov 15–21, 2009

Moreira-Muñoz A (2005) Conservation in a changing world: biodiversity hotspots and the distracting paradigm. J Conserv Plann 1:1–6

Muñoz Pizarro C (1969) Áreas Naturales. En: Segunda Jornada Latinoamericana de Parques Nacionales, Oct 1–4, 1969, Viña del Mar. Ministerio de Agricultura.

Muñoz Pizarro C (1973) Chile: plantas en extinción. Editorial Universitaria, Santiago

Muñoz-Schick M, Yánez J, Núñez H (1996) Libro Rojo de los Sitios Prioritarios para la Conservación de la Biodiversidad en Chile. CONAF, Santiago

Myers AA, Giller PS, (eds) (1988) Analytical biogeography. Chapman and Hall, London

Naughton-Treves L, Buck Holland M, Brandon K (2005) The role of protected areas in conserving biodiversity and sustaining local livelihoods. Annu Rev Env Resour 30:219–252

Olivares P, San Martín J, Santelices R (2005) Ruil (*Nothofagus alessandrii*): Estado del conocimiento y desafíos para su conservación. Departamento de Protección de Recursos Naturales, Comisión Nacional del Medio Ambiente Región del Maule, Talca

Oltremari JV, Jackson RG (2006) Conflicts, perceptions, and expectations of indigenous communities associated with natural areas in Chile. Nat Areas J 26:215–220

Parmesan C (2007) Influences of species, latitudes and methodologies on estimates of phenological response to global warming. Glob Change Biol 13:1860–1872

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42

Pauchard A, Villarroel P (2002) Protected areas in Chile: history, current status and challenges. Nat Areas J 22:318–330

Pauchard A, Aguayo M, Peña E, Urrutia R (2006) Multiple effects of urbanization on the biodiversity of developing countries: the case of a fast-growing metropolitan area (Concepcion, Chile). Biol Conserv 127:272–281

Pearson RG, Thuiller W, Araujo MB, Martínez-Meyer E, Brotons L, McClean C, Miles L, Segurado P, Dawson TP, Lees DC (2006) Model-based uncertainty in species range prediction. J Biogeogr 33:1704–1711

Peters RL, Lovejoy TE (1992) Global warming and biological diversity. Yale University Press, London

Prendergast JR, Quinn RM, Lawton JH (1999) The gaps between theory and practice in selecting nature reserves. Conserv Biol 13:484–492

Pisano E (1996) Implicaciones de la teoría de biogeografía de islas para el diseño de reservas naturales. An Inst Pat (Ser Cienc Nat) 24:117–126

Posadas P, Miranda-Esquivel DR, Crisci JV (2001) Using phylogenetic diversity measures to set priorities in conservation: an example from southern South America. Conserv Biol 15:1325–1334

Quintanilla V (2008) Estado de recuperación del bosque nativo en una cuenca nordpatagónica de Chile, perturbada por grandes fuegos acaecidos 50 años atrás (44º–45ºS). Rev Geogr Norte Grande 39:71–91

Quintanilla V, Castro R (1998) Seguimiento de las cubiertas vegetales post-incendios forestales en la zona mediterránea costera de Chile. Ser Geogr (Univ Alcalá) 7:147–154

Ramírez de Arellano PI (2007) Systematic conservation planning in Chile: sensitivity of reserve selection procedures to target choices, cost surface, and spatial scale. PhD thesis, State University of New York, College of Environmental Science and Forestry, Syracuse, New York, NY

Regan HM, Ben-Haim Y, Langford B et al. (2005) Robust decision-making under severe uncertainty for conservation management. Ecol Appl 15:1471–1477

Rivera A, Acuña C, Casassa G (2006) Glacier variations in central Chile (32°S–41°S). In: Knight PG, (ed) Glacier science and environmental change. Blackwell, Oxford, pp 246–247

Rodrigues ASL, Gaston KJ (2002) Maximising phylogenetic diversity in the selection of networks of conservation areas. Biol Conserv 105:103–111

Root TL, Liverman D, Newman C (2007) Managing biodiversity in the light of climate change: current biological effects and future impacts. In: Macdonald D, Service K, (eds) Key topics in conservation biology. Blackwell, Oxford, UK, pp 85–104

Rovira J, Ortega D, Alvarez A, Molt K (2008) Areas Protegidas en Chile. In: CONAMA (ed) Biodiversidad de Chile: patrimonio y desafíos, 2nd edn. CONAMA, Santiago, pp 506–561

Rozzi R, Massardo F, Anderson C, (eds) (2004) Reserva de Biosfera Cabo de Hornos: una propuesta de conservación y turismo para el desarrollo sustentable en el extremo austral de América. Ediciones de la Universidad de Magallanes, Punta Arenas

Sarkar S, Pressey RL, Faith DP, Margules CR, Fuller T, Stoms DM et al. (2006) Biodiversity conservation planning tools: present status and challenges for the future. Annu Rev Env Resour 31:123–159

Searle JP, Rovira J (2008) Cambio climático y efectos en la biodiversidad: el caso chileno. In: CONAMA (ed) Biodiversidad de Chile: patrimonio y desafíos, 3rd ed. CONAMA, Santiago, pp 502–503

Serey I, Ricci M, Smith-Ramírez C, (eds) (2007) Libro Rojo de la Región del Libertador Bernardo O'Higgins. CONAF, Santiago

Shafer CL (1990) Nature reserves: island theory and conservation practices. Smithsonian Institution Press, Washington, DC

Smith-Ramírez C (2004) The Chilean coastal range: a vanishing center of biodiversity and endemism in South American temperate rainforests. Biodivers Conserv 13:373–393

Squeo FA, Arancio G, Gutiérrez JR, (eds) (2001) Libro Rojo de la Flora Nativa y de los Sitios Prioritarios para su Conservación: Región de Coquimbo. Ediciones Universidad de La Serena, La Serena

Squeo FA, Arancio G, Gutiérrez JR, (eds) (2008) Libro Rojo de la Flora Nativa y de los Sitios Prioritarios para su conservación: Región de Atacama. Ediciones Universidad de La Serena, La Serena, pp 137–163

Tognelli MF, Fernández M, Marquet PA (2009) Assessing the performance of the existing and proposed network of marine protected areas to conserve marine biodiversity in Chile. Biol Conserv 142:3147–3153

Torres-Mura JC, Castro S, Oliva D (2008) Conservación de la Biodiversidad. In: CONAMA (ed) Biodiversidad de Chile: patrimonio y desafíos, 2nd ed. CONAMA, Santiago, pp 413–431

Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin JM, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. Nature 416:389–395

Whittaker RJ, Araujo MB, Paul J, Ladle RJ, Watson JEM, Willis KJ (2005) Conservation biogeography: assessment and prospect. Divers Distrib 11:3–23

Whittaker RJ, Triantis KA, Ladle RJ (2008) A general dynamic theory of oceanic island biogeography. J Biogeogr 35:977–994

Wilson EO, Willis EO (1975) Applied biogeography. In: Cody ML, Diamond MM, (eds) Ecology and evolution of communities. Belknap Press, Cambridge, pp 522–534

Wilson RJ, Gutierrez D, Gutierrez J, Monserrat VJ (2007) An elevational shift in butterfly species richness and composition accompanying recent climate change. Glob Change Biol 13: 1873–1887

Part IV
Case Studies on Selected Families

Chapter 7
Cactaceae, a Weird Family and Postmodern Evolution

Abstract One of the most charismatic American plant families, the Cactaceae, is well represented in Chile. Biogeographic analysis of the Chilean representatives is rarely undertaken, mainly due to the complex taxonomy of the group. Taking account of the most recent taxonomic treatments and distributional knowledge, an attempt is made here to develop a biogeographic regionalization by means of parsimony analysis of endemism (PAE) and the program NDM/VNDM. The first method yields three areas of endemism in northern Chile bordering the Atacama Desert to the North and to the South, and the second method yields one area which includes North-Central Chile. Advantages and restrictions of the methods are discussed. Finally, the evolution of the family is discussed in relation to the rise of the Atacama Desert and the systematic interpretation of the group

"Cacti have a special fascination all of their own. Like the brilliantly colored hummingbirds, the Cactaceae are creatures of the New World" (Barthlott 2001, p 9). With representatives ranging from minute spiny dwarf cacti of a couple centimetres in diameter to the majestic columns of the Arizona giant saguaro, the Cactaceae is the second largest family of angiosperms almost exclusively restricted to the New World. The richest American plant family is Bromeliaceae; both families have one taxon occurring outside America: the Bromeliaceae has *Pitcairnia* as a native genus in West Africa; the Cactaceae has *Rhipsalis* wider distributed in Africa, Madagascar, Mauritius, the Seychelles and Ceylon. The family is present in America from central Canada to Patagonia. The highest diversity is found in the arid environments of North and South America, but contrary to the popular believe due to their spiny morphology, the family is not strictly restricted to arid environments: it also occupies temperate, sub-tropical, and tropical environments reaching mesic southern Chile and Argentina and ranging from the coast to the high Andes (Kraus 1995; Mauseth et al. 2002). The southern limit for the family is the Santa Cruz province in Argentina (ca. 50°S, Anderson 2001), where *Austrocactus, Gymnocalycium, Maihuenia, Maihueniopsis,* and *Pterocactus* occur.

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7.1 Cacti Classification

The morphological characteristics of cacti have long attracted botanists and amateur plant lovers. First exemplars known in Europe supposedly were part of the gifts that Columbus brought to Isabella when returning from his first voyage to the West Indies (Barthlott 2001), and first reports on cultivation of cacti in Europe date back to the middle of the sixteenth century (Mauseth et al. 2002). Cactaceae can be superficially distinguished by the succulent stems (with exceptions) and characteristically clustered spines (Mauseth et al. 2002) (Fig. 7.1).

The subdivision of the cacti into three subfamilies dates back to Schumann (1898). He placed *Pereskia* and *Maihuenia* in the subfamily Pereskioideae, which was already established by Engelmann in 1876 (Leuenberger 2008). In the middle 1990s, *Maihuenia* was transferred to its own subfamily, Maihuenioideae (Wallace 1995). Currently both subfamilies are recognized, together with the Opuntioideae and the most evolved and species-rich Cactoideae (Griffith 2008).

- Pereskioideae is composed of leafy, spiny, often non-succulent trees and shrubs of the genus *Pereskia* (16 species). Traditionally it is considered the most primitive or relictual genus in the Cactaceae, supposedly resembling the "proto-Cactaceae" ancestor. The subfamily is not represented in Chile, but is extensively distributed from the Caribbean along the Andes to Argentina and SE Brazil, surrounding the Amazonas basin (map in Leuenberger 2008).
- Opuntioideae have minute, barbed, deciduous spines (= glochids), and small, often ephemeral leaves, and a bony seed aril. It comprises about 300 species, occupying a geographic range from North America to Patagonia.
- Cactoideae are leafless, spiny stem succulents, considered the most "derived" subfamily, occurring in America, Africa, Madagascar, Mauritius, Seychelles and Ceylon due to the genus *Rhipsalis*.
- Maihuenioideae is composed of the two species of the genus *Maihuenia,* distributed in southern Chile and Argentina (Leuenberger 1997, 2008). The Maihuenioideae is a little subfamily that is the last to have been recognized, and enjoys a huge interest with regard to the evolution of the whole family (Sect. 7.5).

7.2 Chilean Representatives and Their Distribution

The dynamic taxonomy of the group results in very different accounts of the representatives in Chile: Lembcke and Weisser (1979) considered 23 genera, while Marticorena (1990) gave a list of 21 genera and 154 native species for Chile (plus almost 100 infraspecific taxa). More recently, collaborators of the Southern Cone Checklist consider the Chilean Cactaceae as represented by 21genera and 112 species, plus quite a number of varieties and subspecies (Zuloaga et al. 2008). This account, that also presents 88 Chilean endemic species, is considered here as the most recent, valid checklist (Table 7.1). The inclusion of *Miqueliopuntia* as different from *Austrocylindropuntia* is based on more recent results from Griffith and Porter

Fig. 7.1 Chilean cacti: **a** *Eulychnia iquiquensis*, Tocopilla; **b** *Pyrrhocactus curvispinus*, La Campana; **c** *Eriosyce aurata*, Illapel; **d** *Browningia candelaris*, Tarapacá (photo credits: **a**–**c** A. Moreira-Muñoz; **d** Carlo Sabaini);

(2009). All former Chilean Opuntia species have been transferred to other genera like *Maihueniopsis* or *Pterocactus*. *Tephrocactus nigrispinus* (cfr Pinto and Kirberg 2009) is considered by the Southern Cone Checklist as a synonym of *Maihueniopsis nigrispina. Cylindropuntia tunicata* is considered as an introduced species.

Fig. 7.1 (continued) **e** *Copiapoa cinerea*, Tal Tal; **f** *Cumulopuntia sphaerica*, La Serena; **g** *Maihuenia poeppigii*, Las Trancas; **h** *Neoporteria subgibbosa*, Fray Jorge; **i** *Oreocereus leucotrichus*, Chusmiza (photo credits: **e**–**i** A. Moreira-Muñoz)

Clearly the Cactoideae contain most Chilean representatives of the family (Table 7.1), since it is the richest subfamily of the Cactaceae. Most Chilean cactus genera have their distribution in the highs of Peru, Bolivia, and northern Chile (12 genera). 4 genera show more restricted distributions to Argentina and Chile. And 5 genera are endemic to north central Chile (*Copiapoa, Eriosyce, Eulychnia, Neoporteria,* and *Thelocephala*). These genera show an important role in the building of a northern Chilean area of endemism (see Sect. 4.3).

7.2.1 Cacti Distribution in Chile

Lembcke and Weisser (1979) mapped the distribution of 23 genera encompassing Chilean Cactaceae, but new collections and systematic treatments (Pinto 2002, 2003; Kiesling 2002; Zuloaga et al. 2008) imply a renewal of this early account. Only the extreme northern regions have been intensively surveyed and mapped (Pinto and Kirberg 2009). For this chapter, dot maps for Chilean genera have been made by means of the collections in existence at the National Herbarium SGO (Fig. 7.2a). A species richness map is presented as Fig. 7.2b. Distribution maps

Table 7.1 Classification and richness of Chilean cacti (according to Zuloaga et al. 2008)

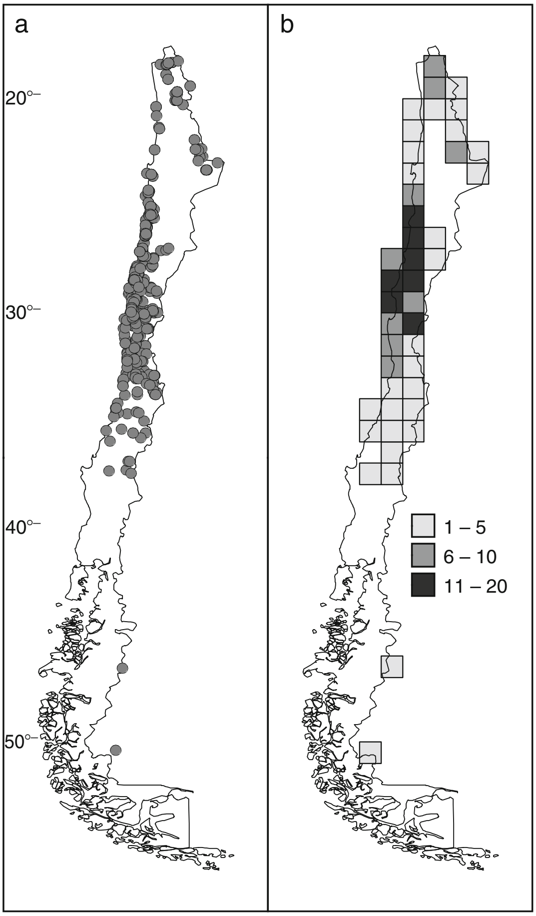
Subfamily	Genus	Nº spp.	Distribution	Chilean native spp.	Chilean endemic spp.
Maihuenioideae	*Maihuenia*	2	Arg, Chile	2	0
Opuntioideae	*Cumulopuntia*	20	Bol, S Peru, N Chile	2	0
	Maihueniopsis	16	Andes Peru, Bol, Chile, Arg	13	9
	Miqueliopuntia	1	Chile	1	1
	Pterocactus	9	Patagonia Arg, Chile	2	0
	Tunilla	9	Andes Peru, Bol, Chile	2	0
Cactoideae	*Austrocactus*	4	Arg, Chile	3	1
	Browningia	11	Peru, Bol, Chile, Paraguay	1	0
	Copiapoa	22	N Chile	22	22
	Corryocactus	12	Bol, S Peru, N Chile	1	0
	Eriosyce	5	Chile	5	5
	Eulychnia	6	Chile	6	6
	Haageocereus	20	Peru, Chile	2	1
	Islaya	4	Peru, Chile	4	3
	Lobivia	24	Andes Peru, Bol, Chile, Arg	2	0
	Neoporteria	6	Chile	6	6
	Neowerdermannia	2	Peru, Bol, Chile, Arg	1	1
	Oreocereus	7	Andes Peru, Bol, Chile, Arg	4	1
	Phyrrocactus	27	Arg, Chile	20	20
	Thelocephala	6	Chile	6	6
	Trichocereus	25	Chile, Arg, S Peru	7	6
				112	88

for each genus within the three subfamilies present in Chile are shown in Figs. 7.3 and 7.4.

With the collection localities, a **species** richness map was made on the base of a 1 × 1 degree grid (Fig. 7.2b). Chilean Cactaceae are mainly distributed in central and northern Chile from 18° to 38°S, concentrated at the coast of the Antofagasta and Atacama regions, between 25° and 31°S (Fig. 7.2b). Genera showing a wider distribution in Chile are *Eulychnia*, *Phyrrocactus*, and *Trichocereus*. In contrast, other genera like *Browningia, Islaya, Neowerdermannia,* and *Lobivia* have a very restricted distribution in Chile, inferior to one latitudinal degree. Most genera show discontinuous distributions, but collection gaps cannot be ruled out. This discontinuity is extreme in genera such as *Austrocactus*, with several collections in Central Chile and in Patagonia (Fig. 7.3).

Skottsberg (1916) reported the species *Pterocactus australis* (=*Opuntia australis*) and *Pterocactus hickenii* (=*Opuntia skottsbergii*) from Lago Buenos Aires (Rio Fenix). A recent report (Kiesling 2002) for *Pterocactus hickenii* on the Chilean side at 46°30′S (Chile Chico) confirms the early observations from Skottsberg (1916). That means that the known southern limit for the family in Chile is at the Lago General Carrera (46°30′S). At the limit with Argentina (ca 50°23′S) most probably *Austrocactus patagonicus* can be found (Hoffmann and Walter 2004).

Fig. 7.2 Distribution of Chilean Cactaceae: **a** collection localities from SGO; **b** species richness map



A dubious report of a southernmost occurrence of *Maihuenia poeppigii* at Torres del Paine National Park, some 1,400 km south of its distribution, has been rejected by Leuenberger (2008). That means that aside from the few localities in the Patagonian steppe at the boundary with Argentina, the Chilean regions Araucanía, Los Lagos, Aisén and Magallanes, encompassing the area from 38° to 56°S, have just a few species according to the Southern Cone Checklist (Zuloaga et al. 2008), and no collections at all in the National Herbarium SGO (Fig. 7.2a).

7.2.2 *Areas of Endemism*

The species richness core that appears at the coast between 25 and 31°S (encompassing 11–20 species) can be superficially interpreted as an area of endemism. This can be tested by means of specific methods: PAE and the optimality method (see also Sect. 4.3).

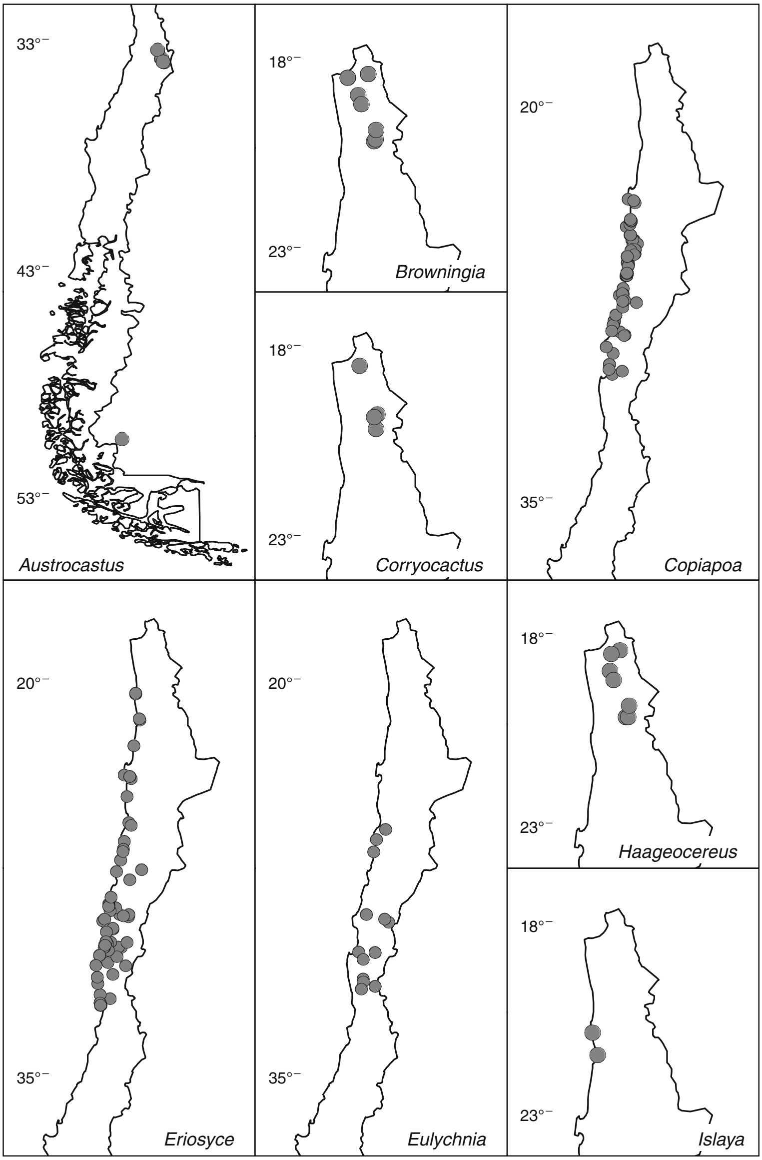


Fig. 7.3 Collection localities of the genera of the Cactoideae

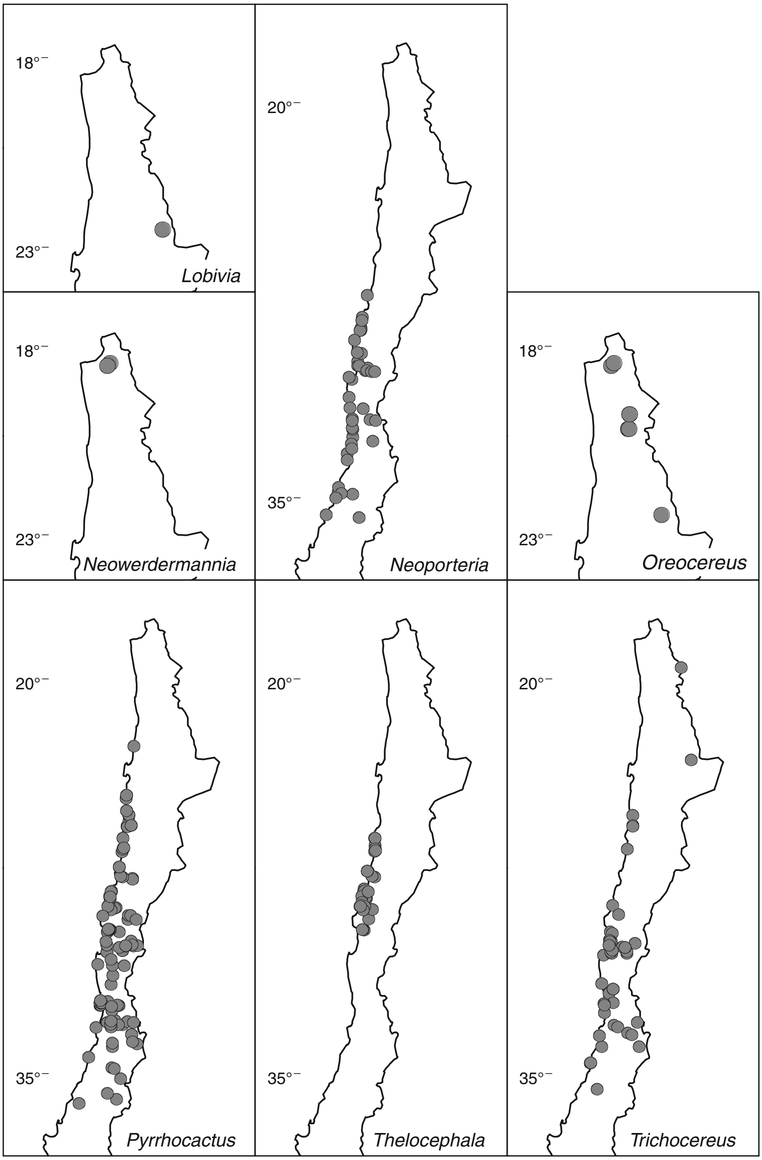


Fig. 7.3 (continued)

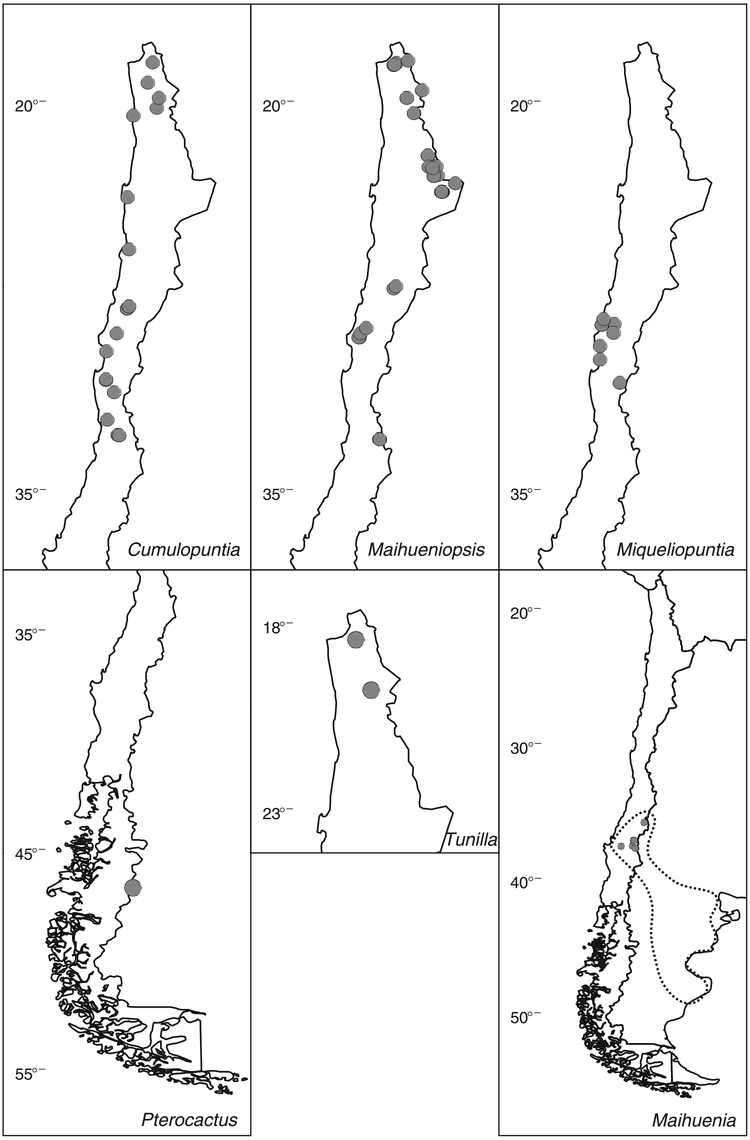


Fig. 7.4 Collection localities of the genera of the Opuntioideae and Maihuenioideae (*Maihuenia*)

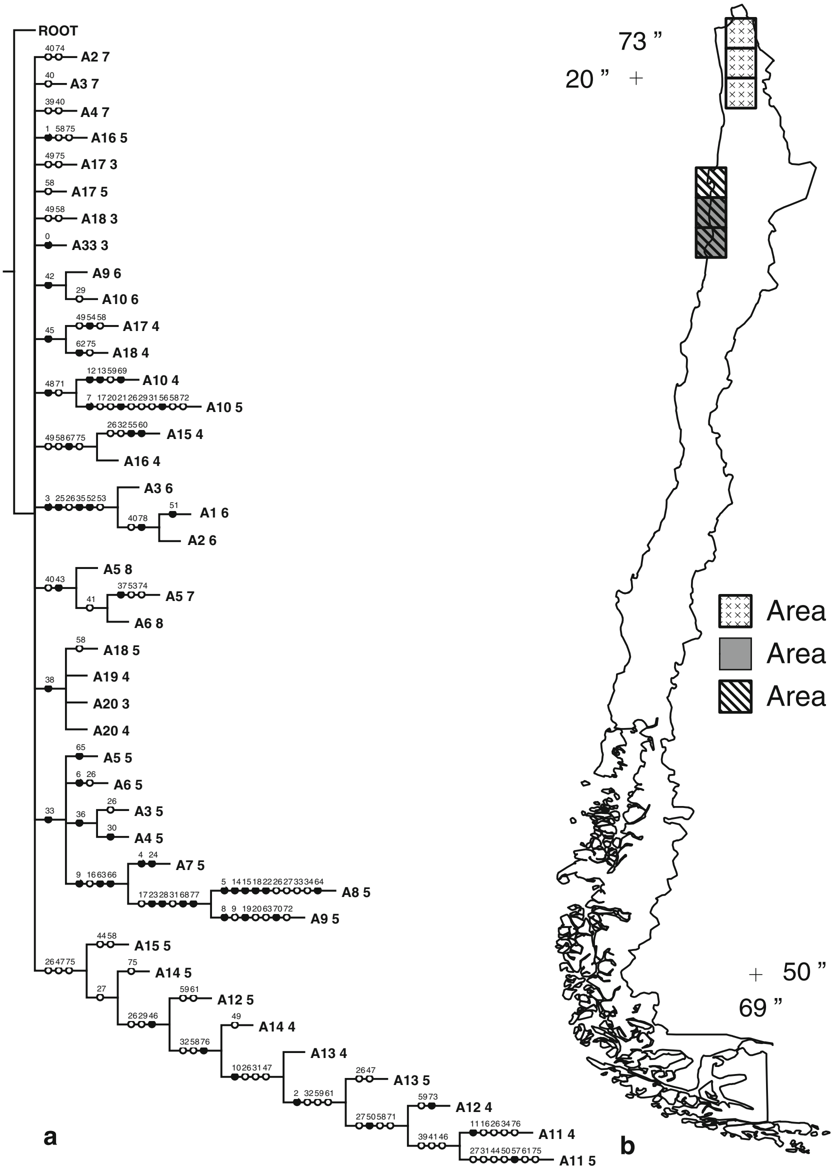


Fig. 7.5 Results from PAE: **a** matrix obtained with Winclada; **b** map of terminals (quadrats) representing areas of endemism

7.2.2.1 PAE

Parsimony Analysis of Endemicity (PAE) was applied by means of a matrix with 42 quadrats and the 79 species, in Winclada. 92 trees were obtained, with 137 steps and CI = 57 (consistence index) and RI = 61 (retention index). The strict consensus cladogram had 146 steps, CI = 54 and RI = 55. This cladogram (Fig. 7.5a) showed an initial politomy and 56 geographic synapomorphies, but only 11 were used to identify areas of endemism because they defined clades based on the presence of two or more geographic synapomorphies. Three areas of endemism were found, two of them with a nested pattern. The first area (Fig. 7.5b) includes three quadrats between 18°–21°S and 69°–70°W, including four endemic species. The second area (Fig. 7.5b) is nested in another wider area; it includes four endemic species, comprises two quadrats at 24°–26°S and 70°–71°W. The third area (Fig. 7.5b) includes the previous area plus another quadrat at 23°–26°S and 70°–71°W, and added three endemic species (for the species list, see Table 7.2).

7.2.2.2 NDM/VNDM

The optimality method was performed with NDM/VNDM v. 2.6 (Goloboff 2005). The georeferenced database of Chilean species of Cactaceae from the National Herbarium SGO consists of 514 records of 79 species, including 473 unique localities. Each locality was superposed to a grid of 1 × 1 degrees. The program was run saving sets with two or more species, and with scores above 2.0; settings were the same as for the analysis of endemic genera (Sect. 4.3). The search was performed until the number of sets was shown stable in 25 repetitions with different random seeds, using edge proportions. Eleven areas of endemism were obtained, and 33 species were endemic to some area. A consensus was applied to the sets, with 40% of similarity in species and the option against any of the other areas in the consensus. The program yielded four consensus areas; some of them overlapping. The endemic species of each consensus are shown in Table 7.2. Consensus area 0 is retrieved from just 1 set, and showed five endemic species and a score of 5.08. It includes three quadrats at 18°–21°S latitude and 69°–70°W longitude. Consensus area 1 was obtained from five sets, including 12 endemic species and a score of 5.23 (although two species have a score below 0.5); including 11 quadrats at 27°–33°S and 70°–72°W. Consensus area 2 was built by four sets, had 14 endemic species and a score of 6.83. It includes seven quadrats at 24°–29°S and 70°–72°W. Consensus area 3 encompassed one set, including three endemic species and a score of 2.52. It includes nine quadrats at 18°–24°S and 67°–70°W (Fig. 7.6).

Both programs usually yield different results (see discussion in Sect. 4.3). PAE tends to retrieve less areas of endemism than NDM. This last program identified 11 areas of endemism, and therefore consensus had to be applied to the results. Even the consensuses can retrieve overlapped areas, as was the case. The areas of endemism identified by PAE are partially overlapped and mostly nested in the ones from NDM. Area 0 from NDM is identical to Area a from PAE, supported by 4 species (e.g. *Browningia candelaris*) (Table 7.2). This Area 0 is nested in Area

Table 7.2 Areas of endemism and their supporting species (for NDM and PAE)

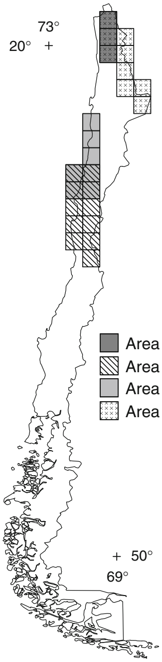


Fig. 7.6 Result from NDM/VNDM

Consensus NDM		Area PAE		
N° area	Species	a	b	c
0	*Browningia candelaris*	X		
	Corryocactus brevistylus	X		
	Haageocereus fascicularis	X		
	Oreocereus hempelianus	X		
	Tunilla soehrensii			
1	*Thelocephala napina*			
	Miqueliopuntia miquelii			
	Copiapoa coquimbana			
	Maihueniopsis ovata			
	Neoporteria clavata			
	Neoporteria nidus			
	Neoporteria villosa			
	Pyrrhocactus eriosyzoides			
	Pyrrhocactus heinrichianus			
	Trichocereus coquimbanus			
2	*Copiapoa serpentisulcata*		X	X
	Eriosyce rodentiophila		X	X
	Thelocephala esmeraldana		X	X
	Trichocereus deserticola		X	X
	Thelocephala napina			
	Copiapoa cinerea			X
	Pyrrhocactus paucicostatus			X
	Pyrrhocactus taltalensis			X
	Copiapoa humilis			
	Copiapoa hypogaea			
	Copiapoa marginata			
	Eulychnia saint-pieana			
	Neoporteria sociabilis			
	Thelocephala odieri			
3	*Maihueniopsis boliviana*			
	Oreocereus leucotrichus			
	Trichocereus atacamensis			

3 that encompasses a wide area of the Chilean Altiplano. The gap that appears in the core of the Atacama is obvious since it has the overall lowest presence of plant taxa (Fig. 7.2b). At the coast south of the Atacama, both programs retrieve areas of endemism: areas b and c from PAE are, excepting one quadrat, nested in NDM's Area 2, due to the presence of e.g. *Eriosyce rodentiophila* and *Thelocephala esmeraldana* (Table 7.2 and Fig. 7.6). NDM's Area 2 much more extends to the South, and partially overlaps with Area 1 that reaches 33°S. Remarkably, Areas 2 and 1 retrieved by NDM, are almost perfectly coincident with Area 2 retrieved by the analysis of the endemic genera (Sect. 4.3). Certainly in the regionalization by

endemic genera (Fig. 4.9) the Cactaceae genera play an important role, and this is corroborated here at the species level.

As discussed for the analysis of endemic genera (Sect. 4.3), these analyses are still at the level of exercises, since they are much dependant on the strength of the database, the grid size and the geographical origin of the grid, and the settings of the programs. Also the observation that the areas of endemism do not show sharp limits and tend to overlap (independent of the programs' settings) is as valid for the endemic genera as for the Cactaceae species.

7.3 Notes on Cacti Conservation

Areas of special interest for cactus conservation are highlighted by the richness and endemism maps (Figs. 7.2, 7.5, and 7.6). The interest that these species gain from private collectors from all over the world put many of the species at conservation risk. At least four species are classified in the red lists (Chap. 6) as "highly endangered" in the regions Atacama and Coquimbo (26º–32ºS) (*Eriosyce rodentiophila, Maihueniopsis domeykoensis, Pyrrhocactus eriosyzoides, Eulychnia breviflora*), and 18 more species are classified as "vulnerable". Another 29 species are considered "not sufficiently known", mostly due to the lack of precise knowledge about their distribution. Among these are taxa of special interest for improving collection efforts and population level studies (e.g. Pinto and Moscoso 2004), to shorten the so-called Wallacean shortfall (Box 6.2). In the extreme north, cacti populations are much more affected due to human activities, especially mining and the extraction for urban gardening in the city of Iquique (Pinto and Kirberg 2009). Coastal populations at this latitude (18º–21ºS) appear much damaged through long drought periods (Fig. 7.7), but whether this is a cyclical situation related to El Niño (Box 7.1) or the sign of a long term desiccation is still a matter of discussion (Schulz 2009; Pinto and Luebert 2009).

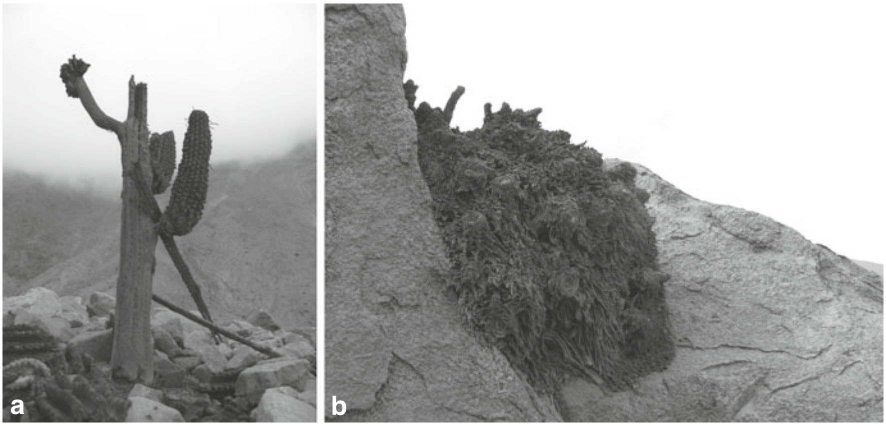


Fig. 7.7 **a** Dead cactus exemplar of *Eulychnia iquiquensis* at the coast of Tocopilla (22ºS); **b** dry exemplar of *Puya boliviensis* at the same locality (see Pinto and Kirberg (2009))

Box 7.1 Rise and Bloom of the Atacama Desert

Coastal deserts occur in western North- and South America at tropical and extratropical latitudes, related to the atmospheric circulation (high pressure belts), and the oceanic circulation (Richter 2001). Along the west coasts, the oceanic upwelling generates a cool, stable coastal atmosphere, forming coastal fog deserts like the Atacama, one of the driest ecosystems on earth (Ezcurra 2006). Nevertheless, the exact time at which the climate in the Atacama Desert became hyperarid is a topic of much debate with ages ranging from 25 mya (Dunai et al. 2005), 14 mya (Alpers and Brimhall 1988) to 3 mya (Hartley and Chong 2002) (see Box 3.1).

Hartley et al. (2005) proposed that the sedimentary succession in the Atacama Desert records deposition under an arid to semiarid climate from the Late Jurassic (150 mya) to the present day. Prior to this, at the Middle Jurassic, conifers, Bennettitales, ferns and sphenopsids dominated the landscape (Herbst and Troncoso 1996) (Sect. 1.2).

These results are in agreement with results presented by Evenstar et al. (2005) on erosional and depositional surfaces analysed via remote sensing, and are corroborated by Clarke (2006), who proposed that “the Atacama Desert is almost certainly the oldest continuously arid region on Earth”. This is in agreement with the geomorphologic/biogeographic analysis done by Ochsenius (1999) who proposed the Atacama as being one of several Triassic-Jurassic palaeodeserts, prior to the break-up of Gondwana. Ochsenius (1999) could further identify Mesozoic relict floras of the intra-Andean valleys from Venezuela to Ecuador, which he described as an Interandean arid track. Several tracks that connected the xeric natural areas of South America have been also highlighted by Roig-Juñent et al. (2003, 2006).

Although the Atacama Desert has existed for at least 90 mya, the initial onset of hyper-aridity was most likely to have developed progressively with the uplift of the Andes as they reached elevations between 1,000 and 2,000 m asl (see Box 1.5). The coupling with the intensification of the cold upwelling current is dated by these authors at 15–10 mya (Middle Miocene). According to Alpers and Brimhall (1988), the Middle Miocene climatic desiccation of the Atacama is related to an increase in upwelling intensity as the Antarctic ice cap became established at approximately 15–13 mya, generating a decrease in temperature of coastal waters supplied by the ancestral Humboldt Current. According to Hartley et al. (2005): “Rapid and extreme climatic fluctuations during the Plio-Pleistocene were not sufficient to destabilize the climate within the Atacama”.

Nevertheless, there is appealing evidence towards Atacamas’s increasing aridity in the Late Pliocene, related to a phase of global cooling, the rain-shadow effects of the growing Andean Cordillera (Box 1.5), and the upwelling of the cold Humboldt Current (Hartley and Chong 2002). Hay et al. (2002) further propose that the global climate system suffered a major change with the advent and spread of C_4 plants during the Late Miocene. The authors called this a “climate change paradox”: these plants radically altered the hydrologic cycle, changed atmospheric heat transport mechanisms, and restructured weathering and erosion processes (Hay et al. 2002).

Climate oscillations occurred in the Pleistocene-Holocene of the Atacama (Latorre et al. 2002, 2003; Maldonado et al. 2005) (Box 3.1). However, it appears unlikely that they would have caused a major shift from arid conditions, except locally through supply of both surface and groundwater (Clarke 2006).

Today, the scanty vegetation of the coastal Atacama is highly related to the humidity available from fog, also known as “camanchaca” (Cereceda et al. 2008) (Fig. 7.8).

Fig. 7.8 Coastal fog supporting the sparse vegetation at Paposo (25ºS) (photo by A. Moreira-Muñoz)

Humidity is highly restricted to the western slope of the coastal cordillera, and rarely reaches the interior (Fig. 7.8). Nevertheless, in exceptional years, the southern Atacama margin around 24° and 30°S suffers a drastic transformation from the almost complete arid bareness to a full-color landscape, known as desierto florido “blooming desert” (Muñoz-Schick 1991) (Fig. 7.9). This highly attractive phenomenon is strictly related to short and intense rainfalls that reach these latitudes from the south every 5–7 years. This is related to the ENSO phenomenon (El Niño Southern Oscillation). El Niño effects are recorded since 1525 (Ortlieb 1994), with a geological and archaeological evidence of its existence of more than 5,000 years (Dillon 1998; Caviedes 2001). Its impact on the intertropical Pacific coast is related to the generation of exceptional rainfall on the coast of Peru and Chile. In this century the most intense of these events were recorded in 1925–1926, 1982–1983, and 1997–1998 (Dillon and Rundel 1990; Arntz and Fahrbach 1996; Dillon 1998).

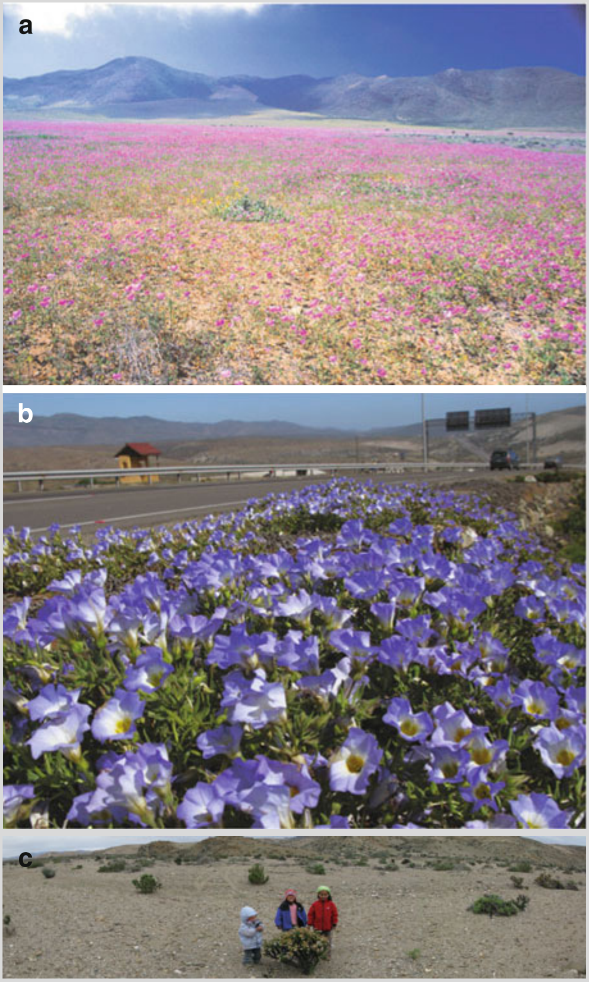


Fig. 7.9 Flowering desert: **a** *Cristaria cyanea* fields, Carrizal Bajo; **b** *Nolana paradoxa* fields, La Serena; **c** expecting the next flowering desert at Llanos de Challe (photo credits: **a**, **b**, **c** A. Moreira-Muñoz)

Remarkably, El Niño-Southern Oscillation (ENSO) related rainfall anomalies in north central Chile seem to be opposite to ENSO-related anomalies in fog-frequency at 30°30′S (Garreaud et al. 2008). El Niño years are associated with less foggy conditions at Fray Jorge forest (see Box 3.1), and La Niña[1] years produce temperature anomalies associated with higher springtime fog frequency. This seems to be very variable along the coast, since the huge coastal blooming in the period 1997–1998 at 21°S (Iquique) was indeed related to the increasing water content of the fog (Muñoz-Schick et al. 2001). Recent results from tree ring analysis of the high Andes (*Polylepis tarapacana* growing at 16°–23°S, between 4,000 and 5,200 m asl) show a high correlation to ENSO, not necessarily to precipitation increase but to a rise in temperature. This suggests nevertheless that the consequences of the phenomenon reach much further than the coastal environments (Christie et al. 2009). Relationships between ENSO and phenomena of smaller amplitude and the low-frequency variability related to the Pacific Decadal Oscillation (PDO) and the Antarctic Oscillation (AAO) are receiving much interest (Garreaud et al. 2008). Moreover, the changes associated with ENSO events have shown important implications for the research in geosciences, especially on agroecosystems, ecosystem restoration, and biodiversity conservation (Holmgren et al. 2006).

The increasing aridity of the Atacama Desert, associated with the Andes uplift (Boxes 1.5 and 3.1), seems to have had important effects on the evolution of the Chilean flora, promoting a rapid evolution in several groups (Stebbins 1952; Solbrig 1976). This seems to be for example the case of *Heliotropium* sect. *Cochranea*. Luebert and Wen (2008) found that isolation episodes may be the reason for the morphological, ecological and geographical differentiation among this group. The uplift of the Andes may have isolated section *Cochranea* on the western side from other lineages of the South American *Heliotropium* on the eastern side of the Andes, promoting vicariant speciation (Luebert and Wen 2008). According to these authors, the gradual isolation of the individual species due to climatic fluctuations may have been helped by geomorphologic events such as mass landslides. A similar situation could have been responsible for the diversification in *Malesherbia* (Gengler-Nowak 2002) and in several Asteraceae genera like *Polyachyrus* and *Chuquiraga* (see Chap. 8).

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[1] For the counter cycle of El Niño, a better denomination would be “El Viejo”, since “La Niña” is a meaningless term in relationship with the origin of the concept associated to the occurrence of warm waters towards Christmas (M. Dillon, pers. comm.)

7.4 Biogeographic Insights: Spatial and Temporal Origins

In spite of the conceptual difficulties in the search for centres of origin (Sect. 3.3), the center of origin for the Cactaceae has been a constant question for researchers. Backeberg (1942) proposed that the evolutionary origin of the cacti was in Central America, with subsequent migrations north and south. Buxbaum (1969) cited both the Caribbean and central South America as likely areas of origination, due to the presence of *Pereskia* and of opuntioid and cactoid lineages that he considered "ancestral".

Wallace and Gibson (2002) hypothesized a central Andean origin for the family. They assumed that Andean *Pereskia*, certain Opuntioideae, and the cactoid *Calymmanthium* are basal cactus lineages, and all reside in Peru, Bolivia, and northern Argentina.

Leuenberger (1986), in his monograph about *Pereskia*, concluded that northwestern South America was a more likely center of origin, proposing a Late Cretaceous origin of the group. Some recent studies (Hershkovitz and Zimmer 1997; Nyffeler 2002; Edwards et al. 2005), suggest that the cacti can't be that old because the sequence divergence between major clades is limited. Edwards et al. (2005) assert that both Opuntioideae and Cactoideae originated in the central Andean region of Peru, Bolivia, and northern Argentina. They refer to the Andean orogeny as the cause of diversification for many plant lineages. Early uplift in the central Andean region (25–20 mya) is hypothesized to have occurred under a fluctuating arid/semi-arid climate regime (Chap. 2), which presents a likely scenario for early cactus diversification. Edwards et al. (2005) further suggest that the placement of Cacteae (an exclusively North American lineage with its center of diversity in Mexico) among the earliest diverging lineages of Cactoideae, implies relatively early movements out of South America across the continent.

Centering the origin far away from Africa might explain the poor representation of cacti in that continent. In fact, all major lineages of the cacti, i.e. Pereskioideae, Maihuenioideae, Opuntioideae, and Cactoideae, occur mostly or exclusively in South America. Furthermore, the closest relatives of the cacti from the "portulacaceous cohort" (Applequist and Wallace 2001) have their highest diversity on continents of the former Gondwana (Hershkovitz and Zimmer 1997). This is generally taken as evidence that the family Cactaceae originated in South America (e.g. Buxbaum 1969). Hence, various groups of *Pereskia*, Opuntioideae, and Cactoideae supposedly dispersed into Central and North America from their postulated northwestern South American center of origin (Leuenberger 1986). The presence of a *Rhipsalis* species in tropical Africa, Madagascar, and Sri Lanka led some authors to propose that this distribution indicates an old vicariance between South America and Africa (e.g. Backeberg 1942) or even an origin of the cacti in the Old World (Croizat 1952). This would imply that the cacti originated before the split of the southern continents during the late Cretaceous and that all other cacti that might have naturally occurred in Africa went extinct. More recently, however, this distribution pattern of *Rhipsalis baccifera*, which is characterized by having very sticky seeds, has been explained as the result of relatively recent long-distance dispersal by birds (Barthlott

1983; Gibson and Nobel 1986; Barthlott and Hunt 1993). This vision is not lacking controversy: "I consider the bird-dispersal scenario to be as dead in the water as any rain forest bird that tries to fly the Atlantic. This really leaves only the vicariance explanation as a viable option… Another question must be asked: Why, of all the cacti that have juicy fruits (and are therefore potentially attractive to birds) should it be *Rhipsalis* that has this wide distribution?" (Maxwell 1998).

Since cacti are not well suited for the fossilization process, the fossil record of the family is very sparse: only several reports related to microfossils exists for the South American Cactaceae. Mautino (2002) reported two types of Miocene pollen grains from Tucumán, northern Argentina. According to Barreda et al. (2007), Cactaceae was one of the important groups that supports the early-Middle Miocene Neotropical province in the actual Chaco Domain, together with the Apocynaceae, Aquifoliaceae, Fabaceae, Sapotaceae, Moraceae, Anacardiaceae, Ulmaceae, Arecaceae, Amaranthaceae (Chap. 1).

In spite the general consensus favouring a spatial origin of cacti in northern South America (Nyffeler 2002), there is still disagreement about the time of the cacti origin. A Late Cretaceous origin between 65 and 90 mya, relatedto the breakup of western Gondwana, has been proposed by Gibson and Nobel (1986) and Mauseth (1990). More recently, on the base of molecular data that show small amount of sequence divergence, a much more recent origin of cacti in the Late Palaeogene (30 mya) has been proposed (Hershkovitz and Zimmer 1997; Nyffeler 2002).

Edwards et al. (2005) still suggest a basal split in Cactaceae in a northern clade comprising *Pereskia* species and a southern clade comprising also *Pereskia* species and *Maihuenia* and other Cactoideae and Opuntioideae. Edwards et al. (2005) recognize that their sampling and resolution within Opuntioideae are insufficient to make inferences about the geographic distribution of its basal members, and recognize recent results that placed its earliest diverging lineages in Chile and Argentina (Griffith 2004a).

7.5 Cactus Postmodern Evolution

For resolving the question about the geographical origin (if there is something like that at all) and the time of origin of the family, we have to obtain a good picture about the phylogeny of the family, including its closest relatives and the morphological characteristics of the proto-cactus or the "first" cactus (i.e. "what did the first cactus look like?", Griffith 2004a).

Phylogenetic cladograms presented by Butterworth and Edwards (2008) still support the hypothesis of *Pereskia* representing the earliest members of the cacti. But the authors recognize that accurate character reconstruction is still challenging.

Regarding the closest family, there has been a long standing view that the Aizoaceae was the sister family to the cacti, but this was proved erroneous. Studies of molecular data and vascular anatomy suggest that the closest relatives to the cacti are the genera *Portulaca, Talinum*, and *Anacampseros* from the Portulacaceae

(Hershkovitz and Zimmer 1997; Applequist and Wallace 2001). Another possible closely related family is the Didiereaceae. Extant Portulacaceae occur in South Africa, Kerguelen Island and New Zealand. Didiereaceae occur on Madagascar. The three families show therefore an old Gondwanic relationship.

As expressed by Gorelick 2008: "Good phylogenies matter. If *Ceraria* and *Portulacaria* are most closely related to traditional Didiereaceae than to Portulacaceae, as appears to be the case (Nyffeler et al. 2008), we may make erroneous inferences about the evolution of succulence in cacti and related families. This philosophical approach is not without problems, because it is often difficult to discern which characters are basal and which are derived, much as it is difficult to distinguish homology from analogy in evolution" (Gorelick 2008).

The difficulties in discerning the appropriate interpretation of characters are better expressed by P. Griffith in two challenging papers. In Griffith's vision (2004b), the classical interpretation of cactus evolution is still influenced by the cultural context of the 1500s, when the exotic members of the family were first seen in Europe. "The striking, but culturally determined, exoticness of the Cactaceae still impacts our concept of what is relictual and derived for the family" (Griffith 2004b). The traditional view, codified in the early twentieth century by Britton and Rose, proposed that leafy cacti are primitive or relictual; on the contrary, stem-succulent cacti seem to be derived. Britton and Rose (1919) proposed the genus *Pereskia*, due to its similarity to other woody flowering plants, the nearest cactus relative to the other families. The most derived are the Cactoideae, exemplified by leafless plants like *Trichocereus*. The *Pereskia*-primitive idea has been so influential that "recent authors have sometimes misinterpreted new data to be consistent with Britton and Rose, even when the data are more readily interpreted as contradictory" (Griffith 2004a). That means that the evolutionary interpretations are bounded to the contextual bias, i.e. the horticultural landscape from traditional botanical gardens and colleges (see also the political aspects of *Pereskia* taxonomy discussed by Leuenberger 2008, p 58). Griffith challenges current evolutionary interpretations proposing that the nearest relatives of Cactaceae were not broad-leaved dicots superficially similar to *Pereskia*; rather, Cactaceae likely evolved from diminutive, often geophytic Portulacaceae; and the southern South American *Maihuenia*, with its terete, succulent leaves and cushion habit form a deep, subfamilial lineage (Wallace 1995; Griffith 2004b).

As recently summarised by Griffith (2008), there are currently three crucial lines of discussion: (a) the phylogenetic position of *Pereskia*; (b) the nature of the outgroups; (c) the character evolution implied by each: "If *Pereskia* represent transitional forms, what do they transition between?" (Griffith 2008, p 37).

The two deepest lineages in Opuntioideae include most species of *Maihueniopsis* and all *Pterocactus,* and are characterized by diminutive, succulents, often of geophytic habit, and leafless at maturity (Griffith and Porter 2009). The authors suggest that Opuntioideae have originated in west-central South America.

As for other plant groups, the spatial split between several clades was most probably caused by the Andean uplift and the formation of intracontinental marine basins during the Cenozoic (Ritz et al. 2007).

In spite of the efforts done by cacti experts and the advent of molecular data, and due to the persisting lack of macrofossils and the difficulties in character interpretation, early cactus evolution remains still an important unanswered question. Will the future offer a fossil encounter of an early cactus outside America, as it was the case for the first Old World hummingbird fossils recently discovered in European Oligocene deposits? (Mayr 2004; Louchart et al. 2008).

References

Alpers C, Brimhall GH (1988) Middle Miocene climatic change in the Atacama Desert, northern Chile: evidence from supergene mineralization at La Escondida. Geol Soc Am 100:1640–1656

Anderson EF (2001) The cactus family. Timber Press, Portland, OR

Applequist WL, Wallace RS (2001) Phylogeny of the portulacaceous cohort based on ndhF sequence data. Syst Bot 26:406–419

Arntz WE, Fahrbach E (1996) El Niño. Experimento climático de la naturaleza. Causas físicas y efectos biológicos. Traducción de C Wosnitza-Mendo y J Mendo. Fondo de Cultura Económica, México

Backeberg C (1942) Cactaceae; Jahrbücher der DKG., Teil 2, Juni 1942: 55, Cactaceae Lindley; Systematische Übersicht (Neubearbeitung) mit Beschreibungsschlüssel

Barreda VD, Anzótegui LA, Prieto AR, Aceñolaza PG et al. (2007) Diversificación y cambios de las angiospermas durante el Neógeno en Argentina. In: Archangelsky S, Sánchez T, Tonni EP (eds) Ameghiniana 50° aniversario, Publicación Especial 11: 173–191

Barthlott W (1983) Biogeography and evolution in neo- and paleotropical Rhipsalinae (Cactaceae) – Sonderb. Naturwiss Verl Hamburg 7:241–248

Barthlott W (2001) Preface. In: Anderson EF, (ed) The cactus family. Timber Press, Portland, OR

Barthlott W, Hunt DR (1993) Cactaceae. In: Kubitzki K, Rohwer JG, Bittrich V, (eds) The families and genera of vascular plants, Vol 2. Flowering plants: Dicotyledons: Magnoliid, Hamamelid and Caryophyllid families. Springer, Berlin, Heidelberg, pp. 161–197

Britton NL, Rose JN (1919–1923) The Cactaceae, 4 vols. Carnegie Inst., New York, NY

Butterworth Ch, Edwards EJ (2008) Investigating Pereskia and the earliest divergences in Cactaceae. Haseltonia 14:46–53

Buxbaum F (1969) Die entwicklungswege der Kakteen in Sudamerika. In: Fittkau EJ, Illies J, Klinge H, et al. (eds) Biogeography and ecology in South America. W. Junk, The Hague, pp 583–623

Caviedes C (2001) El Niño in history: storming through the ages. University Press of Florida, Gainesville, FL

Cereceda P, Larrain H, Osses P, Farías M, Egaña I (2008) The spatial and temporal variability of fog and its relation to fog oases in the Atacama Desert, Chile. Atmos Res 87:312–323

Christie DA, Lara A, Barichivich J, Villalba R, Morales MS, Cuq E (2009) El Niño-Southern Oscillation signal in the world's highest-elevation tree-ring chronologies from the Altiplano, Central Andes. Palaeogeogr Palaeoclimatol Palaeoecol. doi:10.1016/j.palaeo.2007.11.013

Clarke JDA (2006) Antiquity of aridity in the Chilean Atacama Desert. Geomorphology 73: 101–114

Croizat L (1952) Manual of phytogeography, or an account of plant dispersal throughout the world. Junk, The Hague

Dillon MO (1998) Chasing the 1997/1998 El Niño across Peru. Field Museums Memb Publ 69:2–4

Dillon MO, Rundel PW (1990) The botanical response of the Atacama and Peruvian desert floras to the 1982–83 El Niño event. In: Glynn PW, (ed) Global ecological consequences of the 1982–83 El Niño-Southern Oscillation. Elsevier Oceanography Series 52. Elsevier, Amsterdam, pp 487–504

Dunai TJ, González López GA, Juez-Larré J (2005) Oligocene–Miocene age of aridity in the Atacama Desert revealed by exposure dating of erosion-sensitive landforms. Geology 33:321–324

Edwards EJ, Nyffeler R, Donoghue MJ (2005) Basal cactus phylogeny: implications of Pereskia (Cactaceae) paraphyly for the transition to the cactus life form. Am J Bot 92:1177–1188

Evenstar L, Hartley A, Rice C, Stuart F, Mather A, Chong G (2005) Miocene-Pliocene climate change in the Peru-Chile Desert. 6th international symposium on Andean geodynamics (ISAG 2005, Barcelona), extended abstracts, pp 258–260

Ezcurra E, (ed) (2006) Global deserts outlook. United Nations Environment Programme (UNEP), Nairobi

Garreaud RD, Barichivich J, Christie DA, Maldonado A (2008) Interannual variability of the coastal fog at Fray Jorge relict forests in semiarid Chile. J Geophys Res 113:G04011. doi: 10.1029/2008JG000709

Gengler-Nowak KM (2002) Reconstruction of the biogeographical history of Malesherbiaceae. Bot Rev 68:171–188

Gibson AC, Nobel PS (1986) The cactus primer. Harvard University Press, Cambridge, MA

Goloboff P (2005) NDM/VNDM ver. 2.6. Programs for identification of areas of endemism. http://www.zmuc.dk/public/phylogeny/endemism

Gorelick R (2008) Early cactus evolution. Haseltonia 14:3–5

Griffith MP (2004a) What did the first cactus look like? An attempt to reconcile the morphological and molecular evidence. Taxon 53:493–499

Griffith MP (2004b) Early cactus evolution: the postmodern view. Haseltonia 10:3–11

Griffith MP (2008) Pereskia, Portulacaceae, photosynthesis, and phylogenies: implications for early Cactaceae. Haseltonia 14:37–45

Griffith MP, Porter JM (2009) Phylogeny of Opuntioideae (Cactaceae). Int J Plant Sci 170:107–116

Hartley AJ, Chong G (2002) A late Pliocene age for the Atacama Desert: implications for the desertification of western South America. Geology 30:43–46

Hartley AJ, Chong G, Houston J, Mather AE (2005) 150 million years of climatic stability: evidence from the Atacama Desert, northern Chile. J Geol Soc 162:421–424

Hay WW, Soeding E, DeConto RM, Wold CN (2002) The Late Cenozoic uplift – climate change paradox. Int J Earth Sci 91:746–774

Herbst R, Troncoso A (1996) La tafoflora de Juan de Morales del Jurásico Medio (Formación Chacarilla), Región de Tarapacá, Chile. Rev Geol Chile 23:3–15

Hershkovitz MA, Zimmer EA (1997) On the evolutionary origins of the cacti. Taxon 46:217–232

Hoffmann AE, Walter HE (2004) Cactáceas en la flora silvestre de Chile, 2nd edn. Ed. Fundación Claudio Gay, Santiago

Holmgren M, Stapp P, Dickman CR, Gracia C, Graham S, Gutiérrez JR, Hice C, Jaksic F, Kelt DA et al. (2006) A synthesis of ENSO effects on drylands in Australia, North America and South America. Adv Geosci 6:69–72

Kiesling R (2002) *Pterocactus* (Cactaceae), new record for the Chilean flora. Gayana Bot 59:61–63

Kraus R (1995) The environmental conditions of Cactaceae in Chile. Haseltonia 3:110–129

Latorre C, Betancourt JL, Rylander K, Quade J (2002) Vegetation invasions into absolute desert; a 45 000 yr rodent midden record from the Calama–Salar de Atacama basins, northern Chile (lat 22°–24°S). Geol Soc Am Bull 114:349–366

Latorre C, Betancourt JL, Rylander K, Quade J, Matthei O (2003) A vegetational history from the arid prepuna of northern Chile (22°–23°S) over the last 13,500 years. Paleogeogr Paleoclimatol Paleoecol 194:223–236

Lembcke H, Weisser PJ (1979) The distribution of the genera of Chilean Cactaceae. Aloe 17:9–26

Leuenberger BE (1986) *Pereskia* (Cactaceae). Mem NY Bot Gard 41:1–141

Leuenberger BE (1997) *Maihuenia*—monograph of a Patagonian genus of Cactaceae. Bot Jahrb 119:1–92

Leuenberger BE (2008) *Pereskia, Maihuenia*, and *Blossfeldia*—taxonomic history, updates, and notes. Haseltonia 14:54–93

Louchart A, Tourment N, Carrier J, Roux T, Mourer-Chauviré C (2008) Hummingbird with modern feathering: an exceptionally well-preserved Oligocene fossil from southern France. Naturwissenschaften 95:171–175

Luebert F, Wen J (2008) Phylogenetic analysis and evolutionary diversification of *Heliotropium* sect. *Cochranea* (Heliotropiaceae) in the Atacama Desert. Syst Bot 33:390–402

Maldonado A, Betancourt JL, Latorre C, Villagrán C (2005) Pollen analyses from a 50 000-yr rodent midden series in the southern Atacama Desert (25 degrees 30′S). J Quat Sci 20:493–507

Marticorena C (1990) Contribución a la estadística de la flora vascular de Chile. Gayana Bot 47: 85–113

Mauseth JD (1990) Continental drift, climate and the evolution of cacti. Cact Succ J 62:302–308

Mauseth JD, Kiesling R, Ostolaza C (2002) A Cactus Odyssey: journal in the wilds of Bolivia, Peru, and Argentina. Timber Press, Oregon

Mautino LR (2002) Cactaceae en la Formación San José (Mioceno Medio), Tucumán, Argentina. 8º Congreso Argentino de Paleontologia y Bioestratigrafía, Resúmenes: p. 26

Maxwell R (1998) The *Rhipsalis* Riddle – or the day the cacti came down from the trees. http://rhipsalis.com/maxwell.htm (originally appeared in the New Zealand Cactus and Succulent Journal)

Mayr G (2004) Old world fossil record of modern-type hummingbirds. Science 304:861–864

Muñoz-Schick M (1991) Flores del Norte Chico, 2nd edn. Dirección de Archivos, Bibliotecas y Museos, Santiago

Muñoz-Schick M, Pinto R, Mesa A, Moreira-Muñoz A (2001) Oasis de neblina en los cerros costeros del sur de Iquique, región de Tarapacá, Chile, durante el evento El Niño 1997–1998. Rev Chil Hist Nat 74:389–405

Nyffeler R (2002) Phylogenetic relationships in the cactus family (Cactaceae) based on evidence from trnK/matK and trnL-trnF sequences. Am J Bot 89:312–326

Nyffeler R, Eggli U, Ogburn M, Edwards EJ (2008) Variations on a theme: repeated evolution of succulent life forms in the Portulacineae (Caryophyllales). Haseltonia 14:26–36

Ochsenius C (1999) The neotropical aridity. CCOS PCSS Geowissenschaftliche Beiträge, Baden-Württemberg

Ortlieb L (1994) Las mayores precipitaciones históricas en Chile Central y la cronología de eventos ENOS en los siglos XVI–XIX. Rev Chil Hist Nat 67:463–485

Pinto R (2002) *Lobivia ferox* Britton et Rose (Cactaceae): new record for the Chilean flora. Gayana Bot 59:65–72

Pinto R (2003) *Maihueniopsis nigrispina* (Cactaceae, Opuntioideae): nuevo registro para la flora chilena. Chloris Chilensis 6. http://www.chlorischile.cl

Pinto R, Moscoso D (2004) Estudio poblacional de *Echinopsis atacamensis* (Cactaceae) en la Región de Tarapacá (I), norte de Chile. Chloris Chilensis 2. http://www.chlorischile.cl

Pinto R, Kirberg A (2009) Cactus del Extremo Norte de Chile. AMF, Santiago

Pinto R, Luebert F (2009) Datos sobre la flora vascular del desierto costero de Arica y Tarapacá, Chile, y sus relaciones fitogeográficas con el Sur de Perú. Gayana Bot 66:28–49

Richter M (2001) Vegetationszonen der Erde. Klett-Perthes, Ulmer, Gotha and Stuttgart

Ritz CM, Martins L, Mecklenburg R, Goremykin V, Hellwig FH (2007) The molecular phylogeny of *Rebutia* (Cactaceae) and its allies demonstrates the influence of paleogeography on the evolution of South American mountain cacti. Am J Bot 94:1321–1332

Roig-Juñent S, Flores GE, Mattoni C (2003) Consideraciones biogeográficas de la Precordillera (Argentina), con base en artrópodos epígeos. In: Morrone JJ,, Llorente Bousquets J, (eds) Una Perspectiva Latinoamericana de la Biogeografía. Las Prensas de Ciencias, Facultad de Ciencias, UNAM, México, DF, pp 275–288

Roig-Juñent S, Domínguez MC, Flores GE, Mattoni C (2006) Biogeographic history of South American arid lands: a view from its arthropods using TASS analysis. J Arid Environ 66:404–420

Schulz N (2009) Loma-Formationen der Küsten-Atacama/Nordchile unter besonderer Berücksichtigung rezenter Vegetations- und Klimaveränderungen. PhD thesis, Geographical Institute, Erlangen-Nürnberg University

Schumann K (1898) Gesamtbeschreibung der Kakteen. Neumann, Neudamm

Skottsberg C (1916) Botanische Ergebnisse der schwedischen Expedition nach Patagonien und dem Feuerlande 1907–1909. V. Die Vegetationsverhältnisse längs der Cordillera de los Andes südlich von 41 Grad südlicher Breite. K Sven Vetenskapsakademien Handl 56:1–366. Almqvist & Wiksell, Stockholm

Solbrig O (1976) The origin and floristic affinities of the South American temperate, desert and semidesert regions. In: Goodall W, (ed) Evolution of desert biota. University of Texas Press, Austin, TX, pp 7–49

Stebbins GL (1952) Aridity as a stimulus to plant evolution. Am Nat 86:33–44

Wallace RS (1995) Molecular systematic study of the Cactaceae: using chloroplast DNA variation to elucidate cactus phylogeny. Bradleya 13:1–12

Wallace RS, Gibson AC (2002) Evolution and systematics. In: Nobel PS, (ed) Cacti: biology and uses. University of California Press, Berkeley, CA, pp 1–21

Zuloaga FO, Morrone O, Belgrano MJ, (eds) (2008) Catálogo de las Plantas Vasculares del Cono Sur: Argentina, Sur de Brasil, Chile, Paraguay y Uruguay. Monogr Syst Bot, 107: 1715–1830 Missouri Botanical Garden

Chapter 8
Asteraceae, Chile's Richest Family

Abstract Being the richest family worldwide, the Asteraceae is also the richest Chilean family at the genus and species level. According to the most up to date knowledge, it encompasses 123 genera and 838 native species, that pertain to 20 different tribes. The 123 genera have been classified in 7 floristic elements and 9 generalized tracks and the geographical evolution of the family is discussed. Analysis of endemism has been undertaken by means of the program NDM/VNDM, resulting in 6 areas of endemism, some of them overlapping in Central Chile. Finally, several aspects about the conservation of the Chilean Asteraceae are discussed, considering also the high degree of alien invasive taxa and the gaps in the distributional knowledge. An exercise towards bridging these gaps is undertaken by means of niche modeling of *Mutisia* species.

The Asteraceae or Compositae is the richest vascular plant family in the world, with over 1,600 genera and 23,000 species (Anderberg et al. 2007). Only the Orchidaceae (ca 880 genera and 22,000 species) and the Fabaceae (730 genera and 19,000 species) come close to these numbers (Stevens 2001 and onwards).

Members of the Asteraceae are found in almost every environment and on all continents, except Antarctica, but the distribution at the genus and species level is very heterogeneous and with high levels of endemism at different scales (Funk et al. 2005). Asteraceae representatives adopt almost every life-form: herbs, succulents, lianas, epiphytes, trees, or shrubs (Figs. 8.1 and 8.2). They are mainly characterized by the florets grouped in capitula, the fruit being a cypsela mostly with a pappus (Fig. 8.3).

8.1 Classification of Chilean Asteraceae

Systematics of the Asteraceae is a very dynamic field. In the earlier stages of plant taxonomy, Cassini (1819) recognized 19 tribes, while Bentham (1873) proposed a system of 13 tribes. After many vicissitudes, currently under the predominance of molecular systematics, the classification has been improved to include 10 subfamilies and 39 tribes (Funk et al. 2009). The classification at the genus level is also

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Fig. 8.1 Chilean Asteraceae: **a** *Triptilion spinosum*, Antuco; **b** *Ophryosporus triangularis*, Cuesta Buenos Aires; **c** *Chaetanthera pusilla*, Cerro Provincia; **d** *Mutisia cana*, Catemu; **e** *Haplopappus rengifoanus*, Cuesta Buenos Aires (photo credits: **a**–**e** A. Moreira-Muñoz)

very dynamic: every year several new genera are described and many more are resurrected or moved into synonymy (Bremer 1994). For the Chilean flora, one of the most recently resurrected genera is *Ocyroe* (Bonifacino 2008).

The classification at the tribe level is far from having reached consensus, but an attempt towards a synopsis has been proposed by Funk et al. (2005), (2009), as a phylogenetic supertree based greatly on the last findings via molecular systematics (Fig. 8.4).

The Chilean genera have been organized here under this scheme, following Moreira-Muñoz and Muñoz-Schick (2007), updated by means of Anderberg et al. (2007), the Southern Cone checklist (Zuloaga et al. 2008), and recent monographic treatments (e.g. *Chiliotrichum* s.s., Bonifacino 2009). The Asteraceae is the richest family in the Chilean flora (see Sect. 2.2). According to the current update, the family is composed in Chile by 123 native genera and ca. 838 native species (Table 8.1).

Fig. 8.2 Chilean Barnadesieae (Asteraceae): **a** *Dasyphyllum diacanthoides*, Antuco; **b** *Chuquiraga oppositifolia*, Juncal (photo credits: **a**, **b** A. Moreira-Muñoz)

A high number of these species (374 or 45%) are endemic to Chile (Table 8.1). Regarding the tribe composition, 20 of 39 currently recognized tribes (according to Funk et al. 2009) are recorded in Chile, i.e. half of the global diversity at the tribus level is present in Chile. Best represented in Chile are the Astereae (20 genera), Nassauvieae and Gnaphalieae (15) (Table 8.1).

At the species level the best represented tribe is by far the Senecioneae, due to the presence of *Senecio* (ca 224 species, 103 of them endemic), the species-richest Chilean plant genus (Sect. 2.2) (Teillier and Marticorena 2006). Other Compositae species-rich tribes in Chile are the Astereae (173 species) and Nassauvieae (114); species-rich genera are also *Haplopappus* (54 species), *Leucheria* (42), *Baccharis* (40), and *Chaetanthera* (38).

The relative proportion of the genera in the respective tribes gives us another perspective: the Chilean genera from the Onoserideae, Mutisieae, and Nassauvieae represent 67, 57 and 60% of the generic richness respectively, while Chilean Mutisieae and Nassauvieae represent one third of the species richness of these tribes (Table 8.1). In contrast, tribes such as Cardueae, Anthemideae, Inuleae or Eupatorieae, have a very sparse representativeness in Chile.

8.2 Floristic Elements of Chilean Asteraceae

Similar to the analysis done for the whole flora at the genus level (Chap 3) a specific analysis of floristic elements and generalized tracks was undertaken for the genera of the Asteraceae. As for the flora in general (Sect. 3.2), it seems that disjunction is

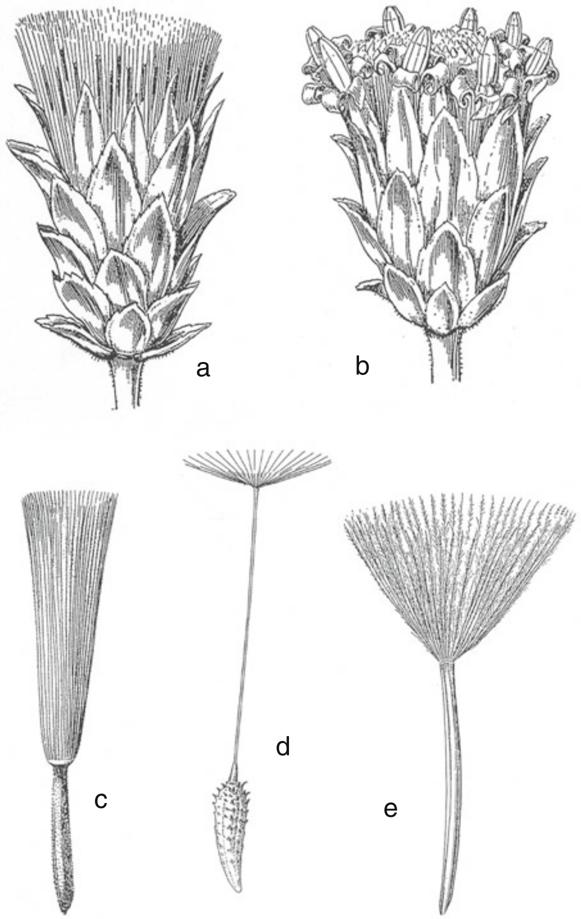

Fig. 8.3 Asteraceae fruits: **a** female capitulum, *Baccharis linearis*; **b** male capitulum, *B. linearis*; **c** achene with pappus, *Pleocarpus revolutus*; **d** achene with pappus, *Taraxacum officinale*; **e** achene with pappus, *Hypochaeris incana* (illustrations from E. Sierra, in Muñoz Pizarro 1966))

the norm under the Chilean Asteraceae. Floristic elements and generalized tracks of Chilean Asteraceae genera are synthesized in Tables 8.2, 8.3 and Fig. 8.5.

Most genera within the Chilean Asteraceae (53 genera, 43%) can be classified into a Neotropical element, further composing four different tracks: the "wide Neotropical", "wide Andean", "Central Andean", and "South Amazonian" tracks. The second most important element in the Chilean Asteraceae is the Antitropical element, which reaches 21% with 26 genera. This Antitropical element can be assigned to a "wide Antitropical track" that connects Chile with temperate North America and Eurasia (9 genera, e.g. *Adenocaulon*, *Hypochaeris*) and a "Pacific-Antitropical track" that includes most genera disjunct between central Chile and western North America (13 genera, e.g. *Bahia*, *Blennosperma*, and *Gutierrezia*). Four genera form a "circum-Pacific track", showing a distribution in western North America, South America, and Australasia (*Flaveria*, *Gochnatia*, *Microseris*, and *Soliva*).

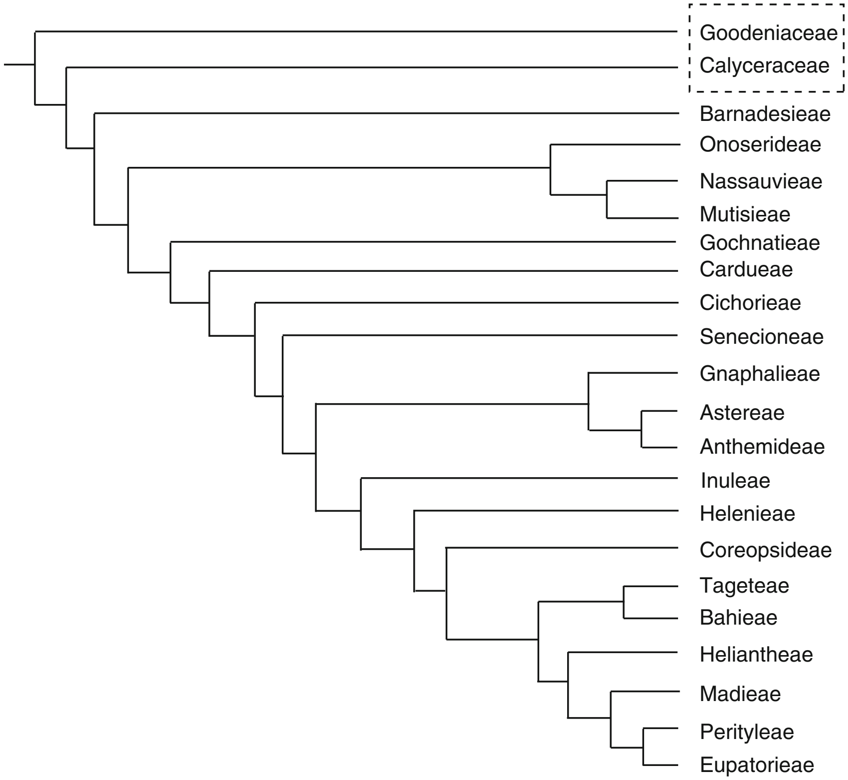

Fig. 8.4 Phylogenetic relationships of Chilean Asteraceae tribes. Goodeniaceae and Calyceraceae appear as outgroups (adapted from Funk et al. (2005, 2009))

The South-temperate element (11 genera), encompasses genera distributed only in central/southern Chile and Argentina (e.g. *Belloa*, *Eriachaenium*, and *Triptilion*). *Acrisione* is a subendemic Chilean genus with a couple reported localities in Argentina (Cabrera 1975).

The pantropical element is composed by 9 genera (e.g. *Achyrocline*, *Centipeda*, *Mikania*) distributed along the world's tropical belt.

The australasiatic element comprises also a generalized track that represents the disjunct distribution between Chile and Australasia, as shown by the four genera *Abrotanella*, *Lagenophora*, *Leptinella*, and *Trichocline.*

The Chilean endemic element is composed of 16 genera. Under those, 6 genera are endemic to the oceanic islands off Chile: *Lycapsus* (Perityleae) and *Thamnoseris* (Cichorieae) are restricted to the Desventuradas Islands (San Félix and San Ambrosio); *Dendroseris* (Cichorieae), *Robinsonia* (Senecioneae), *Centaurodendron*, and *Yunquea* (both Cardueae) are restricted to the Juan Fernández archipelago (see Chap 5). On the other hand, 10 genera are endemic to mainland Chile, pertaining mostly to the Nassauvieae (*Calopappus*, *Leunisia*, *Marticorenia*,

Table 8.1 Summary of Chilean Asteraceae: tribes present in the Chilean flora, tribal distribution, global numbers of genera and species, Chilean numbers, and relative presence in Chile (updated from Moreira-Muñoz and Muñoz-Schick 2007; Anderberg et al. 2007; Zuloaga et al. 2008; Funk et al. 2009). For detailed genera and species numbers see Appendix

Tribe	Distribution	Gen. n° global	Gen. n° Chile	%	Spp. n° global	Spp. n° Chile	%	Endemic Chilean spp.
Barnadesieae	South America	9	3	33.3	91	9	9.9	3
Onoserideae	Southern Andes	6	4	66.7	52	5	9.6	3
Nassauvieae	Neotropics	25	15	60.0	315	114	36.2	39
Mutisieae	Neotropics, few in Asia, Africa, Australia	14	8	57.1	200	71	35.5	29
Gochnatieae	South America, few Mexico, USA	4	1	25.0	88	1	1.1	1
Cardueae	Mediterranean, Asia, N hemisphere	72	3	4.2	2, 400	10	0.4	10
Cichorieae	Temperate N hemisphere, few S Am, Islands	93	9	9.7	1, 400	55	3.9	31
Senecioneae	Cosmopolitan	150	9	6.0	3, 500	258	7.4	118
Gnaphalieae	Cosmopolitan, esp. Australia, S Africa, S Am	190	15	7.9	1, 240	74	6.0	27
Astereae	Cosmopolitan	222	20	9.0	3, 100	174	5.6	88
Anthemideae	Cosmopolitan, Mediterranean, Asia, S Africa	111	4	3.6	1, 800	6	0.3	0
Inuleae	Subcosmopolitan, Eurasia, S Africa, S Am	66	2	3.0	687	2	0.3	0
Helenieae	Anfitrops, esp. W USA	13	1	7.7	120	7	5.8	6
Coreopsideae	North/South Am, few Australia, India	30	3	10.0	550	5	0.9	1
Tageteae	Neotropics, esp. W USA	32	2	6.3	270	4	1.5	0
Bahieae	Neotropics, esp. W USA, few Africa, Pacific	20	2	10.0	83	3	3.6	1
Heliantheae	Pantropics, esp. Neotrops	114	10	8.8	1, 461	16	1.1	7
Madieae	Anfitropics, esp. W USA	36	3	8.3	200	4	2.0	1
Perityleae	SW USA, Chile/Peru, Desventuradas Is	7	3	42.9	84	4	4.8	2
Eupatorieae	Subcosmop	182	6	3.3	2, 200	16	0.7	7
Total			123			838		374

Table 8.2 The generic composition of floristic elements and generalized tracks in the Chilean Asteraceae (updated from Moreira-Muñoz and Muñoz-Schick (2007), by permission of John Wiley and Sons)

Element	Track	Definition	N° genera	Genera
1. Pantropical		Tropics	9	*Achyrocline, Centipeda, Conyza, Cotula, Mikania, Pluchea, Sigesbeckia, Spilanthes, Wedelia*
2. Australasiatic	2.1 Australasiatic	Southern hemisphere: America, Australasia	4	*Abrotanella, Lagenophora, Leptinella, Trichocline*
3. Neotropical	3.1 Wide Neotropical	NW USA, México to Chile	17	*Ageratina, Ambrosia, Baccharis, Chaptalia, Coreopsis, Erechtites, Gamochaeta, Grindelia, Helenium, Heterosperma, Schkuhria, Stevia, Tagetes, Trixis, Verbesina, Viguiera, Villanova*
	3.2 Wide Andean	Costa Rica, Colombia to Chile	9	*Aristeguietia, Chuquiraga, Cuatrecasasiella, Diplostephium, Luciliocline, Mutisia, Perezia, Werneria, Xenophyllum*
	3.3 Central Andean	Altiplano Perú, Chile, Bolivia, Argentina	18	*Aphylloclados, Chaetanthera, Chersodoma, Haplopappus, Helogyne, Laennecia, Leucheria, Lophopappus, Mniodes, Nardophyllum, Nassauvia, Ocyroe, Pachylaena, Parastrephia, Plazia, Polyachyrus, Proustia, Urmenetea*
	3.4 South Amazonian	Andes and southern Brazil	9	*Chevreulia, Dasyphyllum, Facelis, Lucilia, Micropsis, Noticastrum, Ophryosporus, Picrosia, Tessaria*
4. Antitropical	4.1 Wide antitropical	Cool regions both hemispheres	9	*Adenocaulon, Anaphalis, Antennaria, Artemisia, Erigeron, Hieracium, Hypochaeris, Solidago, Taraxacum*

Table 8.2 (continued)

Element	Track	Definition	N° genera	Genera
	4.2 Circum-Pacific	Temperate regions N Am, S Am and Australasia	4	*Flaveria, Gochnatia, Microseris, Soliva*
	4.3 Pacific-antitropical	Chile – W USA	13	*Agoseris, Amblyopappus, Bahia, Blennosperma, Encelia, Flourensia, Gutierrezia, Lasthenia, Madia, Malacothrix, Perityle, Psilocarphus, Symphyotrichum*
5. South-temperate		Temperate Chile/Argentina	11	*Acrisione, Belloa, Brachyclados, Chiliotrichum, Doniophyton, Eriachaenium, Gamochaetopsis, Lepidophyllum, Macrachaenium, Notopappus, Triptilion*
6. Endemic		Continental Chile	10	*Calopappus, Guynesomia, Gypothamnium, Leptocarpha, Leunisia, Marticorenia, Moscharia, Oxyphyllum, Pleocarphus, Podanthus*
		Chilean islands	6	*Centaurodendron, Dendroseris, Lycapsus, Robinsonia, Thamnoseris, Yunquea*
7. Cosmopolitan		Worldwide, most continents	4	*Bidens, Centaurea, Gnaphalium, Senecio*

Table 8.3 Floristic elements of Chilean Asteraceae genera

Element	N° Genera	%
Pantropical	9	7.3
Australasiatic	4	3.3
Neotropical	53	43.1
Antitropical	26	21.1
South-temperate	11	8.9
Endemic	16	13.0
Cosmopolitan	4	3.3
	123	100.0

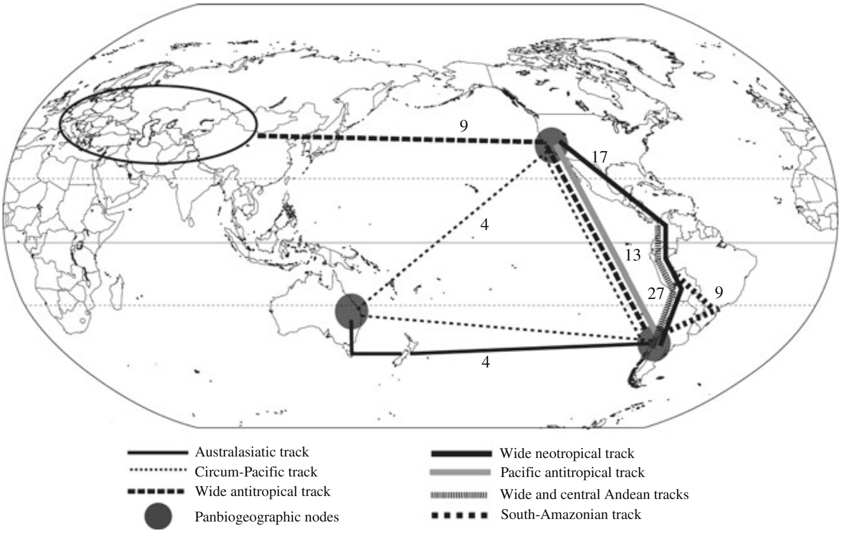

Fig. 8.5 Generalized tracks of Chilean Asteraceae genera (updated from Moreira-Muñoz and Muñoz-Schick (2007), by permission of John Wiley and Sons)

Moscharia, *Oxyphyllum, Pleocarphus*). Heliantheae are represented by *Podanthus* and *Leptocarpha*; Onoserideae by *Gypothamnium*; and Astereae by *Guynesomia*. Dot maps for the distribution of these endemic genera have been published in Moreira-Muñoz and Muñoz-Schick (2007).

Finally, the cosmopolitan element includes only four widespread genera: *Bidens* (Coreopsideae), *Centaurea* (Cardueae), *Gnaphalium* (Gnaphalieae), and *Senecio* (Senecioneae).

The proportion of floristic elements in the Chilean Asteraceae is similar to that of the whole vascular flora (compare with Table 3.2). Remarkably is the highest presence of neotropical genera (43%) within the Asteraceae, resting from the cosmopolitan genera which in the whole flora reach a 17% while in the Asteraceae corresponds only to a 3%.

8.3 Biogeographic regionalization of the Chilean Asteraceae

The latitudinal range of distribution of each genus of the Chilean Asteraceae has been already illustrated in Moreira-Muñoz and Muñoz-Schick (2007), on the base of the collections at the National Herbarium (SGO).

There is no obvious relationship between the geographic relationships and the distribution in Chile along the latitudinal gradient: while the few australasiatic genera tend to occupy more austral localities than the neotropical genera, there is one exception: *Trichocline,* which reaches northernmost Chile. In contrast, not all the neotropical genera just reach the subtropical latitudes of Central Chile: some of them approach southernmost Chile, such as *Gamochaeta, Nardophyllum, Nassauvia*, or the rich and widespread genus *Baccharis*. Apart from *Baccharis*, the most widely distributed genera are *Perezia*, *Leucheria*, *Conyza*, *Gamochaeta* and *Senecio,* that occupy the whole Chilean latitudinal extent from Parinacota (17°35′S) to Cabo de Hornos (56°S). Of course we find genera with a more restricted distribution, e.g. most genera pertaining to the Central Andean track reach the southern Atacama and not disperse to the South. Chilean endemic genera are restricted to Central Chile, such as *Calopappus*, *Leunisia*, *Marticorenia, Moscharia*. Only *Leptocarpha* reaches more southern latitudes at 45°S.

The generic richness plotted on a grid of 1 × 1 degrees shows three centres of richness (Fig. 8.6a): a reduced one at 18°–19°S in the Altiplano encompassing many Neotropical genera shared with Peru and NW Argentina; a second and biggest

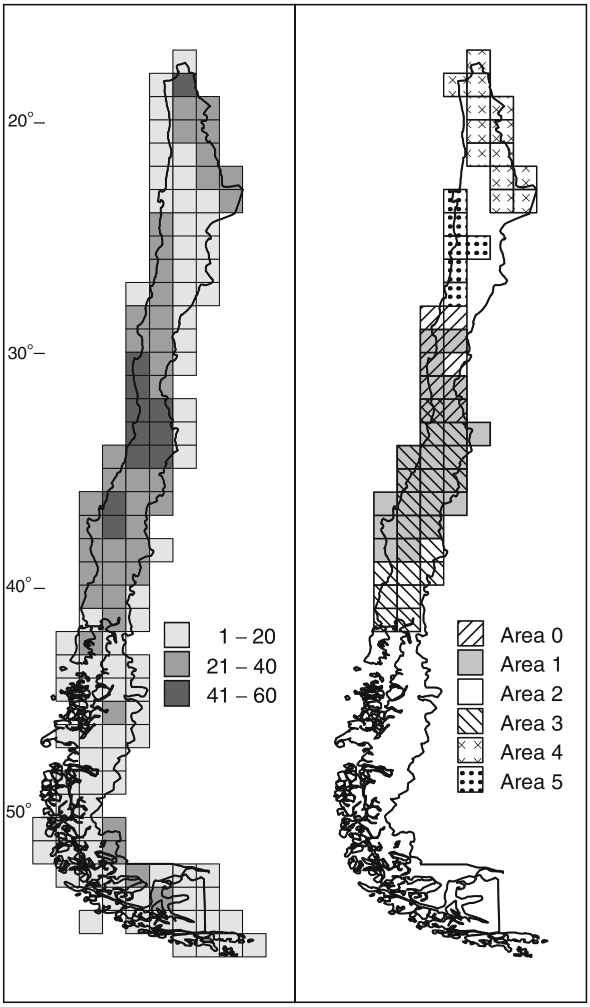

Fig. 8.6 **a** Generic richness of Chilean Asteraceae on a 1 × 1 degree grid; **b** areas of endemism (based on consensus) obtained by NDM/VNDM

centre at 31°–35°S, encompassing many Chilean endemic genera; and a third centre at 36°–38°S (coast). This last one seems to be an extension of the Central Chilean centre, separated most probably due to collection gaps. The number of genera shows an obvious decline in the Atacama Desert and South of 38°S, entering the temperate zone that suffers a general reduction in the plant generic richness. This figure has to be taken only as referential, since collection gaps cannot be ruled out, and much effort needs to be done on the improvement of the georeferencing of the Herbaria collections and the acquirement of new field data.

Reiche (1905) made, with the knowledge of his time, a biogeographic analysis of the Chilean composites, further proposing the first biogeographic regionalization for the Chilean flora (see also Sect. 4.3). He proposed five floristic regions and five subregions based on the endemic or restricted genera and species of the family (Table 8.4 and Fig. 8.7). Reiche further drew a second map in which he proposed the dispersal routes for the Chilean Compositae (Fig. 8.7).

Reiche considered both the genera present in certain zones, as well as the genera that were absent, i.e. the turnover in geographic distribution. This is the essence of modern methods of endemism analysis like PAE or NDM/VNDM (Goloboff 2005) (see Sects. 4.3 and 7.2). Remarkably, Reiche made a similar analysis intuitively and with a much more limited distributional knowledge than we manage today. To replicate the analysis, a database with 19,900 records of 116 genera of the Asteraceae native to continental Chile was built. Collections pertain to the Herbaria SGO and CONC (C. Marticorena pers. comm.). Records were checked regarding georeference, corresponding to 15,809 unique localities that were overlapped by a grid of quadrats of 1° × 1° degree covering Chile.

The optimality method was carried out with NDM/VNDM v. 2.6 with the same options as for the endemic genera and Cactaceae species (Sects. 4.3 and 7.2). The

Table 8.4 Floristic regions of the Chilean Compositae (Reiche 1905)

	Regions and subregions	Extention	Characteristic taxa
I	North Coastal	22°–29°S coast	*Gypothamniun, Oxyphyllum, Amblyopappus*
II	North Andes	18°–31°S Andes	*Diplostephium, Schkuhria, Plazia, Werneria*
III	Central and southern Andes	31°–52°S Andes	*Nassauvia, Leucheria, Perezia, Mutisia*
	(A) Coquimbo to Chillán	31°–36°S Andes	*Leucheria, Perezia*
	(B) Chillán to Magallanes	36°–52°S Andes	*Adenocaulon, Leucheria, Baccharis magellanica*
IV	Central coast	30°–36°S	*Chaptalia, Moscharia, Triptilion*
	(A) Coquimbo to Maule	30°–36°S	Absence of *Polyachyrus*
	(B) Maule to Concepción	36°–37°S	*Dasyphyllum diacanthoides*
	(C) Concepción to the south	37°–56°S	*Lagenophora, Leucheria*
V	Magallanes and Tierra del Fuego	52°–56°s	*Chiliophyllum fuegianum, Artemisia magellanica*

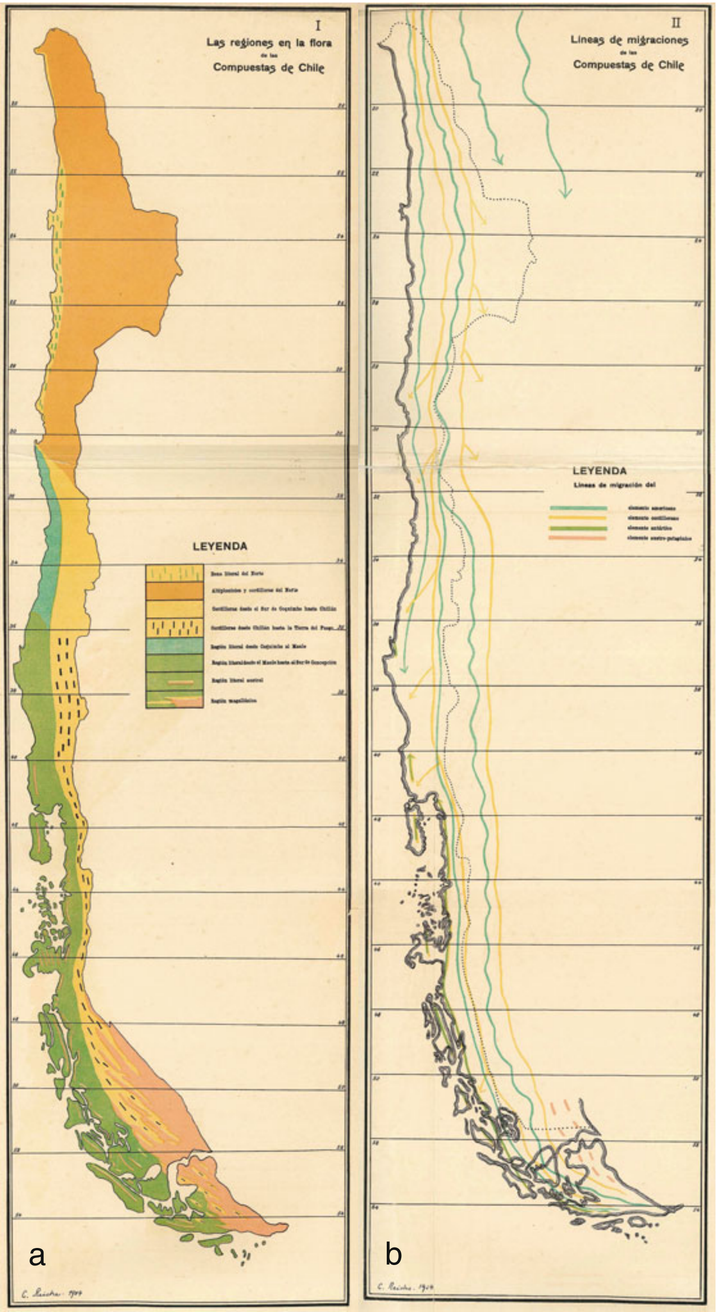

Fig. 8.7 Biogeographic maps of Chilean Asteraceae, from Reiche (1905): **a** floristic regions; **b** migration routes

search was performed until the number of sets was shown stable with different random seeds, using edge proportions.

16 areas of endemism were obtained, and 41 genera were endemic to some area. A consensus was further applied to the obtained sets, with 10% of similarity in species (genera) and the option against any of the other areas in the consensus (Fig. 8.6b).

This resulted in 6 consensus areas, some of them overlapping. The consensus area with the lower score has 2.27, and the higher has 5.88 (this score is relative, considering that 1 is the highest score a genus can get, meaning it is found in all quadrats of the area of endemism: i.e. a consensus built by 3 species (genera) can reach maximally a score of 3).

Consensus Area 0 was obtained from two sets, showing four endemic genera and a score of 2.3. It includes 10 quadrats between 28° and 33°S. Genera supporting this area are *Brachyclados, Flourensia, Guynesomia* and *Pleocarphus*.

Consensus Area 1 was obtained from seven sets, built by the distribution of 13 genera and having a score of 3.81 (that is relatively low for a total of 13 genera). It includes 25 quadrats between 29° and 39°S. Its supporting genera are *Ageratina, Anaphalis, Aristeguietia, Blennosperma, Calopappus, Chaptalia, Gochnatia, Marticorenia, Micropsis, Mikania, Moscharia, Podanthus* and *Psilocarphus*.

Consensus Area 2 is built by one set, made up of 3 genera and getting a score of 2.5 (that is relative high for just 3 genera). It encompasses the whole country's latitudinal extent, including 121 quadrats between 17° and 56°S. The widespread genera supporting this area are *Baccharis, Perezia* and *Senecio*. This Area is included in the map as a blank base (Fig. 8.6b).

Consensus Area 4 was obtained from 4 sets, had 13 genera and a score of 5.63 including 13 quadrats in the northernmost Chilean Altiplano between at 17° and 24°S. This area has a rather high score. Its genera are *Chersodoma, Cotula, Coreopsis, Diplostephium, Helogyne, Heterosperma, Lophopappus, Luciliocline, Mniodes, Parastrephia, Pluchea, Trixis* and *Xenophyllum.*

Consensus Area 5, obtained from one set, had 3 genera. It shows a score of 2.83 and includes six quadrats between 23° and 28°S. Its genera are *Erechtites, Gypothamnium* and *Oxyphyllum*.

Consensus Area 3 was set aside in the final result, because the genera got very low scores (< 0.5). The area included 22 quadrats between 32° and 42°S, and the genera were *Belloa, Chevreulia, Dasyphyllum, Lucilia* and *Noticastrum*.

Taking account of the accumulation of knowledge in 100 years, the areas of endemism presented here logically differentiate from the proposal by Reiche (1905), but there are a couple of remarkable similarities: consensus area 5 is highly coherent with the North coastal floristic region (Table 8.4), sustained by the genera *Oxyphyllum* and *Gypothamnium*. Also Area 4 was recognized by Reiche as a "North Andean" region, although not so strictly limited as in the present results (Fig. 8.6b). Reiche's "Central and Southern Andes" and "Central Coastal" regions are partly consistent with Areas 0 and 1. Reiche proposed a sharp limit between coastal and Andean units, which are not retrieved by NDM. This can be an effect of the scale and origin of the grid and that can only be overruled with better distributional data.

The low richness of Magallanes does not allow recognition of a specific floristic region, as proposed by Reiche.

Future analyses will have to include not only genera but species, and especial attention has to be paid to the adequate taxonomy of the taxa and further increase in distributional knowledge.

8.4 Asteraceae Evolutionary Biogeography

After analyzing the distribution of the genera and visualizing the migration routes for the Compositae (Fig. 8.7b), Reiche reached the conclusion that only an old circumpolar continent connecting South America with New Zealand could be the cause of the close floristic relationships between the genera that composed his "antarctic element" (Reiche 1905). Impossible to be known to Reiche, only during the 1990s several authors proposed that the family seems to have an ancient origin in the South Hemisphere related to the Gondwana break-up (Bremer 1993; Bremer and Gustafsson 1997). DeVore and Stuessy (1995) proposed a Southern Hemisphere origin for the three families Goodeniaceae, Calyceraceae, and Asteraceae, with Goodeniaceae separating from Calyceraceae–Asteraceae when America got isolated from Australia/Antarctica (in the Early Eocene, 43–53 Ma) (Boxes 1.3 and 8.1).

Box 8.1 Goodeniaceae and Calyceraceae in the Familiar Relationships of the Asteraceae

Molecular analyses suggest that the closest families to the Asteraceae are the Goodeniaceae and Calyceraceae. The Goodeniaceae show a predominant distribution in Australia, New Zealand and the Pacific. The distribution of *Selliera*, on the Australian Continent, Pacific islands, and Chile, is particularly interesting. The Calyceraceae are completely restricted to southern South America. From the 6 genera and 60 species, 5 genera (*Boopis*, *Calycera*, *Gamocarpha*, *Moschopsis*, and *Nastanthus*) and 30 species are to be found in Chile (Fig. 8.8). Fossil pollen from the Calyceraceae related to *Gamocarpha* type has been recently reported by Palazzesi et al. (2010) from Miocene deposits (Chubut, Patagonia).

The fossil record of the family is sparse and consists mostly of dispersed pollen grains. Turner (1977) suggested a Cretaceous origin for the Asteraceae, while the revision made by Graham (1996) appears to indicate an Eocene origin for the Asteraceae in South America. Eocene fossil Asteraceae pollen has been found more recently also in Palaeocene/Eocene (55 mya) deposits in South Africa (Zavada

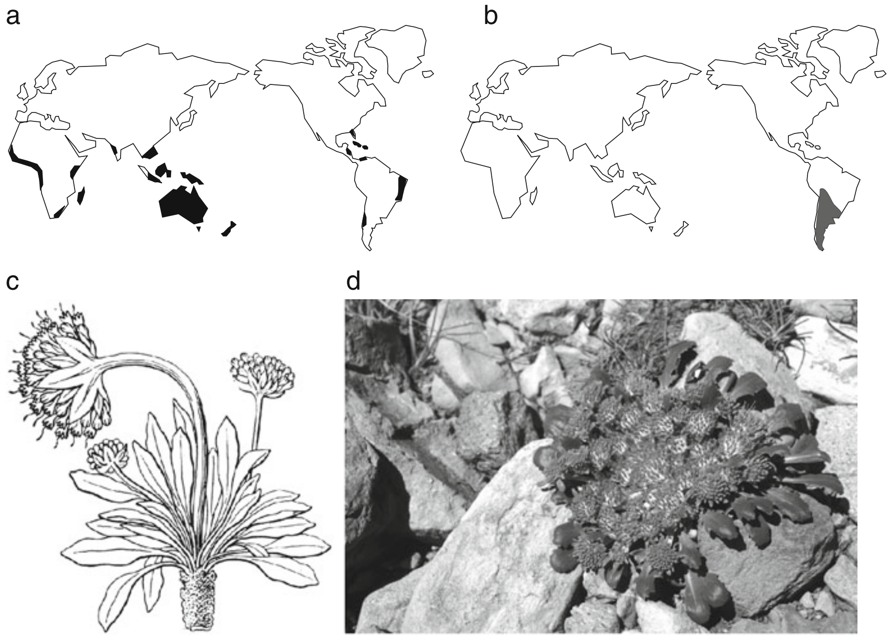

Fig. 8.8 Global distribution of the sister families to the Asteraceae: **a** Goodeniaceae; **b** Calyceraceae; **c** illustration of *Boopis alpina*, from Poeppig and Endlicher (1835–1845) (Chap 2); **d** *Nastanthus spathulatus* (photo by A. Moreira-Muñoz)

and de Villiers 2000; Scott et al. 2006). Anderberg et al. (2007) emphasize several uncertainties of identification and/or dating of all pre-Oligocene records. Early to Middle Oligocene records are found in western USA, Chile, central Europe (Anderberg et al. 2007), and in the Late Oligocene of North America and Patagonia (Katinas et al. 2007). Recently Palazzesi et al. (2009) reported the presence of fossil pollen grains in the Miocene of Patagonia, pertaining to the basal Barnadesieae; Stuessy et al. (1996) have suggested an origin in the early Oligocene (38 mya) for Barnadesieae (Box 8.2).

Box 8.2 The Barnadesieae/Barnadesioideae

The tribe (currently considered as a subfamily), comprises 9 genera and 91 species, and is located at the base of the cladogram as a sister group to the rest of the tribes (Fig. 8.4). The genera of the Barnadesieae are mainly characterized by the absence of a chloroplast DNA inversion characteristic of the rest of the family (Jansen and Palmer 1987; Bremer 1994). The tribe has an exclusively South American distribution, with genera distributed from Venezuela to Patagonia, including Eastern Brazil, but surrounding the Amazon basin (Fig. 8.9). In Chile three genera occur: *Chuquiraga*, *Dasyphyllum* and *Doniophyton* (Fig. 8.9). The disjunct distribution of the arborescent *Dasyphyllum* species (= subgenus *Archidasyphyllum*) of southern Chile/Argentina is (Fig. 8.2), in comparison with the distribution of the rest of the genus, very challenging. Cabrera (1959) proposed the subgenus *Archidasyphyllum* as the most primitive within the tribe, but newer phylogenetic analyses by Gruenstaeudl et al. (2009) support a basal evolutionary split within the subfamily into a clade comprising *Chuquiraga*, *Doniophyton*, and *Duseniella* and a clade comprising all other genera. *Archidasyphyllum* species (i.e. Chilean *Dasyphyllum*) appear most closely related to *Fulcaldea* and *Arnaldoa* from the western northern Andes. This relationship, together with the east-west disjunction across the Andes between both subgenera, suggests the future elevation of these taxa to the generic rank (Gruenstaeudl et al. 2009).

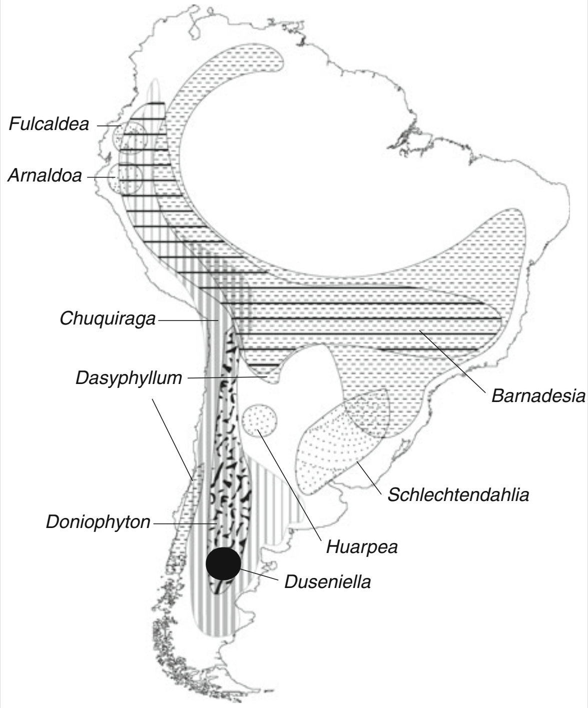

Fig. 8.9 Distribution of Barnadesieae (from Moreira-Muñoz (2006), by permission of Jardín Botánico Chagual)

Most tribes appear in the fossil record only in the middle Miocene (14 mya) (Graham 1996). The fossil record encompasses both primitive clades (e.g. Mutisieae) as well as derived ones (e.g. Heliantheae). This supports the idea of an older age than the Eocene for the family (Graham 1996). The fossil record gets richer into the Miocene (5 mya), where representatives of most of the present tribes have been found (Graham 1996).

The geographical spread of the Asteraceae during the Miocene (10–20 mya) was probably correlated with the development of extensive dry to semi-arid ecosystems with seasonal precipitation (Anderberg et al. 2007). The family members show several adaptations to exploit conditions of limited water availability under climates with seasonal rainfall (Hendry 1996). This, coupled with the development of effective dispersal mechanisms and effective chemical defenses against herbivores, enabled the Asteraceae to spread in the grassland vegetation types which became widespread during the Late Miocene, and pre-adapted them to the cooler, xeric conditions arising during the Pliocene (Anderberg et al. 2007).

Luebert et al. (2009) emphasize the role of the Andean uplift and the Atacama aridity (see also Boxes 1.5 and 7.1) in the evolution of the endemic Asteraceae genera *Oxyphyllum* and *Gypothamnium*. Interestingly, the sympatric distribution range of these two genera arose under different scenarios: *Oxyphyllum* seems to be one of the northernmost representatives of a group with its highest presence in central Chile, like the closely related *Leucheria, Moscharia*, and *Polyachyrus*. Contrary to this pattern, the ancestral group related to *Gypothamnium*, encompassing genera like *Onoseris* and *Lycoseris*, is distributed in the tropical areas of north-western South America and Mesoamerica (Luebert et al. 2009). Therefore, the current superposed distribution is to be traced along two different evolutionary lines, both related to the uplift of the Andes and the continuous drought of the Atacama. According to Luebert et al. (2009) the Andes played its role in the origin and diversification of the Atacama Desert flora in three different ways: (1) acting as a corridor that allowed the north–south geographical range expansion of taxa, causing the pattern of some related groups to establish a distribution range along the Andes; (2) the Andes have acted as a vicariant barrier separating closely related groups on the eastern and western sides; (3) they served as a new niche for speciation in high-elevation environments, which may explain the fact that there are phylogenetically related taxa in the basal areas of both sides of the Andes and also at high elevations (see also Hershkovitz et al. 2006, for the evolution of *Chaetanthera* on Andean elevations). Muellner et al. (2005) further reported a complex system of recolonization routes after Pleistocene glaciations in the temperate Andes by *Hypochaeris palustris*.

In spite of the fact that it seems so recent, several authors propose the Pliocene/Pleistocene, in relation to the final uplift of the Andes, as the time of origin of several endemic genera of the Mutisieae in Central Chile, such as *Moscharia* and *Polyachyrus* that apparently descended from a Pliocene/Pleistocene ancestor (Katinas and Crisci 2000). Simpson (1973) also interpreted the splitting of the Prenanthoides group in *Perezia*, as a recent Pleistocene event. Also *Abrotanella* (Senecioneae) (Swenson and Bremer 1997) and *Chuquiraga* (Barnadesieae) (Ezcurra 2002) have a supposedly Pleistocene origin.

8.4.1 Origin and Dispersal Routes

The many trans-Pacific relationships led Bremer (1993) to suggest the Pacific basin as related to the early evolution of the family. This Pacific relationship is to be found among the Chilean Asteraceae in the circum-Pacific, australasiatic, and Pacific antitropical tracks, encompassing 21 genera belonging to different tribes (Table 8.2). The early evolution of the family seems to be related to the fragmentation of West Gondwana during the Palaeocene, but there is still the question of how the representatives of the family reached the rest of the world. Same as for the whole flora (Sect. 3.3), currently many researchers are appealing to long-distance dispersal scenarios to explain the global spread of the family.

The genera of the Cichorieae shared between South America and North America, such as *Microseris*, supposedly have undergone a greater radiation in North America with later dispersion towards South America and Australia/New Zealand (Chambers 1963; Vijverberg et al. 1999; Lee et al. 2003). Recently discovered Peruvian *Microseris* populations are supposedly derived from Chilean progenitors instead of being remnants of stepping-stone dispersal from North America through the Andes to Chile (Lohwasser et al. 2004). Analogous molecular analyses of *Hypochaeris* suggest that the closest relatives to the South American species are in Northwest Africa. This has been interpreted as a direct dispersion Africa-South America, without a previous stop in Europe-North America (Tremetsberger et al. 2005).

The remarkable arborescent Cardueae, Cichorieae and Senecioneae from Juan Fernández have been also interpreted as the result of long-distance dispersal from the mainland, but the closest relatives are unknown, and the oceanic nature of the islands has been long part of the debate (Chap. 5). This is valid also for the endemic genera from the Desventuradas Islands, *Lycapsus* and *Thamnoseris* (Chap. 5). The oldest taxa of the Senecioneae were apparently herbs and the arboreal habit and the palmate venation of the leaves arose later; the arboreal genus *Robinsonia* is an example. The genus suffered an explosive radiation in the Juan Fernández Islands, reaching eight species endemic to this archipelago (Sanders et al. 1987), but the probable origin and extension of this genus is unknown (Chap. 5). Small (1919) proposed the Senecioneae as the basal group for the phylogeny of the family, in agreement with the "Age and area" theory of Willis (1922). The theory supposes that the more diversified groups had more time to evolve and therefore they are the oldest. Present evidence suggests that at least for the Asteraceae this is not the case, and that Senecioneae is nested well within the family (Fig. 8.4). Also from the Senecioneae, current Pacific disjunction in *Abrotanella* has been also proposed as the result of long-distance dispersal (Swenson and Bremer 1997; Wagstaff et al. 2006), in spite of lacking a pappus suited for this.

8.4.2 Dispersal Capacities

There is a common believe that Asteraceae taxa have a good dispersal capacity, due to their wind-dispersed achenes; therefore the taxa should have reached far away territories by means of long-distance dispersal. But specific experiments have shown that the dispersal capacity is sometimes very restricted: even wind-dispersed achenes can travel only several meters under specific environmental conditions (Sheldon and Burrows 1973; McEvoy and Cox 1987).

Taking account of the fruit characteristics, taxa having a pappus not suited for wind dispersal, such as *Abrotanella* and its Pacific disjunct distribution, have been interpreted as the result of vicariant form-making prior to the Palaeogene, in relation to processes of subduction, accretion and orogenesis associated with the tectonic evolution of the Pacific region (Heads 1999). To the same deduction came Grehan (2007) while analyzing the disjunct distribution of *Microseris*. Another eight genera with a Pacific distribution do not have a pappus suited for wind transport: *Blennosperma*, *Centipeda*, *Flaveria*, *Lagenophora*, *Lasthenia*, *Leptinella*, *Soliva*, and *Psilocarphus*.

The high level of endemism at the genus and species level also challenges the supposedly good dispersal capacity, since theoretically floristic exchange would obscure endemism and disjunct patterns. Also the low presence of cosmopolitan genera (only four) in the Chilean Asteraceae flora contrasts with the assumption that the Asteraceae have facilities of dispersion by wind or animals. Emphasizing the notable patterns of endemism existent in all taxonomic levels, and challenging any proposed centre of origin, Heads (2009) maintains that the Asteraceae might descend from a globally widespread ancestor. This ancestor or few ancestors "might have undergone a phase of active mobilism in the Mesozoic in which they occupied much of Earth's land surface, before settling down into a Cenozoic phase of immobilism and speciation" (Heads 2009, p 765).

There seems to be still a lot to do in Asteraceae biogeography: "Perhaps the size of the family, its global distribution, the lack of macrofossils and paucity of discriminating characters in fossil pollen, and the lack of an agreed upon phylogeny have restricted attempts to understand its history" (Funk et al. 2009, p 755).

8.5 Conservation v/s Invasions

Almost a third of the Chilean Asteraceae genera (35) show very restricted to medium-small distribution ranges between just one locality to 5 latitudinal degrees (Moreira-Muñoz and Muñoz-Schick 2007). This is not irrelevant, since one of the most important criteria for classifying endangered species is the geographic range extent (IUCN 2001). Furthermore, half of the genera (53) have their distribution in central Mediterranean Chile from 27° to 37°S, in an intensively modified human landscape (see Sect. 6.1). As shown by the map of generic richness (Fig. 8.6), centres of richness located between 31°–35°S and 36°–38S°, coincide with the most populated regions (Santiago, Valparaíso, Concepción). This means a huge challenge for the conservation of these taxa, since the intensive land occupation creates huge gaps in protected areas (see Figs. 6.2 and 6.3).

An early recognized target of conservation is the species *Dasyphyllum excelsum* (Box 8.2), which is considered as Endangered in the Species Red List (Sect. 6.1).

Dasyphyllum excelsum, a characteristic tree of the sclerophyllous forest of Central Chile, pertains to the basal Barnadesieae and is therefore a critical species for the understanding of the early evolution of the family. Regional Red Books (see Chap 6) also include many Asteraceae species. Almost 80 Asteraceae species have been catalogued as vulnerable or endangered in the Atacama, Coquimbo and O'Higgins regions (see Sect. 6.1). Considering the serious lack of adequate distributional data to allow a good assessment, these types of assessments must be applied with caution: sometimes a species that is considered highly vulnerable or even extinct can be rediscovered with adequate field work, as in the case of *Plazia cheiranthifolia*, that was considered as regionally extinct and was newly rediscovered in the Coquimbo region (Faúndez and Saldivia 2008).

Nevertheless, this seems to be sadly not the case for the Fernandezian endemic composites since the islands' flora is the most endangered of the country and one of the most threatened island territories worldwide (see Chap 5). This directly affects several Asteraceae species: two species, *Robinsonia berteroi* and *R. macrocephala* are already extinct (Danton and Perrier 2005), while ca. 30 species (i.e. all of the islands's Asteraceae!) are classified ranging from critically endangered (CR) to vulnerable (VU) (Danton and Perrier 2006).

On the other hand, the Chilean Asteraceae flora, on the islands as well as on the continent, is constantly "enriched" by alien species that are becoming rapidly naturalized. Castro and Muñoz-Schick (2006) reported the presence of 58 Compositae genera and 99 species naturalized in continental Chile.

Only 15 (26%) of these genera were present in the flora as native genera. Most of the genera (43; 74%) are new for the Chilean flora. The newly incorporated genera tend to be less diverse than the others, since these are represented by a mean of 1.4 species, while genera already present in Chile contain a mean of 2.4 introduced species. This fact suggests that the phylogenetic relationships could affect the effectiveness of introduced species: genera already represented in Chile by means of native species have major possibilities of being enriched by introduced species. The mechanisms underlying these observations are unknown, but Castro and Muñoz-Schick (2006) speculate a sort of pre-adaptation of several species to occupy a specific niche in a new territory. Of course this is a very interesting field of research due to the richness of "invaders" in the family. The competition that one would expect in closely related species is a totally undeveloped field of research. The Asteraceae are certainly one of the best study objects in the research of invasions (sensu Pauchard et al. 2009).

Most of the introduced Asteraceae genera are represented by one species. Several genera represented by two to four species are: *Acmella*, *Anthemis*, *Carduus*, *Carthamus*, *Chrysanthemum*, *Cirsium*, *Conyza*, *Hypochaeris*, *Lactuca*, *Tanacetum*, *Ambrosia*, *Calendula*, *Chamomilla*, *Leontodon*, *Xanthium*, *Cotula*, *Crepis* and *Sonchus* (see examples in Fig. 8.10). The most diverse genera are represented by five introduced species, from the genera *Bidens*, *Centaurea*, *Hieracium* and *Senecio*. These genera are originally present in Chile, although the relation is not proportional: *Senecio* has more than 220 native species (Teillier and Marticorena 2006)

Fig. 8.10 *Chrysanthemum coronarium* and *Chrysanthemoides monilifera*, two highly invasive Asteraceae species in coastal central Chile (original illustration by Sergio Elórtegui Francioli)

while *Bidens*, *Centaurea* and *Hieracium* have between six and seven native species, i.e. introduced species can soon overpass native species in these genera.

Regarding the geographic origin, most of the naturalized Compositae come from Mediterranean Europe and northern Africa (72% of the species). Only 10% comes from other South American countries. Interestingly, the naturalized Compositae flora also shows a "natural" spatial segregation: the northern assemblage is different from the one from Central Chile and from the southern one, the central assemblage being the species-richest. This fact may reflect the different human colonization history of the territory, or/and that the environmental differences indeed affect the establishment of the introduced flora (Castro and Muñoz-Schick 2006).

8.5.1 Invading Biogeography

Invasive species, not just Asteraceae, are putting biogeography in trouble; Schram (2008) asks: "…does biogeography have a future in a globalized world…?" Or in the words of Nijman and Vonk (2008): "…in a globalised world, with species reintroductions, invasions of alien species, and large-scale extinctions, unravelling the true biogeographic relationships between areas and species may become increasingly difficult" (Nijman and Vonk 2008). But the analysis of invasions shows also good research opportunities: several authors consider invasions as "natural experiments" for the study of spatially explicit phenomena like dispersal, colonization, range expansion, and population dynamics. In this sense, the study of invasions contributes to our understanding of the spatial dimensions of ecological processes, and to biogeography! (Pauchard 2007; Crawford and Hoagland 2009; Pauchard et al. 2009). One of the most promising research topics is the range expansion of naturalized Asteraceae species. Several of them can be traced back to the moment of their arrival and it seems attractive to evaluate possible scenarios of maximal future expansion, via GIS niche modeling, and phylogeography (Ortiz et al. 2008). Distributional modeling has been indeed used for the analysis of Chilean native *Senecio* species (Rovito et al. 2004).

It is worth to emphasize the need of strengthening the herbaria collections, for the native as well as for the naturalized species, thus minimizing the "Wallacean shortfall" (Box 6.2). In spite of new research programs like niche modeling on GIS platforms (Sect. 6.2), which can support conservation initiatives, good botanical collections are essential to a better performance of the models. An exercise done with the native *Mutisia* species is presented in Box. 8.3 (Fig. 8.11). A better knowledge of the geographic distribution and ecological situation of the Chilean Asteraceae will enable us to propose new lines of inquiry that will allow us a better understanding of the family's evolution in time and space.

Box 8.3 Niche Modeling of *Mutisia* Species

Niche modelling techniques are getting widely used, together with GIS techniques and remote sensing, to identify and understand current distributions as well as to predict range shifts in the future (Guisan and Thuiller 2005; Kosak et al. 2008; Gillespie et al. 2008). In Chile the application of niche modelling is a very promising field of research (e.g. Zizka et al. 2009, for Chilean Bromeliaceae). Moreira-Muñoz et al. (2009) showed an example of its application with the distribution modelling of Chilean *Mutisia* species. Twenty one species were modelled, based on the collections from the SGO Herbarium and the monograph (Cabrera 1965), encompassing 700 georeferenced localities in Chile and adjacent localities in Argentina, Perú and Bolivia. Twenty percentage of the data was set apart for testing the fit of the models in the program MaxEnt. Nineteen environmental variables were obtained from Worldclim (www.worldclim.org), together with the digital elevation model (DEM). Results yielded a bad fit for 7 species that were those with less than 13 collection localities. Five environmental variables better explained the distribution of the analyzed species: altitude, Min T° colder month, Mean T° of the humid quarter, Mean T° warmer trimester, precipitation warmer trimester. The program was run again and models of probability were obtained and transferred to binary maps with the cut-value obtained for each species. These results are still preliminary; the models seem to be very sensitive to the number of presences. Testing of the climatic surfaces seems to be also necessary, as well as adequate georeferencing, which is critical for the work with Herbarium collections (see the richness map of Chilean *Mutisia* species in Fig. 8.11).

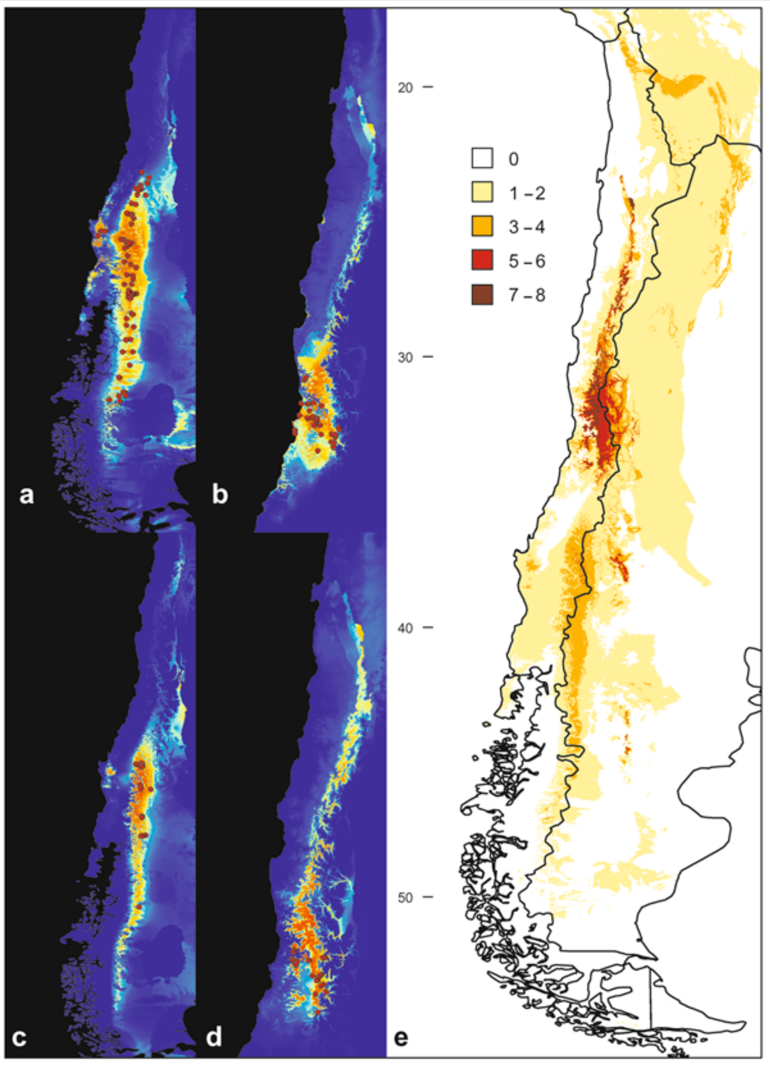

Fig. 8.11 Distribution niche modelling of Chilean *Mutisia* species: **a** *M. decurrens*; **b** *M. latifolia*; **c** *M. oligodon*; **d** *M. rosea*; **e** richness map based on niche modelling

References

Anderberg AA, Baldwin BG, Bayer RG, Breitwieser J, Jeffrey C, Dillon MO, Eldenäs P, Funk V et al. (2007) Compositae. In: Kubitzki K, (ed) Asterales. Kadereit JW, Jeffrey C (vol eds), The families and genera of vascular plants, vol 8. Springer, New York, NY, pp 61–621

Bentham G (1873) Notes on the classification, history and geographic distribution of Compositae. J Linn Soc Bot 13:355–577

Bonifacino JM (2008) Reinstatement of *Ocyroe* (Compositae: Astereae). Brittonia 60:205–212

Bonifacino JM (2009) Taxonomic revision of the *Chiliotrichum* group sensu stricto (Compositae: Astereae). Smithson Contrib Bot 92:1–115

Bremer K (1993) Intercontinental relationships of African and South American Asteraceae: a cladistic biogeographic analysis. In: Goldblatt P, (ed) Biological relationships between Africa and South America. Yale University Press, New Haven, CT and London, pp 105–135

Bremer K (1994) Asteraceae: cladistics and classification. Timber Press, Portland, OR

Bremer K, Gustafsson MHG (1997) East Gondwana ancestry of the sunflower alliance of families. Proc Nat Acad Sci USA 94:9188–9190

Cabrera AL (1959) Revisión del género *Dasyphyllum* (Compositae). Rev Mus Plata (Ser. 2) 9: 21–100

Cabrera AL (1965) Revisión del género *Mutisia* (Compositae). Opera Lilloana 13:1–227

Cabrera AL (1975) Nota sobre cinco Compositae de la República Argentina. Bol Soc Arg Bot 16:255–260

Cassini H (1819) Suit du sixiéme mémoire sur la familie des Synanthérées, contenat les caractères des tribus. J Phys Chem, Hist Nat Arts 88:189–204

Castro S, Muñoz-Schick M (2006) Compuestas naturalizadas en Chile: Importancia de la flora exótica como agente del cambio biotic. Rev Chagual (Jard Bot Santiago) 4:29–38

Chambers KL (1963) Amphitropical species pairs in *Microseris* and *Agoseris* (Compositae: Cichorieae). Q Rev Biol 38:124–140

Crawford PHC, Hoagland BW (2009) Can herbarium records be used to map alien species invasion and native species expansion over the past 100 years? J Biogeogr 36:651–661

Danton P, Perrier C (2005) Notes sur la disparition d'une espèce emblématique: *Robinsonia berteroi* (DC.) Sanders, Stuessy and Martic. (Asteraceae), dans l'île Robinson Crusoe, archipel Juan Fernández (Chili). J Bot Soc Bot France 31:3–8

Danton P, Perrier C (2006) Nouveau catalogue de la flore vasculaire de l'archipel Juan Fernández (Chili). Acta Bot Gall 153:399–587

DeVore ML, Stuessy TF (1995) The place and time of origin of the Asteraceae, with additional comments on the Calyceraceae and Goodeniaceae. In: Hind DJN, Jeffrey C, Pope GV, (eds) Advances in Compositae systematics, vol. 1. Royal Botanic Gardens, Kew, pp 23–40

Ezcurra C (2002) Phylogeny, morphology, and biogeography of *Chuquiraga*, an Andean-Patagonian genus of Asteraceae-Barnadesioideae. Bot Rev 68:153–170

Faúndez L, Saldivia P (2008) *Plazia cheiranthifolia*, especie 'extinta', redescubierta en la precordillera de Ovalle, region de Coquimbo, Chile. Noticiario Mens Mus Nac Hist Nat 360:18–21

Funk VA, Bayer RJ, Keeley S, Chan R, Watson L, Gemeinholzer B, Schilling E, Panero JL, Baldwin BG, Garcia-Jacas N, Susanna A, Jansen RK (2005) Everywhere but Antarctica: Using a supertree to understand the diversity and distribution of the Compositae. Biol Skr 55: 343–374

Funk VA, Susanna A, Stuessy TF, Bayer RJ, (eds) (2009) Systematics, evolution, and biogeography of Compositae. International Association for Plant Taxonomy, Vienna

Gillespie TW, Foody GM, Rocchini D, Giorgi AP, Saatchi S (2008) Measuring and modelling biodiversity from space. Prog Phys Geogr 32:203–221

Goloboff P (2005) NDM/VNDM ver. 2.6. Programs for identification of areas of endemism. http://www.zmuc.dk/public/phylogeny/endemism

Graham A (1996) A contribution to the geologic history of the Compositae. In: Hind DJN, Beentje HJ (eds) Compositae: Systematics. Proceedings of the international Compositae conference, Kew, 1994, vol 1: 123–140

Grehan JR (2007). A brief look at Pacific biogeography: the trans-oceanic travels of Microseris (Angiosperms: Asteraceae). In: Ebach MC, Tangney RS, (eds) Biogeography in a changing world. Systematics association special volumes. CRC Press, Boca Raton, FL, pp 83–94

Gruenstaeudl M, Urtubey E, Jansen RK, Samuel R, Barfuss MHJ, Stuessy TF (2009) Phylogeny of Barnadesioideae (Asteraceae) inferred from DNA sequence data and morphology. Mol Phyl Evol 51:572–587

Guisan A, Thuiller W (2005) Predicting species distributions: offering more than simple habitat models. Ecol Lett 8:993–1009

Heads M (1999) Vicariance biogeography and terrane tectonics in the South Pacific: analysis of the genus *Abrotanella* (Compositae). Biol J Linn Soc 67:391–432

Heads M (2009) Inferring biogeographic history from molecular phylogenies. Biol J Linn Soc 98:757–774

Hendry GAF (1996) Fructan and the ecology and evolution of the Compositae. In: Caligari PDS, Hind DJN (eds) Compositae: biology and utilization. Proceedings of the international Compositae conference, Kew Royal Botanic Gardens, 1994, vol 2, pp 121–128

Hershkovitz MA, Arroyo MTK, Bell C, Hinojosa LF (2006) Phylogeny of *Chaetanthera* (Asteraceae: Mutisieae) reveals both ancient and recent origins of the high elevation lineages. Mol Phyl Evol 41:594–605

IUCN (2001) The IUCN List of Threatened Species. Categories and Criteria (version 3.1). http://www.iucn.org/themes/ssc/redlists/RLcats2001booklet.html

Jansen RK, Palmer JD (1987) A chloroplast DNA inversion marks an ancient evolutionary split in the sunflower family, Asteraceae. Proc Nat Acad Sci USA 84:5818–5822

Katinas L, Crisci JV (2000) Cladistic and biogeographic analyses of the genera *Moscharia* and *Polyachyrus* (Asteraceae, Mutisieae). Syst Bot 25:33–46

Katinas L, Crisci JV, Tellería MC, Barreda V, Palazzesi L (2007) Early history of Asteraceae in Patagonia: evidence from fossil pollen grains. NZ J Bot 45:605–610

Kosak KH, Graham CH, Wiens JJ (2008) Integrating GIS-based environmental data into evolutionary biology. Trends Ecol Evol 23:141–148

Lee J, Baldwin BG, Gottlieb LD (2003) Phylogenetic relationships among the primarily North American genera of Cichorieae (Compositae) based on analysis of 18S–26S nuclear rDNA ITS and ETS sequences. Syst Bot 28:616–626

Lohwasser U, Granda A, Blattner FR (2004) Phylogenetic analysis of *Microseris* (Asteraceae) including a newly discovered Andean population from Peru. Syst Bot 29:774–780

Luebert F, Wen J, Dillon MO (2009) Systematic placement and biogeographical relationships of the monotypic genera *Gypothamnium* and *Oxyphyllum* (Asteraceae: Mutisioideae) from the Atacama Desert. Bot J Linn Soc 159:32–51

McEvoy PB, Cox CS (1987) Wind dispersal distances in dimorphic achenes of ragwort, *Senecio jacobaea*. Ecology 68:2006–2015

Moreira-Muñoz A (2006) Posición filogenética y distribución de los generous de Compuestas chilenas, con algunas notas biogeográficas. Rev Chagual (Jard Bot Santiago) 4:12–28

Moreira-Muñoz A, Muñoz-Schick M (2007) Classification, diversity, and distribution of Chilean Asteraceae: implications for biogeography and conservation. Divers Distrib 13: 818–828

Moreira-Muñoz A, Morales V, Pliscoff P (2009) Aplicación del programa 'Maxent' para modelar la distribución geográfica de las especies del género *Mutisia* (Asteraceae). XXX Congreso Nacional de Geografía Talca, Chile, 14 de octubre de 2009

Muellner AN, Tremetsberger K, Stuessy TF, Baeza CM (2005) Pleistocene refugia and recolonization routes in the southern Andes: insights from *Hypochaeris palustris* (Asteraceae, Lactuceae). Mol Ecol 14:203–212

Muñoz Pizarro C (1966) Sinopsis de la Flora Chilena, 2nd edn. Ediciones Universidad de Chile, Santiago

Nijman V, Vonk R (2008) Blurring the picture: introductions, invasions, extinctions – biogeography in a global world. Contrib Zool 77:67–70

Ortiz MA, Tremetsberger K, Terrab A, Stuessy TF, Garcia-Castano JL, Urtubey E, Baeza CM, Ruas CF, Gibbs PE, Talavera S (2008) Phylogeography of the invasive weed *Hypochaeris radicata* (Asteraceae): from Moroccan origin to worldwide introduced populations. Mol Ecol 17: 3654–3667

Palazzesi L, Barreda V, Tellería MC (2009) Fossil pollen grains of Asteraceae from the Miocene of Patagonia: Barnadesioideae affinity. Rev Palaeobot Palynol 155:83–88

Palazzesi L, Barreda V, Tellería MC (2010) First fossil record of Calyceraceae (Asterales): Pollen evidence from southern South America. Rev Palaeobot Palynol 158:236–239

Pauchard A (2007) Invasions as spatially explicit processes: contributions to ecology (Letter to the editor). Front Ecol Environ 5:123–124

Pauchard A, Kueffer C, Dietz H, Daehler CC, Alexander J, Edwards PJ, Arévalo JR, Cavieres L et al. (2009) Ain't no mountain high enough: plant invasions reaching high elevations. Front Ecol Environ 7:479–486

Reiche C (1905) La distribución geográfica de las Compuestas de la flora de Chile. An Mus Nac Chile Secc Bot 17:1–45

Rovito SM, Arroyo MTK, Pliscoff P (2004) Distributional modelling and parsimony analysis of endemicity of Senecio in the Mediterranean-type climate area of Central Chile. J Biogeogr 31:1623–1636

Sanders RW, Stuessy TF, Marticorena C, Silva M (1987) Phytogeography and evolution of *Dendroseris* and *Robinsonia*, tree-Compositae of the Juan Fernández Islands. Opera Bot 92:195–215

Schram FR (2008) Does biogeography have a future in a globalized world with globalized faunas? Contrib Zool 77:127–133

Scott L, Cadman A, Mcmillan I (2006) Early history of Cainozoic Asteraceae along the Southern African west coast. Rev Palaeobot Palynol 142:47–52

Sheldon JC, Burrows FM (1973) The dispersal effectiveness of the achene-pappus units of selected Compositae in steady winds with convection. New Phytol 72:665–675

Simpson BB (1973) Contrasting modes of evolution in two groups of *Perezia* (Mutisieae; Compositae) of southern South America. ***Taxon*** 22:525–536

Small J (1919) The origin and development of the Compositae. New Phytol 18:201–234

Stevens PF (2001 onwards) Angiosperm Phylogeny Website. http://www.mobot.org/MOBOT/research/APweb/

Stuessy TF, Sang T, DeVore ML (1996) Phylogeny and biogeography of the subfamily Barnadesioideae with implications for early evolution of the Compositae. In: Hind DJN, Beentje HJ (eds) Compositae: Systematics. Proceedings of the international Compositae conference, Royal Botanic Gardens, Kew, 1994, vol. 1, pp 463–490

Swenson U, Bremer K (1997) Pacific biogeography of the Asteraceae genus *Abrotanella* (Senecioneae, Blennospermatinae). Syst Bot 22:493–508

Teillier S, Marticorena A (2006) El género *Senecio* (Asteraceae): el más diverso de Chile. Rev Chagual (Jard Bot Santiago) 4:39–48

Tremetsberger K, Weiss-Schneeweiss H, Stuessy TF, Samuel R, Kadlec G, Ortiz MA, Talavera S (2005) Nuclear ribosomal DNA and karyotypes indicate a NW African origin of South American Hypochaeris (Asteraceae, Cichorieae). Mol Phylogenet Evol 35:102–116

Turner BL (1977) Fossil history and geography. In: Heywood VH, Harborne JB, Turner BL, (eds) The biology and chemistry of the Compositae, vol. 1. London, Academic Press, pp 21–39

Vijverberg K, Mes THM, Bachmann K (1999) Chloroplast DNA evidence for the evolution of *Microseris* (Asteraceae) in Australia and New Zealand after long-distance dispersal from western North America. Am J Bot 86:1448–1463

Wagstaff SJ, Breitwieser I, Swenson U (2006) Origin and relationships of the austral genus *Abrotanella* (Asteraceae) inferred from DNA sequences. Taxon 55:95–106

Willis JC (1922) Age and area: a study in geographical distribution and origin of species. Cambridge University Press, Cambridge

Zavada M, de Villiers S (2000) Pollen of the Asteraceae from the Paleocene-Eocene of South Africa. Grana 39:39–45

Zizka G, Schmidt M, Schulte K, Novoa P, Pinto R, König K (2009) Chilean Bromeliaceae: diversity, distribution and evaluation of conservation status. Biodivers Conserv 18:2449–2471

Zuloaga FO, Morrone O, Belgrano MJ, (eds) (2008) Catálogo de las Plantas Vasculares del Cono Sur: Argentina, Sur de Brasil, Chile, Paraguay y Uruguay. Monographs in systematic botany, vol 107. Missouri Botanical Garden, St. Paul, MO, 1715–1830

Chapter 9
Nothofagus, Key Genus in Plant Geography

Abstract The genus *Nothofagus* is the only representative of the Nothofagaceae. It comprises 36 species distributed in disjunct territories of the southern hemisphere: southern South America, New Zealand, East Australia, New Caledonia and New Guinea. This southern distribution pattern, together with the rich fossil record that is also found in Antarctica, sustains the status of the genus as a “key genus” in plant geography. The evolution of the genus is discussed, confronting different visions, and integrating the phylogeny of related genera, such as the fungi species of the genus *Cyttaria*.

Nothofagus has been considered as a “key genus” in plant geography (Darlington 1965; Van Steenis 1971) for at least three reasons: (1) because of the characteristic disjunct pattern of its species between South America and Australasia, together with the dominant character of these species in their territories of occurrence (Donoso 1993; Veblen et al. 1996) (Fig. 9.1); (2) because of its abundant fossil record, expressed in a rich array of macro and microfossils found in the southern territories including Antarctica (Dettmann et al. 1990); and (3) because the use of the genus as a model for testing different biogeographic methods and the various contesting visions that different studies have reached (Humphries 1981; Heads 1985, Linder and Crisp 1995, Cook and Crisp 2005; Knapp et al. 2005).

9.1 Taxonomy and Phylogeny

The genus *Nothofagus* was described by Blume in 1850, as a member of the family Fagaceae, associated with *Fagus* in the subfamily Fagoideae (hence the name: “false *Fagus*”). The family Nothofagaceae was proposed in 1962 by Kuprianova mainly on the basis of pollen characteristics. Since then, morphological and molecular studies highly support recognition of the family (Nixon 1982; Hill and Jordan 1993).

Li et al. (2004) have placed the Nothofagaceae as a sister clade of the rest of the families of the Fagales. However, the phylogenetic relationship of *Nothofagus* with members of the family Fagaceae remains unclear. Several authors have proposed a close relationship between *Nothofagus* and *Fagus* (Van Steenis 1971; Hill and

A. Moreira-Muñoz, *Plant Geography of Chile*, Plant and Vegetation 5,
DOI 10.1007/978-90-481-8748-5_9,

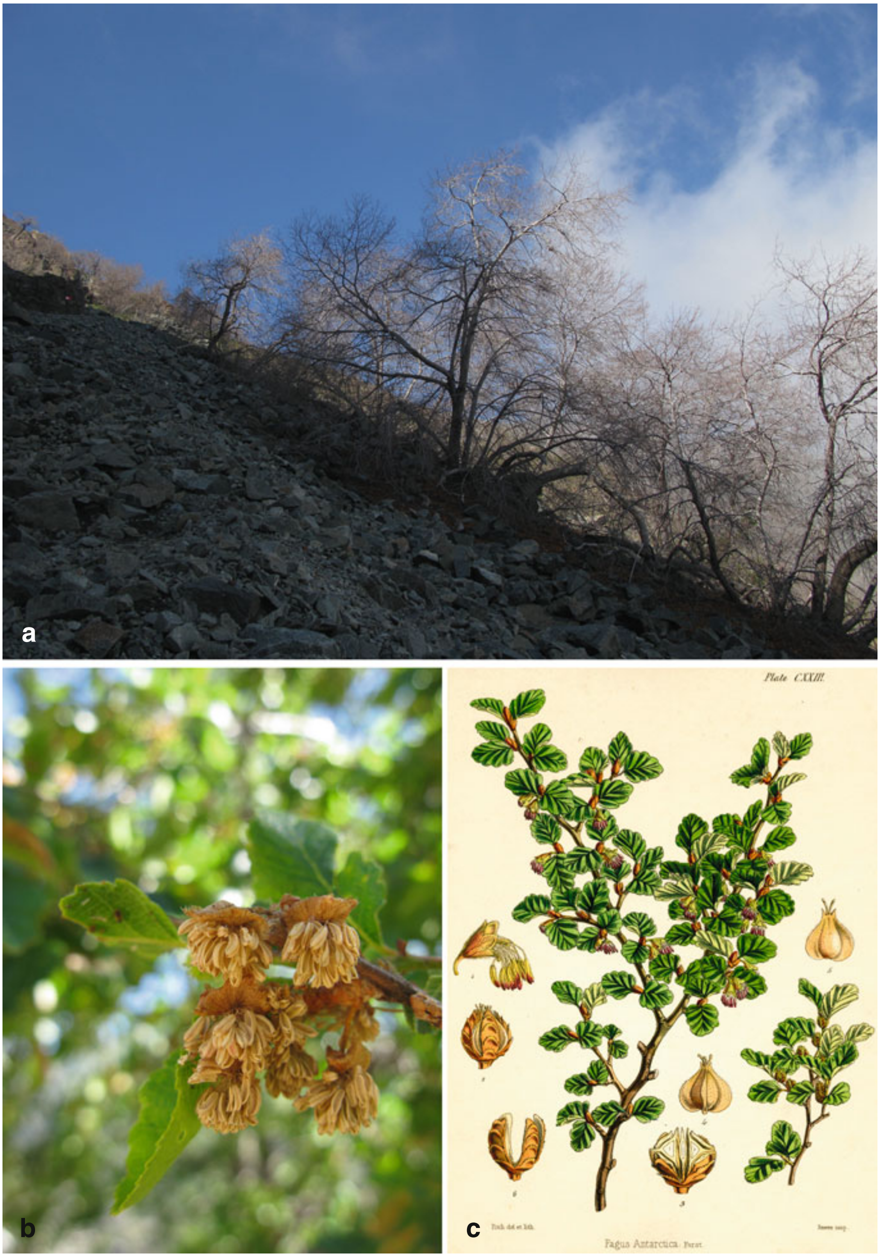

Fig. 9.1 *Nothofagus* species: **a** *N. macrocarpa*, Cerro El Roble; **b** *N. glauca*, flowers, Altos de Lircay (photos A. Moreira-Muñoz); **c** *N. antarctica* (plate 123 in Hooker JD (1847) The Botany of the Antarctic Voyage . . . London (Chapter 2))

Fig. 9.1 (continued) **d** *N. alpina*; **e** *N. alessandrii*, Los Ruiles; **f** *N. dombeyi* and *N. glauca*, Altos de Lircay; **g** *Cyttaria* sp., Altos de Lircay (photo/illustration credits: **e**, **f** A. Moreira-Muñoz; **g** S. Elórtegui Francioli; **d** plate 197 in Poeppig and Endlicher (1835–1845) Nova genera et species plantarum . . . Leipzig (Chapter 2))

Jordan 1993), on the base of morphological similarities like the cupule. However, Nixon (1989) argues that *Nothofagus* is not closely related to *Fagus*, but it shares some important apomorphic features with the family Betulaceae. In accordance with Nixon's point of view, temperate *Nothofagus* species share some leaf characters with representatives of the Betulaceae. These characters, such as a leaf margin with compound teeth, and analogous venation types, are distinct from those of *Fagus* (Li and Zhou 2007). These authors suggest that extant *Nothofagus* species could be classified into two groups: tropical species usually having an entire leaf margin, and temperate species having teethed or crenate margins. Since the venation types of these two groups are also different, Li and Zhou (2007) further suggest that the genus may be split in several genera.

Van Steenis (1971) indeed divided the genus *Nothofagus* into two sections: *Nothofagus* and *Calusparassus*: the first section encompassing the deciduous species from South America and the deciduous *N. gunnii* from Tasmania. Van Steenis (1971) interpreted the characteristics of the cupule as very relevant for the phylogeny, suggesting a “progression rule” in the ornamentation of the cupule and a reduction in seed number (Fig. 9.2). In the section *Calusparassus* he included the evergreen species of Australasia and the three South American evergreen species (*N. betuloides, N. dombeyi,* and *N. nitida*). Most recent taxonomic studies tend to dismiss the deciduous/evergreen character as important in the classification, favoring instead the morphological characteristics of the pollen. The deciduous/evergreen character would have more ecological than phylogenetic significance (Ramírez et al. 1997). The possibility of hybridization between deciduous species (Donoso et al. 1990) and between deciduous and evergreen species (Stecconi et al. 2004) supports this view. According to the differences in pollen, several authors recognize four monophyletic groups classified as subgenera: *Brassospora, Nothofagus,*

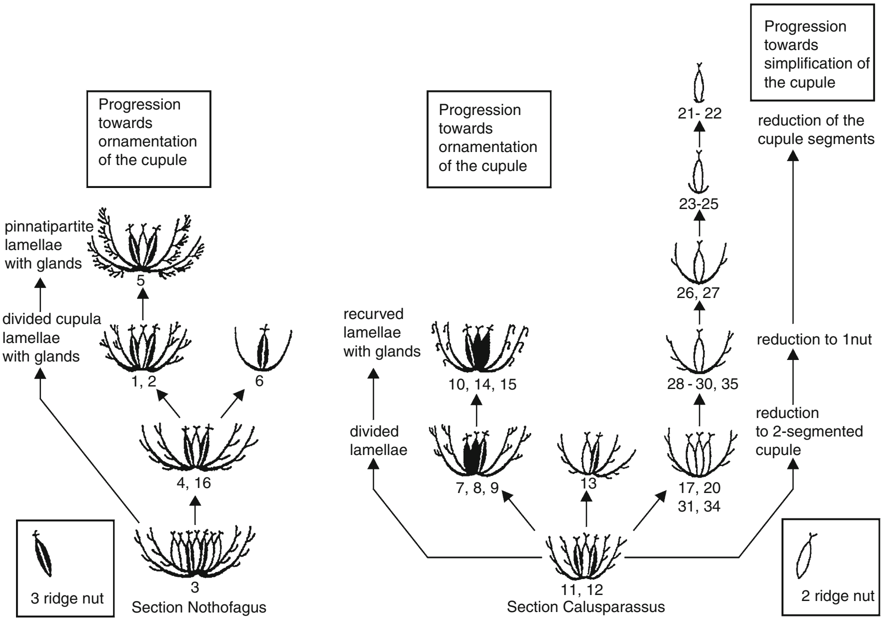

Fig. 9.2 Illustration of the cupules of *Nothofagus* species (adapted from Van Steenis 1971, also reproduced in Gottlieb 2001). Numbers refer to the species in Table 9.1

Table 9.1 Species composition and geographical distribution of the *Nothofagus* subgenera. Source: several authors in Veblen et al. (1996) and Rodríguez and Quezada (2003) for South American species. (Numbers after the species refer to numbers in Fig. 9.2). *Nothofagus leonii* is considered as a hybrid between *N. glauca* and *N. macrocarpa*

Subgenus	Pollen type	Distribution	N° sp.	Species
Nothofagus	*fusca* type b	South America (SA)	5	*N. antarctica* (4), *N. betuloides* (7), *N. dombeyi* (9), *N. pumilio* (6), *N. nítida* (8)
Fuscospora	*fusca* type a	South America (SA)	1	*N. alessandrii* (3)
		Tasmania (TAS)	1	*N. gunnii* (16)
		New Zealand (NZ)	3	*N. truncata* (12), *N. fusca* (11), *N. solandri* (13)
Lophozonia	*menziesii*	South America (SA)	4	*N. alpina* (5), *N. glauca* (2), *N. macrocarpa*, *N. obliqua* (1)
		New Zealand (NZ)	1	*N. menziesii* (10)
		Australia (AUS) – Tasmania (TAS)	1	*N. cunninghamii* (15)
		Australia (AUS)	1	*N. moorei* (14)
Brassospora	*brassi*	New Caledonia (NC)[a]	5	*N. balansae* (33), *N. baumanniae* (34), *N. codonandra* (32), *N. discoidea* (35), *N. aequilateralis* (31)
		New Guinea (NG)	14	*N. brassii* (20), *N. carrii* (23), *N. crenata* (28), *N. flaviramea* (24), *N. grandis* (29), *N. nuda* (18), *N. perryi* (17), *N. pseudoresinosa* (27), *N. pullei* (22), *N. resinosa* (21), *N. rubra* (30), *N. starkenborghii* (19), *N. stylosa* (25), *N. womersleyi* (26)

[a] New Caledonian species still need a careful taxonomic revision, according to Munzinger (2010).

Fuscospora and *Lophozonia* (Hill and Read 1991; Hill and Jordan 1993; Manos 1997) (Fig. 9.3).

Hill and Jordan (1993) proposed the subgenus *Fuscospora* as basal in the phylogeny, including the species *N. alessandrii*,[1] also proposed by van Steenis (1971) as the most ancient species of the genus because of their domes of 7 flowers (Fig. 9.2). However, Manos (1997), based on morphological and molecular analysis, placed the subgenus *Lophozonia* at the basis of the phylogeny, as shown in Fig. 9.3. Nevertheless, Manos (1997) recognized that *Fuscospora* shows many ancestral characters, so it does not appear as monophyletic in all the trees. The subgenera *Nothofagus* and *Brassospora* appear as the most derived groups.

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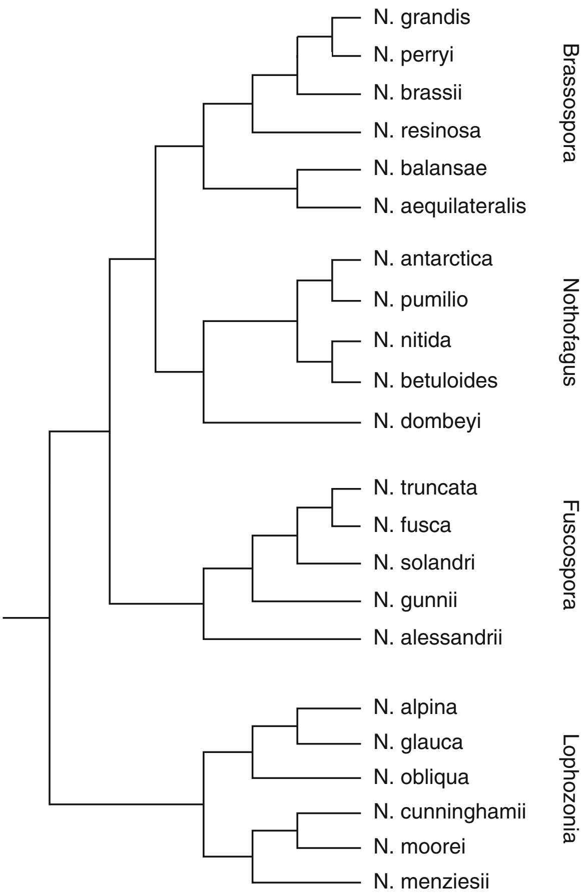
[1] Apart from its phylogenetic relevance, this is one of the most threatened plant species in Chile (Torres-Díaz et al. 2007, see also Sect. 6.2).

Fig. 9.3 Phylogenetic hypothesis for *Nothofagus* (adapted from Manos (1997), updated for subgenus *Nothofagus* from Acosta and Premoli (2010))



The interespecific relationships within of the subgenus *Nothofagus* has been recently studied by Acosta and Premoli (2010). They analyzed morphology and sequences of chloroplast and nuclear DNA and found good support for the monophyly of the subgenus, and according to the results shown by nuclear DNA, the evergreen species *N. dombeyi* and *N. betuloides* differentiated more recently. These species together with *N. nitida* are sisters to the deciduous *N. antarctica. Nothofagus pumilio* (deciduous) seems to have a different and earlier evolutionary history (Fig. 9.3). Chloroplast DNA did not show a clear specific differentiation, but varied instead with geographic location.

9.2 Diversity and Distribution

The extant 36 species of the genus *Nothofagus* are distributed in the territories of the South Pacific, from 33° to 55°S in South America (Chile and Argentina), and from 0° to 47°S in Australasia: New Guinea (including the Islands d'Entrecasteaux and

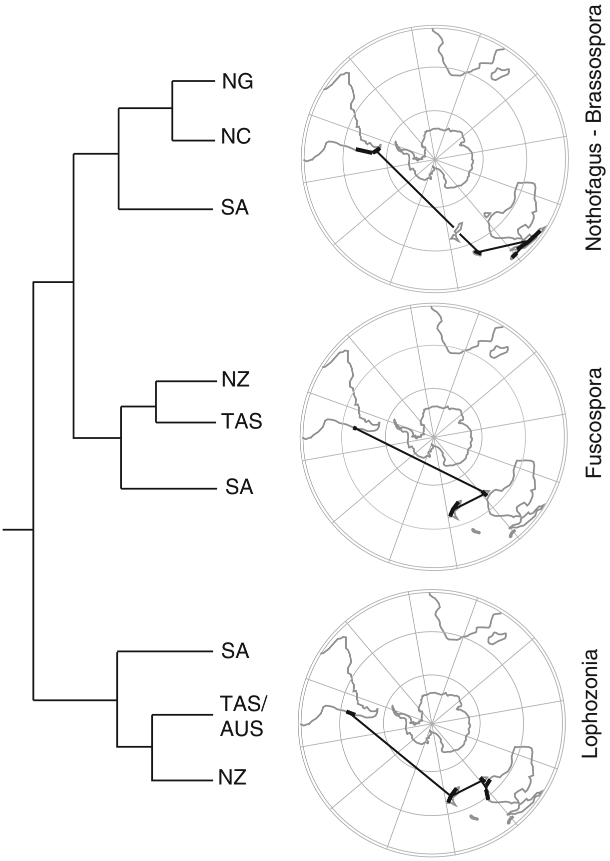


Fig. 9.4 Area cladogram (areagram) of *Nothofagus* subgenera; tracks represent the disjunct distribution of the subgenera: abbreviations of the territories according to Table 9.1 (adapted from Moreira-Muñoz 2004)

New Britain), New Caledonia, Australia, Tasmania and New Zealand (van Steenis 1971) (Fig. 9.4 and Table 9.1).

The geographic relationships have been represented in Fig. 9.4 as an area cladogram, following the phylogenetic hypothesis of Manos (1997). Figure 9.4 also show the tracks that join the species that compose the subgenera, showing three disjunctions: between species in *Lophozonia*, between species in *Fuscospora*, and the disjunct pattern between the subgenera *Nothofagus* and *Brassospora*.

The distribution of the genus in Chile encompasses half of the country's latitudinal extent from 33°S to the South (Fig. 9.5). Two cores of species richness can be identify: a little one at 36°–37°S and a second spreader one between 39° and 42°S. Several species occupy both cores, i.e. *N. alpina, N.antarctica, N. dombeyi, N. obliqua,* and *N. pumilio*, while *N. glauca* is restricted to the northern centre. The southern centre lacks *N. glauca* but incorporates *N. betuloides* and *N. nitida* from 40° to the South. *N. alpina* reaches only 41°S (Fig. 9.5).

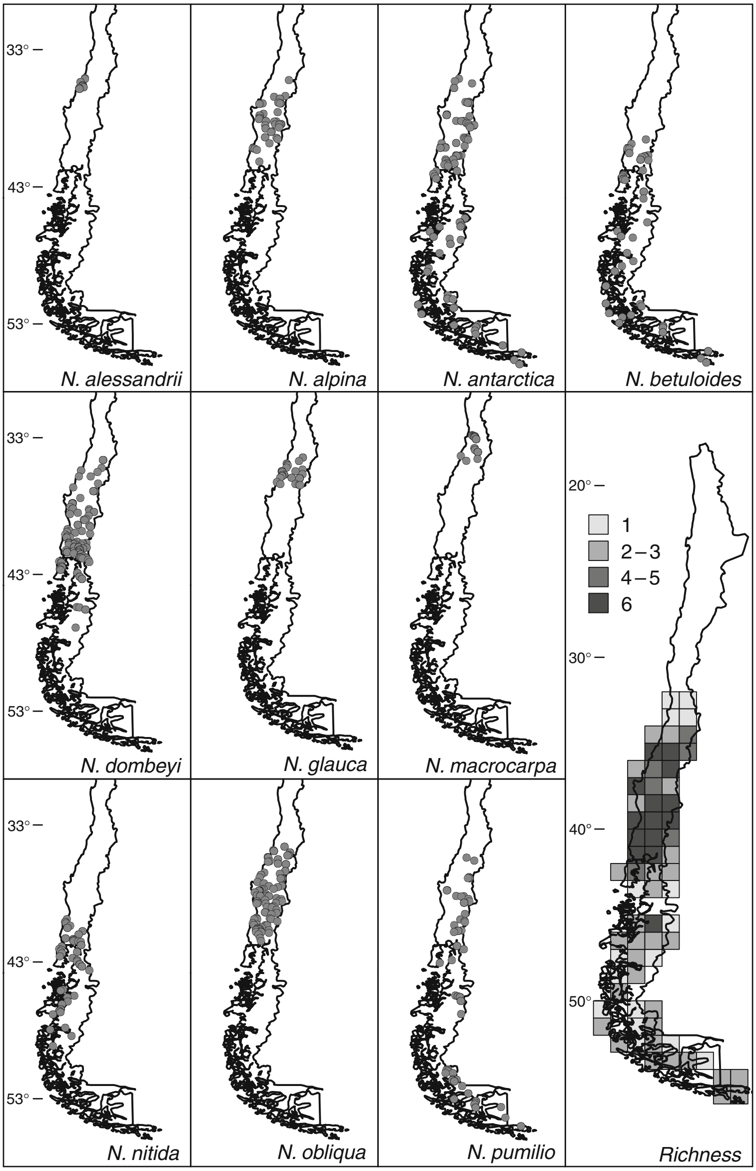


Fig. 9.5 Distribution and species richness of *Nothofagus* in Chile (collections SGO)

9.3 Speciation v/s Extinction

Hill (2001a), among others, suggests that *Nothofagus* was much more diverse in the past and the number of species remaining today is relatively small compared to its peak diversity, possibly during the Late Oligocene-Early Miocene. He also argues that this was also the time of maximum spatial distribution of the genus (although in Chile the northernmost expansion was during the Maastrichtian; see Chap. 1). Hill (2001a) emphasizes that it is difficult to study the evolutionary history of *Nothofagus* based exclusively on evidence from extant species.

Nothofagus fossils are found in almost all regions of occurrence of the extant species. Fossils have also been discovered in Antarctica, particularly in the Antarctic Peninsula and its nearby islands (Torres 1984, 2003) (Box 9.1). Among macrofossils, leaves are most common, followed by fossil wood and cupules; these latter are extremely rare, reported only from Tasmania (Hill 2001b). Fossil wood resembling extant Nothofagaceae has been traditionally classified under the organ genus *Nothofagoxylon* (Poole 2002).

While the description and interpretation of both macro-and microfossils of *Nothofagus* is not without difficulties (Hill 2001a), the fossil record of the genus is one of the most informative in the palaeobotany of the southern hemisphere. Even its absence is informative: the lack of fossils of the genus in India and Africa suggests an origin and radiation after the separation of these territories at the beginning of the fragmentation of West Gondwana. Both stratigraphically and geographically, pollen fossils are the most common. Fossil pollen is especially useful because it is produced in large quantities, is morphologically distinctive and very well preserved in sediments (Dettmann et al. 1990; Hill and Dettmann 1996; Hill 2001a). The oldest known occurrence involves the presence of the four types of pollen (*brassii, fusca a, fusca b, menziesii*) in deposits from the upper Cretaceous of Antarctica (Campanian = ca 83 mya) and South America (Maastrichtian = ca 70 mya) (Table 9.2). The four types have been also found in more modern deposits from Australia, Tasmania and New Zealand. This suggests an ancestral continuous distribution of the four subgenera, from South America to Australasia via Antarctica, until the removal of *Nothofagus* forests from Antarctica during the Pliocene (Hill and Dettmann 1996) (Box 9.1).

Table 9.2 Microfossil *Nothofagus* (pollen) for different epochs and territories during the Late Cretaceous and the Cenozoic. Simplified from Swenson et al. (2001)

	Lophozonia	*Fuscospora*	*Nothofagus*	*Brassospora*
Miocene (23–5 mya)	–	–	–	New Guinea
Eocene (53–34 mya)	New Zealand, Tasmania	–	–	New Zealand
Palaeocene (65–53 mya)	Australia	Australia, Tasmania, New Zealand	Australia, Tasmania, New Zealand	Australia, Tasmania
Campanian/ Maastrichtian (83–65 mya)	Antarctica, South America	Antarctica, South America	Antarctica, South America	Antarctica, South America

Box 9.1 The Green Dress of Antarctica

Antarctica was covered by forests from the Permian onwards (Chap. 1, Fig. 1.10) (Torres 2003; Francis et al. 2008). The evolution of the Antarctic climate from a greenhouse into the Neogene icehouse is captured within a rich record of micro- (pollen) and macrofossils (leaves, wood, and flowers) from the Antarctic Peninsula and the Transantarctic Mountains (Francis et al. 2008). In the Early Cretaceous, the Antarctic forest ecosystem was dominated by a conifer-fern community similar to that in the warm temperate araucarian–podocarp rainforests of present-day New Zealand's North Island (Falcon-Lang et al. 2001). In the Late Cretaceous flowering plants radiated throughout Gondwana changing the Antarctic physiognomy to one more similar to the angiosperm-dominated cool temperate Valdivian rainforests of present-day Chile. Characteristic taxa were Nothofagaceae, Myrtaceae, Eucryphiaceae (=Cunoniaceae), Lauraceae, Monimiaceae, Araucariaceae, Cupressaceae, Podocarpaceae and Winteraceae (Eklund 2003; Poole and Gottwald 2001; Poole and Cantrill 2006). The similarities to the Valdivian rainforests strengthened into the Cenozoic and become dominant up until the Eocene (Poole and Cantrill 2006). By the Eocene (48 mya), Antarctic rainforests were also inhabited by a rich vertebrate assemblage (Reguero

Fig. 9.6 Illustration of the biotic assemblage from the Oligocene of the Antarctic Peninsula. Steppes were inhabited by ratites, palaeolamas, penguins' ancestors. Forests of *Araucaria* and *Nothofagus* were inhabited by little marsupials, among others. The continent's inland showed already the beginning of the gradual massive glaciation (original drawing by Sergio Elórtegui Francioli)

et al. 2002). Forests were increasingly reduced in area and diversity, due to the global climate cooling and the initial formation of the Antarctic ice sheets at the Eocene/Oligocene boundary (34–35 mya) (Fig. 1.10 and 9.6) (Zachos et al. 2001; Francis and Poole 2002; Siegert et al. 2008). The development of the Antarctic Circumpolar Current (ACC), related to the openings of the Drake Passage and the Tasman Gateway (~45–30 mya), may have generated Antarctica's own glaciation and processes of continental cooling (Denton et al. 1991; Convey et al. 2008). There is no agreement on exactly when between 41 and 24 mya the ACC was initiated (Lawver and Gahagan 1998, 2003; Scher and Martin 2006; Livermore et al. 2007), but it most certainly allowed the ice sheets persistence on Antarctica during the Oligocene (till 27 mya). From this stage until the middle Miocene (~15 mya), the global ice volume remained low, due to a warming trend that reduced the extent of Antarctic ice. This warm phase peaked in the Mid-Miocene climatic optimum (17–15 mya), and was followed by a gradual cooling and reestablishment of a major ice-sheet on Antarctica (Zachos et al. 2001, see Sect. 1.2).

Antarctic vegetation became steadily more depauperate towards the end of the Miocene (Fig. 1.18). The Miocene–Pliocene was probably more similar to the current Magellanic tundra of southern Chile/Argentina (see Sect. 1.2), including local stands of angiosperms like *Nothofagus* and a few conifer taxa (Francis et al. 2008). It is likely that the vegetation went through a krummholz phase (e.g. *Nothofagus* decreasing in stature) prior to becoming dominant by low prostrate shrubs in the Pliocene tundra (Poole and Cantrill 2006). The timing of the Antarctic extinctions caused by the climate cooling are still under debate due to the paucity of Neogene fossil sites, possibly following the mid-Miocene warm interval at c. 17 mya or a mid-Pliocene warm interval at about 3 mya (Ashworth and Cantrill 2004). Pollen evidence from the Ross Sea basin indicates that tundra vegetation existed in East Antarctica from the Oligocene into the Early Miocene (Ashworth et al. 2007). As Antarctica's climate cooled further into the Plio-Pleistocene deep-freeze, and the continent became deprived of summer heat and liquid water, it lost almost all its vascular plants (Francis et al. 2008), with the only exception of *Deschampsia antartica* and *Colobanthus quitensis*.

As the four major lineages (subgenera) already existed in the Late Cretaceous (80 mya), before the total breakup of Gondwana, extant taxa could have undergone a process of sympatric speciation in a continuous geographic range (Swenson et al. 2001). The possibilities of hybridization between extant species support this hypothesis. Subsequent events of fragmentation of the biota would merely exacerbate the process of speciation. However, today's scenario might be mainly the result of extinctions (Manos 1997; Swenson et al. 2001). Fossil leaves and cupules similar to *N. betuloides* and *N. dombeyi* (subgenus *Nothofagus*) found in Oligocene deposits on Tasmania show the presence and subsequent extinction of this group in Australasia (Hill 2001b). Also the micro-fossil record shows the extinction of

Brassospora species in South America, Antarctica and New Zealand, and species of the subgenus *Nothofagus* in Antarctica, Tasmania and New Zealand (Manos 1997).

The greatest diversity of species of *Nothofagus* in south-eastern Australia happened between the Oligocene and Miocene, including the four subgenera and 10 species (Hill 2001a, b). Currently there are only two species in Australia (Table 9.1). The extinction in Australia includes the subgenera *Brassospora* and *Nothofagus* (as well as 10 genera of the Podocarpaceae and two genera of the Araucariaceae, according to Crisp et al. 2004).

9.4 Vicariance v/s Dispersal and Centres of Origin

The current disjunct distribution of the subgenera and the lack of any obvious means of trans-oceanic dispersal have led many authors to infer a vicariance explanation for the distribution, related to the fragmentation of Gondwana (Van Steenis 1971; Humphries et al. 1986; Gottlieb 2001). However, the species of the four extant subgenera do not group neatly into four geographic regions; instead there is considerable overlap (Heads 2006) (Fig. 9.4). There is also no clear congruence between species cladograms and the breakup sequence of Gondwana, and so a simple vicariance model has been rejected (Knapp et al. 2005; Cook and Crisp 2005). Thus discussion on the biogeography of the genus has developed into the usual vicariance vs. dispersal debate (Sect. 3.3), and shows little sign of resolution (Heads 2006).

The impression of JD Hooker upon his early visit to the southern territories was a scenario of an ancient continuous biota (including *Nothofagus* and other disjunct groups), then fragmented by geological and climatic events. Later biogeographers invented complicated narratives including centers of origin and dispersal. Darlington (1965) proposed, for example, a center of origin of *Nothofagus* in the northern hemisphere (Asia), with subsequent migration events to the South. Cranwell (1963), on the contrary, proposed a southern origin and subsequent radiation. Van Steenis (1971) raised the idea of contemporary developments of *Fagus-Nothofagus* from a parental "Fagacean" matrix in Southeast Asia, where there are now representatives from nearly every genus of the family Fagaceae. Van Steenis supported his evolutionary scenario by means of "land bridges", whose emergence at different times would have connected the territories of the extant disjunct species (see Sect. 10.4).

This hypothesis has been replaced by modern models of plate tectonics, giving support for the vicariance hypothesis, and several authors found that the phenomena of speciation are quite consistent with the events of fragmentation of Gondwana from the Cretaceous onwards (Linder and Crisp 1995). Swenson et al. (2001) specifically proposed vicariance events affecting the three subgenera: an event in the subgenus *Lophozonia* that occurred in the Eocene (35 mya), which corresponds to the separation of Antarctica/South America/Australia (Chap. 1); an event affecting *Fuscospora* when New Zealand/New Caledonia separated from Gondwana (Cretaceous, 80 mya), and which corresponds to the separation between New Zealand and New Caledonia and the rest of Gondwana; and possible also in the

Cretaceous an event that would have separated the species of *Brassospora* between New Caledonia and New Guinea. Disjunct taxa that are not explained by vicariance are explained as the result of long-distance dispersal, as in *N. gunnii, N. alessandrii* and *N. menziesii*.

Recently, Knapp et al. (2005) calibrated a relaxed molecular clock for 12 species (not including the subgenus *Brassospora*) using fossil ages, i.e. minimum ages. This analysis suggests that the relationships of the Australian and New Zealand *Lophozonia* and *Fuscospora* species are too recent to have roots in Gondwana, suggesting long-distance oceanic dispersal. The evolutionary relationship between the Australasian and South American *Fuscospora* lineages, however, seems to be consistent with vicariance.

Knapp et al. (2005) provided the first "unequivocal molecular clock evidence" that, whilst some *Nothofagus* transoceanic distributions are consistent with vicariance, trans-Tasman Sea distributions can only be explained by long-distance dispersal (see discussion in Box 3.3). Knapp et al. (2005) interpreted the absence of *Lophozonia* and *Fuscospora* pollen types in the New Zealand Cretaceous as evidence for Cenozoic dispersals of *Nothofagus* to New Zealand. The origins of New Zealand's biota have been the subject of much debate due to many authors proposing a complete drowning of these islands in the Oligocene and a relative recent recolonization (see Box 10.1). But others are much more cautious in the interpretation of the geological evidence.

Knapp et al. (2005) suggested that the biogeographic history of *Nothofagus* is more complex than envisaged under simplistic dispersal or vicariance scenarios. Also Cook and Crisp (2005) emphasized that both vicariance and dispersal played a role in the distributional patterns of extant *Nothofagus*. But Heads (2006) proposed that "the vicariant main massings of the four subgenera are compatible with largely allopatric differentiation and no substantial dispersal since at least the Upper Cretaceous (Upper Campanian), by which time the fossil record shows that the four subgenera had evolved". He further suggested that the complex geological origin of New Caledonia-New Guinea in which several allochtonous terranes played their role, has to do with the early differentiation of species in the subgenus *Brassospora*. He finally proposed that the breakup of Gondwana, was possibly too late to have been involved in the evolution of the extant subgenera. All four extant subgenera have a fossil record in the Upper Cretaceous, which gives a minimum age for all of them (Heads 2006).

Knapp et al. (2005) and Heads (2006) coincided in calling for the need for caution in evaluating fossil evidence. The fossil record doesn't necessarily capture when a species first appeared. Knapp et al. finally proposed that "the strength of our molecular analyses highlights the importance of future research into potential mechanisms of long-distance dispersal, and in particular reinvestigation of the transoceanic dispersal properties of *Nothofagus* seeds". There seems not too much to do in this respect, however, since the limited dispersal capacity of the fruits was already experimentally tested by Preest (1963), who showed that they cannot float and are not transported by birds. Burrows and Lord (1993) further calculated a limit of 10–15 km for wind transport.

9.5 Nothofagus and Associated Taxa

Several attempts have been made to integrate the biogeographic analysis of *Nothofagus* with its parasites, (e.g. Humphries et al. 1986). A very interesting relationship is that composed by several *Nothofagus* species and their associated *Cyttaria* species. *Cyttaria* is a fungi genus exclusively related to *Nothofagus* species, encompassing 7 species in Chile/Argentina and 4 in Australasia (Barrera 2004; McKenzie et al. 2000) (Fig. 9.1).

The phylogenetic hypothesis of this group (Crisci et al. 1988) shows an interesting relationship with the phylogeny of *Nothofagus* (Fig. 9.7): the most basal species of *Cyttaria* parasitize on species of the South American subgenus *Nothofagus*, while the most derived *Cyttaria* species parasitize on *Lophozonia* species, both South American and Australasian.

An independent phylogenetic analysis supports the monophyly of these two subgenera of *Nothofagus*. However, the phylogeny of *Cyttaria* challenges the relations between the subgenera, suggesting a closer relationship between *Lophozonia* and *Nothofagus*. Specifically regarding the relations of parasitism, "Fahrenholz's rule" predicts that in groups of permanent parasites the classification of the parasites usually corresponds directly to the natural relationships of the hosts (Mitter and Brooks 1983; Humphries et al. 1986).

These facts aggregate another point of complexity to the already questioned dispersal capacity of *Nothofagus*. *Nothofagus menziesii*, usually treated as a long-distance dispersal taxon (Knapp et al. 2005), is parasited by three species of *Cyttaria* of which *C. pallida* and *C. nigra* are exclusive parasites. That a species could disperse with its own parasites is as improbable as an orchid dispersing with its mycorrhiza (Sect. 3.3).

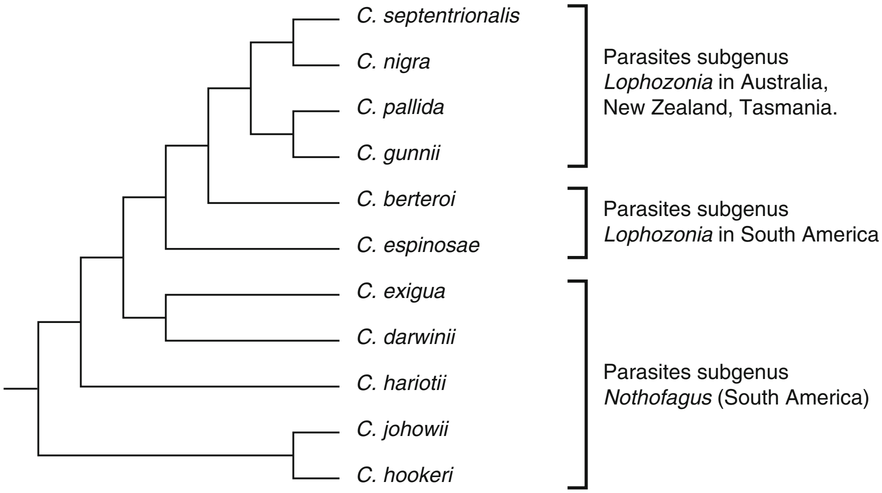


Fig. 9.7 *Cyttaria* species and their hosting subgenera (from the phylogeny by Crisci et al. 1988)

9.6 Synthesis and Outlook

In spite of the fact that *Nothofagus* has long been a traditional study object in biogeography, few facts really show “unequivocal evidence” (sensu Knapp et al. 2005). Results from the most recent studies on extant and fossil leaves (Li and Zhou 2007), on molecular phylogeny (Acosta and Premoli 2010), on molecular dating (Knapp et al. 2005), and species main massings (Heads 2006) suggest several challenges for the future research.

(1) *Nothofagus* most likely originated in high latitude regions of the Southern Hemisphere, encompassing Antarctica, southern South America, New Zealand and Australia, during the Early Campanian (Late Cretaceous). The genus quickly diversified there, and then dispersed gradually to lower latitudes during the Latest Cretaceous and Palaeogene; whether this process of dispersal was over terrestrial surfaces or across oceanic barriers is still a matter of discussion;

(2) A more profound analysis of closely related taxa of host-specific parasites, like *Cyttaria*, could throw more light on this still controversial issue. Other relations of parasitism like the one with the temperate South American *Misodendrum* could be also explored (see Muñoz-Schick 2004)

(3) *Nothofagus* fossil pollen is usually considered as more reliable than macrofossils like leaf impressions (Hill 2001a), but Li and Zhou (2007) argue that research on fossil leaf impressions has emerged into a new era, greatly contributing to the investigations on biogeography, evolution and systematics. Specific morphological features still need to be analyzed under contrasting evolutionary scenarios/hypotheses.

(4) Molecular phylogenies need to be based on both nuclear and chloroplast DNA, together with comprehensive sampling methods (Acosta and Premoli 2010). Recent results from phylogeographic analysis of *Nothofagus* are adding interesting results to longstanding controversies like the “refugial debate” (Azpilicueta et al. 2009) (Box 1.7). In molecular dating, the interpretation of minimal v/s maximal ages in the fossil record is especially critical (Heads 2006).

(5) All this means that *Nothofagus*, extant and fossil, will most probably continue to be a “key genus in plant geography”. The gained status as endangered species of several members of the family, as is the case with *Nothofagus alessandrii* (see Sect. 6.2), confirm the urgent necessity of improve conservation actions on order to assure the possibilities of future research in this challenging biogeographic group.

References

Acosta MC, Premoli AC (2010) Evidence of chloroplast capture in South American *Nothofagus* (subgenus *Nothofagus*, Nothofagaceae). Mol Phylogenet Evol 54:235–242

Ashworth AC, Cantrill DJ (2004) Neogene vegetation of the Meyer Desert Formation (Sirius Group) Transantarctic Mountains, Antarctica. Palaeogeogr Palaeoclimatol Palaeoecol 213: 65–82

Ashworth AC, Lewis AR, Marchant DR (2007) Mid-Miocene extinction in Antarctica. 2007 GSA Denver annual meeting (28–31 Oct 2007)

Azpilicueta MM, Marchelli P, Gallo LA (2009) The effects of Quaternary glaciations in Patagonia as evidenced by chloroplast DNA phylogeography of Southern beech *Nothofagus obliqua*. Tree Genet Genomes 5:561–571

Barrera E (2004) Especies chilenas de *Cyttaria* Berkeley (Cyttariaceae). Rev Chagual (Jard Bot Santiago) 2:62–65

Burrows CJ, Lord JM (1993) Recent colonisation by *Nothofagus fusca* at Cass, Canterbury. NZ J Bot 31:139–146

Convey P, Gibson JAE, Hillenbrand C-D, Hodgson DA, Pugh PJA, Smellie JL, Stevens MI (2008) Antarctic terrestrial life – challenging the history of the frozen continent? Biol Rev 83:103–117

Cook LG, Crisp MD (2005) Not so ancient: the extant crown group of *Nothofagus* represents a post-Gondwanan radiation. Proc R Soc B Biol Sci 272:2535–2544

Cranwell LM (1963) Nothofagus: living and fossil. In: Gressitt JL, (ed) Pacific basin biogeography. Bishop Museum Press, Honolulu, HI, pp 387–400

Crisci JV, Gamundí I, Cabello MN (1988) A cladistic analysis of the genus *Cyttaria* (Fungi-Ascomycotina). Cladistics 4:279–290

Crisp M, Cook L, Stean D (2004) Radiation of the Australian flora: what can comparisons of molecular phylogenies across multiple taxa tell us about the evolution of diversity in present-day communities? Philos Trans R Soc B Biol Sci 359:1551–1571

Darlington PJ Jr (1965) Biogeography of the southern end of the world. Harvard University Press, Cambridge, MA

Denton GH, Prentice ML, Burckle LH (1991) Cainozoic history of the Antarctic ice sheet. In: Tingey RJ, (ed) The geology of Antarctica. Clarendon Press, Oxford, pp 365–433

Dettmann ME, Pocknall DT, Romero EJ, Zamaloa MdelC (1990) *Nothofagidites* Erdman ex Potonie 1960: a catalogue of species with notes on the paleogeographic distribution of *Nothofagus* BL (Southern Beech). N Z Geol Surv Palaeontol Bull 60:1–79

Donoso C (1993) Bosques templados de Chile y Argentina: variación, estructura y dinámica. Editorial Universitaria, Santiago

Donoso C, Morales J, Romero M (1990) Hibridación natural entre roble (*Nothofagus obliqu*a (Mirb.) Oerst.) y raulí (*Nothofagus alpina* (Poepp. & Endl.) Oerst.) en bosques del sur de Chile. Rev Chil Hist Nat 63:49–60

Eklund H (2003) First Cretaceous flowers from Antarctica. Rev Palaeobot Palynol 127:187–217

Falcon-Lang HJ, Cantrill DJ, Nichols GJ (2001) Biodiversity and terrestrial ecology of a mid-Cretaceous, high-latitude floodplain, Alexander Island, Antarctica. J Geol Soc 158:709–724

Francis JE, Poole I (2002) Cretaceous and Tertiary climates of Antarctica: evidence from fossil wood. Palaeogeogr Palaeoclimatol Palaeoecol 182:47–64

Francis JE, Ashworth A, Cantrill DJ, Crame JA, Howe J et al. (2008) 100 million years of Antarctic climate evolution: evidence from fossil plants. In: Cooper AK, Barrett PJ, Stagg H, et al. (eds) Antarctica: a keystone in a changing world. Proc 10th international symposium on Antarctic earth sciences. National Academies Press, Washington, DC, pp 19–27

Gottlieb M (2001) Zur Phylogenie un Phyto-/Paläophytogeographie der Südbuchen. Gattung *Nothofagus*. Mitt Dtsch Dendrol Ges 86:85–106

Heads M (1985) Biogeographic analysis of *Nothofagus* (Fagaceae). Taxon 34:474–480

Heads M (2006) Panbiogeography of *Nothofagus* (Nothofagaceae): analysis of the main species massings. J Biogeogr 33:1066–1075

Hill RS (2001a) Biogeography, evolution and palaeoecology of *Nothofagus* (Nothofagaceae): the contribution of the fossil record. Aust J Bot 49:321–332

Hill RS (2001b) *Nothofagus* cupules from Late Oligocene-Early Miocene sediments at Balfour, northwest Tasmania, Australia. Int J Plant Sci 162:683–690

Hill RS, Read J (1991) A revised infrageneric classification of *Nothofagus* (Fagaceae). Bot J Linn Soc 105:37–72

Hill RS, Jordan GJ (1993) The evolutionary history of *Nothofagus* (Nothofagaceae). Aust Syst Bot 6:111–126

Hill RS, Dettmann ME (1996) Origin and diversification of the genus Nothofagus. *In:* Veblen TT, Hill RS, Read J, (eds) The ecology and biogeography of *Nothofagus* forests. Yale University Press, New Haven, CT, pp 11–24

Humphries CJ (1981) Biogeographic methods and the southern beeches. In: Forey PL, (ed) The evolving biosphere. Cambridge University Press, Cambridge, pp 283–297

Humphries CJ, Cox JM, Nielsen ES (1986) Nothofagus and its parasites: a cladistic approach to coevolution. In: Stone AR, Hawksworth DL, (eds) Coevolution and systematics. Clarendon Press, Oxford, pp 55–76

Knapp M, Stöckler K, Havell D, Delsuc F, Sebastiani F, Lockhart PJ (2005) Relaxed molecular clock provides evidence for long-distance dispersal of *Nothofagus* (southern beech). PLoS Biol 3:38–43

Lawver LA, Gahagan LM (1998) Opening of Drake Passage and its impact on Cenozoic ocean circulation. In: Crowley TJ, Burke KC, (eds) Tectonic boundary conditions for climate reconstructions. Oxford Monographs on Geology and Geophysics 39. Oxford University Press, Oxford, pp 212–223

Lawver LA, Gahagan LM (2003) Evolution of Cenozoic seaways in the circum-Antarctic region. Palaeogeogr Palaeoclimatol Palaeoecol 198:11–37

Li RQ, Chen ZD, Lu AM, Soltis DE, Soltis PS, Manos PS (2004) Phylogenetic relationships in Fagales based on DNA sequences from three genomes. Int J Plant Sci 165:311–324

Li HM, Zhou ZK (2007) Fossil nothofagaceous leaves from the Eocene of western Antarctica and their bearing on the origin, dispersal and systematics of *Nothofagus*. Sci China Ser D Earth Sci 50:1525–1535

Linder HP, Crisp MD (1995) *Nothofagus* and Pacific biogeography. Cladistics 11:5–32

Livermore R, Hillenbrand C-D, Meredith M, Eagles G (2007) Drake Passage and Cenozoic climate: an open and shut case? Geochem Geophy Geosyst 8:Q01005. doi: 10.1029/2005 GC001224

Manos PS (1997) Systematics of *Nothofagus* (Nothofagaceae) based on rDNA spacer sequences (ITS): taxonomic congruence with morphology and plastid sequences. Am J Bot 84:1137–1155

McKenzie EHC, Buchanan PK, Johnston PR (2000) Checklist of fungi on *Nothofagus* species in New Zealand. N Z J Bot 38:635–720

Mitter C, Brooks DR (1983) Phylogenetic aspects of coevolution. In: Futuyama DJ, Slatkin M, (eds) Co-evolution. Sinauer Associates, Sunderland, MA, pp 65–98

Moreira-Muñoz A (2004) *Nothofagus* Bl., pieza clave en la reconstrucción biogeográfica del hemisferio austral. Rev Chagual (Jard Bot Santiago) 2:48–56

Munzinger J (2010) Origin of the Flora of New Caledonia, past and present knowledge. Abstract southern Connection congress, Feb 15–19, 2010, Bariloche, Argentina

Muñoz-Schick M (2004) El género *Misodendrum* DC. en Chile. Rev Chagual (Jard Bot Santiago) 2:57–61

Nixon KC (1982) In support of recognition of the family Nothofagaceae Kuprianova. Bot Soc Am Publ 162:102

Nixon KC (1989) Origins of Fagaceae. In: Crane PR, Blackmore S, (eds) Evolution, systematics, and fossil history of the Hamamelidae, vol 1. Clarendon Press, Oxford, 23–43

Poole I (2002) Systematics of Cretaceous and Tertiary *Nothofagoxylon*: implications for southern Hemisphere biogeography and evolution of the Nothofagaceae. Aust Syst Bot 15:247–276

Poole I, Gottwald H (2001) Monimiaceae sensu lato, an element of Gondwanan polar forests: evidence from the Late Cretaceous-early Tertiary wood flora of Antarctica. Aust Syst Bot 14:207–230

Poole I, Cantrill DJ (2006) Cretaceous and Cenozoic vegetation of Antarctica integrating the fossil wood record, vol 258. Geological Society, London, Special Publications, 63–81

Preest DS (1963) A note on the dispersal characteristics of the seed of New Zealand podocarps and beeches and their biogeographical significance. In: Gressitt JL, (ed) Pacific Basin biogeography. Bishop Museum Press, Honolulu, Hawaii, pp 415–424

Ramírez C, San Martín C, Oyarzún A, Figueroa H (1997) Morpho-ecological study on the South American species of the genus *Nothofagus*. Plant Ecol 130:101–109

Reguero MA, Marenssi SA, Santillana SN (2002) Antarctic Peninsula and South America (Patagonia) Paleogene terrestrial faunas and environments: biogeographic relationships. Paleogeogr Paleoclimatol Paleoecol 179:189–210

Rodríguez R, Quezada M (2003) Fagaceae. In: Marticorena C, Rodríguez R, (eds) Flora de Chile, vol 2. Ed. Universidad de Concepción, Concepción, pp 64–75

Scher HD, Martin EE (2006) Timing and climatic consequences of the opening of the Drake Passage. Science 312:428–430

Siegert MJ, Barrett P, Decont R, Dunbar R, Cofaigh CO, Passchier S, Naish T (2008) Recent advances in understanding Antarctic climate evolution. Antarctic Sci 20:313–325

Stecconi M, Marchelli P, Puntieri J, Picca P, Gallo L (2004) Natural hybridization between a deciduous (*Nothofagus antarctica*, Nothofagaceae) and an evergreen (*N. dombeyi*) forest tree species: evidence from morphological and isoenzymatic traits. Ann Bot 94:775–786

Swenson U, Hill RS, McLoughlin S (2001) Biogeography of *Nothofagus* supports the sequence of Gondwana break-up. Taxon 50:1025–1041

Torres T (1984) *Nothofagoxylon antarcticus* n. sp., Madera fósil del Terciario de la isla Rey Jorge, isles Shetland del Sur, Antártica. Ser Cient INACHI 31:39–52

Torres T (2003) Antártica: un mundo oculto bajo el hielo. Instituto Antártico Chileno, Punta Arenas

Torres-Díaz C, Ruiz E, González F, Fuentes G, Cavieres LA (2007) Genetic diversity in *Nothofagus alessandrii* (Fagaceae), an endangered endemic tree species of the coastal maulino forest of Central Chile. Ann Bot 100:75–82

Van Steenis CGGJ (1971) *Nothofagus*, key genus of plant geography, in time and space, living and fossil, ecology and phylogeny. Blumea 19:5–98

Veblen TT, Hill RS, Read J (eds) (1996) The ecology and biogeography of *Nothofagus* forests. Yale University Press, London

Zachos J, Pagani M, Sloan L, Thomas E, Billups K (2001) Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292:686–693

Part V

Where to from Here? Projections of Chilean Plant Geography

Chapter 10
All the Possible Worlds of Biogeography

> *For history is like a nymph glimpsed bathing between leaves: the more you shift perspective, the more is revealed. If you want to see her whole you have to dodge and slip between many different viewpoints*
>
> (Fernández-Armesto 1997, p 228).

Abstract Today anyone intending to integrate the different views that shape modern biogeography must confront the differences inherent to the diverse approaches involved in the discipline. In spite of the attempts to integrate different approaches into one coherent program of synthetical biogeography, the biogeographic arena is getting more and more fragmented due to a plethora of methods, and the ultimate synthesis is getting more and more elusive. The so-called "crisis of biogeography" seems to be related to a more general crisis of reductionistic modern science in its failure to account for the real world problems, as challenged by scientists inspired by postmodern theory. To what extent biogeography assumes and reflects the conflicts, presumptions and challenges inherent to (post)modern science must be kept in mind while analysing the Chilean plant geography.

10.1 The Fragmented Map of Modern Biogeography

As noted by Riddle (2005), among others, modern biogeography seems to suffer a protracted identity crisis, since there is an evident lack of fully integrative approaches. The plethora of methods that are in common use (see a revision by Crisci et al. 2003; Morrone and Crisci 1995) leaves no opportunity for this integration. Nelson and Ladiges (2001) characterized current biogeography as a "mess of methods" (Fig. 10.1).

No few attempts have been undertaken to propose a more integrative research program in biogeography (e.g. Croizat 1958; Myers and Giller 1988; Salomon 2001; Crisci et al. 2006). Any proposal will be challenging and conflicting: e.g. Donoghue and Moore's (2003) "integrative biogeography" program has been criticized because it has been used to reinforce equivocal divisions, such as that between phylogenetically and ecologically focused methods (Parenti and Ebach 2009). Indeed, together

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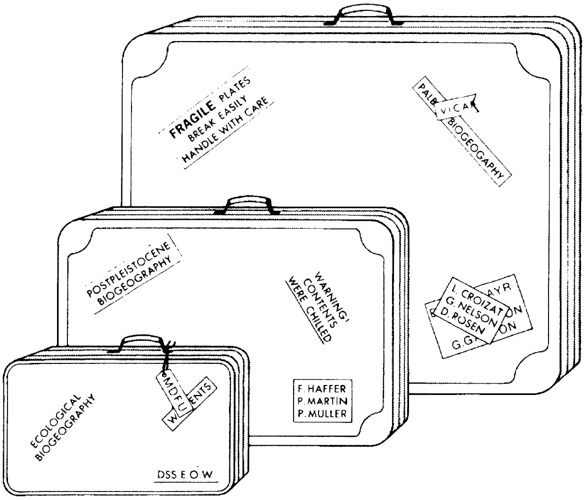

Fig. 10.1 Biogeographers' diverse conceptual and methodological "suitcases", according to Udvardy (1981), by permission of Columbia University Press

with the traditional conflict between dispersalism versus vicariance (Chap. 3), one of the most striking divides has been the one between ecological and historical biogeography. This "probably reflects the predominance of narrative rather than analytical methods in biogeography because narratives allow authors to cast their explanations in terms of rival beliefs rather than rigorous inferences. On the other hand, when analytical methods are used in biogeography, the patterns obtained from them may be neither wholly historical nor wholly ecological, and considerable refinement, testing and reasoning is needed if the effects of these processes are to be distinguished" (Rosen 1988, p 33). Several authors have maintained that this is rather an artificial conflict (e.g. Parenti and Ebach 2009) and there are several researchers working towards a more appropriate framework to overcome these binary opposites to generate a "free play of the opposites" (Crisci and Katinas 2009, p 1031).

10.2 Postmodern Biogeography: Deconstructing the Map

> We are living in a time in which postmodernism is constantly confronting the hegemonic speech of science to denounce its excesses and to expose its limits (Morrone 2003, p. 87)

After the period of discovery that marked the origin of modern nature sciences (with A. von Humboldt) "historical and ecological biogeography and their many subdivisions evolved, diverged, and eventually flourished (or languished) as increasingly more distinct disciplines" (Lomolino and Heaney 2004, p 1). This diversification and growth of distinctive scientific disciplines established a presumed *need* to specialize that resulted in more and more splintering. As a consequence of scientific specialization "…the grand view, the ultimate synthesis across space and time, became murky and more elusive" (Lomolino and Heaney 2004, p 1). But there seems to be still hope for this **great synthesis**, as it might "encourage creative development and applications of the **comparative approach**, deconstructing and reassembling more comprehensive explanations for the diversity and distribution of biotas" (Lomolino and Heaney 2004, p 2).

The deconstruction suggested by Lomolino and Heaney (2004) is in tune with the revision that is today occurring in many disciplines. After decades of reductionism, science has failed in helping to construct a more harmonic and inclusive world for humans and non humans, coming to the current global crisis of ethic values and nature destruction (Chap. 6). The reaction towards actual scientific splintering has canalized critics and alternatives in the so called postmodern science. This new pretended scientific paradigm has rapidly gained advocates and opponents (between the last e.g. Dawkins 1998; Attwell and Cotterill 2000). Advocates maintain that only postmodern science would "nurture the human hunger for quality: for beauty, balance, creative advance" (Ferré 1997, see also Dear and Wassmansdorf 1993). In his context, used and abused dualistic concepts like "objectivity" and "subjectivity" have been questioned: "objects are to be understood through their relations rather than as 'pure objects'… our knowledge of objects is neither objective nor subjective, but a complex outcome of knowing and action in an environment" (Jones 2008, p 1606).

The critical view of postmodernism left nothing untouched and our *Weltbild* is changing rapidly; the potential consequences are immense, and may provide the only possibility to heal our "fragmented culture" (Goodwin 2007) (see further Sect. 10.5). The way in which we do science is inseparable from the culture and the historical moment. As already discussed in Chap. 7: "…the striking, but culturally determined, exoticness of the Cactaceae still impacts our concept of what is relictual and derived for the family" (Griffith 2004).

Perhaps the first explicit proposal for a deconstruction of biogeography is a guest editorial that appeared in the *Journal of Biogeography* as: "Mesozoic tectonics and the deconstruction of biogeography" (Heads 1990). There, Heads proposed an alternative view for the evolution of the Australasian biota, arguing that "approaches to biogeography have been based all too often on consideration of particular lineages, emphasizing purely theoretical ancestor-descendant relationships and have maintained a blind spot towards the general effect of phases of modernization on a landscape and its biota". Since then M. Heads has been championing the developments in biogeographic theory integrating the findings of Croizat and philosophers like Derrida (Heads 2005a). Nowadays, deconstruction is being promoted not as an alternative to traditional academic research, but as a systematic approach in science: "deconstruction should be consciously performed as a methodological strategy" (Marquet et al. 2004, p 192; see also Ebach et al. 2003; Terribile et al. 2009). This method favoured recently a better interpretation of the fossil evidence of Ericaceae in New Zealand (Jordan et al. 2010) (see also Box 10.1).

Box 10.1 Circular Logic in the Drowning of New Zealand

The best example of the contest between geological versus biogeographical hypotheses affects interpretations on the origin of the New Zealand biota, which has been perhaps the most important of any regions in the world for biogeographic analysis (Nelson 1975; Gibbs 2006). According to a recent revision by Goldberg et al. (2008) “molecular studies of terrestrial animals and plants in New Zealand indicate that many taxa arrived since isolation of the land, and that diversification in most groups is relatively recent”. This is in accordance with the dispersalist view that most of New Zealand’s biota disappeared during the Oligocene (Pole 1994; Winkworth et al. 2002; McGlone 2005; McDowall 2008), and the area was recolonized over the last 22 million years across a huge oceanic gap via long-distance dispersal events, rather than simply persisting there for 80 million years. Waters and Craw (2006) criticized the apparent logical circularity in proposing the persistence of several groups like *Agathis* (Fig. 10.2), ratites, wrens, mammals, for 80 million years in “splendid isolation”. They invoke lack of geological evidence neglecting biogeographical evidence, but finally concluded that “available geological data thus neither confirm nor reject Oligocene drowning of New Zealand” (Waters and Craw 2006, p 352).

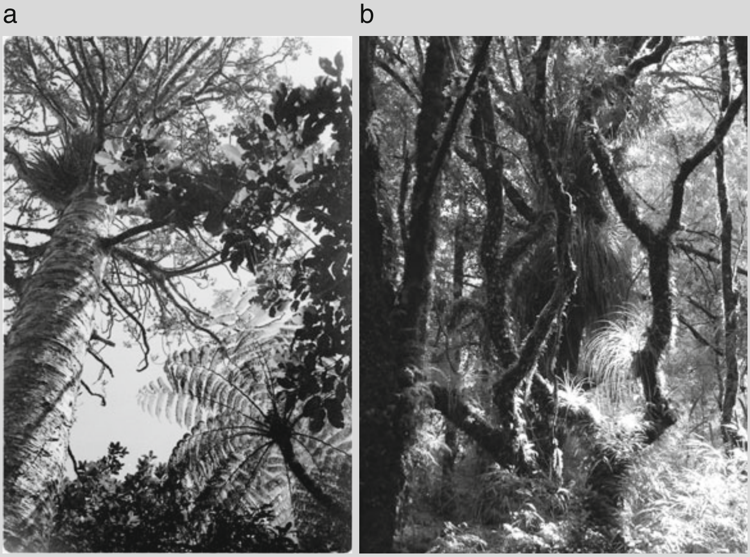

Fig. 10.2 Southern forests: **a** broad-leaved forest with *Agathis* and ferns at Coromandel, New Zealand; **b** Valdivian forest at Oncol, Chile. Photo credits: **a** A. Moreira-Muñoz; **b** S. Elórtegui Francioli

In support of the long splendid isolation is the continuous presence of *Agathis* in New Zealand (Stöckler et al. 2002; Lee et al. 2007), together with other plant taxa. Wanntorp and Wanntorp (2003) propose a continuous presence of *Gunnera* since the Cretaceous and others appoint for drastic drowning, but not all submersion of land (to ca 20% of the present land area, sensu Cooper and Cooper 1995). If we have a look at two independent recent global palaeoreconstructions, New Zealand does not appear submerged in the last 120 million years, neither at 25 mya in the Oligocene (Hall 2002; Sdrolias et al. 2003).

According to Michaux and Leschen (2005) "we have no way of knowing how much of the microcontinent [the Campbell Plateau] was above water by 25 mya: some must have done so to account for the persistence of palaeoendemics". They concluded that "the New Zealand Subantarctic Islands, Fiordland, Southland, Otago, and southern South America preserve a unique collection of west Gondwanan flora and fauna". These findings are coherent with results by Knapp et al. (2007): "ratites, wrens, mammals, and New Zealand Araucariaceae fossils do not support the hypothesis that New Zealand was completely submerged during the Oligocene". Physiognomic and floristic similarities between southern Chile and New Zealand last till today (Ezcurra et al. 2008).

Newest evidence from faunistic groups seems to support the continental nature and the persistence of New Zealand's biota: i.e. in the case of centipedes and meat harvestmen (Edgecombe and Giribet 2008; Boyer and Giribet 2009). Recent evidence also suggests that the subterranean freshwater fauna survived the presumed Oligocene inundation of New Zealand (Wilson 2008), as well as the fossil ancestors of extant tuatara recently found and dated at 19–16 mya (early Miocene) (Jones et al. 2009).

The dispersalist view was already contested by JD Hooker (see Sect. 3.3): "If the number of plants common to Australia and New Zealand is great, and quite unaccountable for by transport, the absence of certain very extensive groups of the former country is still more incompatible with the theory of extensive migration by oceanic or aerial currents. This absence is most conspicuous in the case of Eucalypti, and almost every genus of Myrtaceae, of the whole immense genus of *Acacia*, and its numerous Australian congeners . . ." (Hooker 1853, as quoted by Turrill 1953, p 152).

10.3 Sloppy Biogeography v/s Harsh Geology?

> Evolution is not a constant battle between the eaters and those to be eaten, but rather changes in organisms that are living and surviving on a dynamic Earth (Ebach and Humphries 2003).

As explained by McLoughlin (2001), detailed biogeographic understanding of the Southern Hemisphere floras must ultimately depend on a thorough understanding of the timing of geological and biological events that led to modern floristic distributions. In this sense, the fragmentation of Gondwana should have a big impact on biogeography and evolution of the southern floras. For most parts of Gondwana, the amalgamation and breakup phases and palaeoclimatic regimes are well documented via palaeomagnetic studies, radiometric dating, tectonostratigraphic analyses, palaeontological investigations and comparison of sedimentary facies (McLoughlin 2001) (see Table 1.1). Biogeographic hypotheses are being confronted with palaeogeographic scenarios, in an attempt to discover the processes underlying patterns. Biogeographic explanations are thus getting complicated: different models for the Gondwana fragmentation are entering the discussion and none of them fits well for every biotic group (Krause et al. 2006; Upchurch 2008).

Upchurch et al. (2002), expressed it in this way: "Clearly, there is not a perfect fit between the biogeographical patterns and palaeogeographical history, but there are several reasons why it would be premature to **reject** the biological signal: (i) palaeogeographical reconstructions are themselves **hypotheses** that potentially contain errors; (ii) congruence may increase as time-slicing and area selection are refined; (iii) the degree of congruence partly depends on *a priori* expectations regarding the effect of barriers on dispersal (e.g. phylogenetic divergence may commence before a barrier is fully developed); and (iv) the repeated area relationships are statistically supported signals that stand by themselves as patterns that require explanation" (Upchurch et al. 2002, pp 618–619). Croizat (1958) was the first to call for this independent view of biogeography as a discipline with own methods and tools. He proposed that biogeographers should not base all their study on geologically "well established" hypotheses. Biogeography, as a mature and independent discipline, should be able to develop its own hypotheses and theories **to compare** these with the geological theories. That is the way Alfred Wegener (1915) could develop his worldwide accepted theory (continental drift). At his time he was emphatically criticized by most geologists, but in the end the evidence imposed itself.

In the words of Heads (2005b, p 64): "assuming a priori that any particular geological event, such as the break-up of Gondwana, is relevant to biogeography is a fatal flaw of much biogeography, both dispersalist and vicariance… In fact, a great deal of evidence suggests biogeographic patterns involving New Zealand, New Guinea, New Caledonia, etc. were determined by earth history events both prior and subsequent to the break-up of Gondwana".

In concordance with this, recently some authors are calling for avoiding the circular logic in confronting biogeographical hypothesis with geological evidence (e.g. Renner 2005; Waters and Craw 2006) (Box 10.1). "Constraining nodes in a phylogenetic tree by geological events risks circularity in biogeographical analyses because it already assumes that those events caused the divergence, rather than testing temporal coincidence" (Renner 2005, p 552).

"Unfortunately, at the time we wrote this paper [on Proteaceae], we were misled by conservative geologists who had not got around to accepting continental drift, and our phytogeographic understanding was much distorted by this" (Johnston 1998, as quoted by McCarthy 2005b). McCarthy continues: "some still tend to elevate geological speculation over basic distributional realities. Implicit in papers that indulge in extravagant dispersalism and a plethora of just-right fossil absences is the notion that the basic principles of biogeography are wispy and yielding while geophysical theories are made of sterner stuff. Such papers appear to extend the legend that planetary scientists work in a field devoid of speculation, the belief that when a biogeographer and a geologist confront each other on a narrow path, the biogeographer must step aside" (McCarthy 2005b).

> Under a vicariance paradigm the classical pre-drift reconstruction of Pangea cannot adequately explain trans-Pacific tracks. Therefore, alternative paleogeographic models may be invoked as explanatory hypotheses: the lost continent Pacifica, island integration, a new reconstruction of eastern Gondwanaland, an expanding earth. None of these alternative models is fully compatible with all geological and biogeographic data available at present. It is stressed that biogeographic data and theories should not be made subservient to geological theories (Sluys 1994, p 42).

Also Linder and Crisp (1995) found that the biogeographic pattern found in *Nothofagus* (Chap. 9) was not congruent with geological hypotheses and wrote: "This is not congruent with the current geological theories, nor with the patterns evident from insect biogeography. We suggest that concordant dispersal is an unlikely explanation for this pattern, and propose that the solution might be found in alternative geological hypotheses" (Linder and Crisp 1995, p 5).

Here lies a big paradox in modern biogeography: palaeoreconstructions have been traditionally done integrating geological and paleontological information, i.e. biogeographical evidence, stratigraphic evidence, isotopic signature and palaeomagnetic data (Rapalini 2005). The integration of these different lines of evidence is full of conflict depending on the point of view and the data analysed. But usually botanists take the most accepted reconstruction, and try to fit the extant disjunct distributions with the major events in e.g. the splitting of Gondwana (e.g. split of Africa-America, split of Antarctica-South America, see Table 1.1). But the regional tectonic reconstructions suggest that the tectonic history is much more complicated and everywhere in the southern hemisphere there are geological and biotic composite areas: in Australasia (Morley 2001), New Zealand (Craw 1988), the Subantarctic Islands (Michaux and Leschen 2005), Tasmania (Heads 1999), New Guinea (Heads 2002) and certainly in southern South America (Crisci et al. 1991; Katinas et al. 1999).

10.4 Just Some Possible Worlds

As revised in the preceding section, alternative biogeographic scenarios are often in conflict with tectonic reconstructions, and gain therefore much less acceptation in the scientific community. Alternative palaeoreconstructions rest often on alternative methods that are not fully developed, like Dobson's (1992) spatial logics, which allows building alternative hypothesis of plates' fragmentation. Palaeoreconstructions with specific biogeographic implications for the Chilean flora will be briefly revised hereafter.

10.4.1 Connections Over Land Bridges

The idea of former land bridges on the sites of today's oceans, contrary to the current paradigm of plate tectonics, is not an old one, and like a circular idea, is constantly re-presented and re-rejected. Probably the first one who proposed and illustrated former lands between today's continents was Hermann von Ihering (1907), while studying the biogeographical connections of the Neotropical biota. He proposed ancient land connections between America and Africa and between Antarctica and Australasia that he called *Archinotis* and *Archhelenis,* respectively (Fig. 10.3a). Also Croizat (1952) proposed vast emerged lands between the shapes of current continents (Fig. 10.3b). The theory of land bridges was extendedly defended by CG van Steenis (1962). The idea of the land bridges has been recently called for again by Morley, explaining the biogeographical relationships between the American and African tropics (Morley 2003), the pantropics (Zhou et al. 2006) and between Cenozoic disjunct relict floras from Eurasia – North America (Milne 2006). Davis et al. (2002) favoured Palaeocene-Oligocene migrations between North America and South America via the Caribbean Basin for the Malpighiaceae, avoiding the classical dichotomy vicariance/long-distance dispersal.

10.4.2 And What About a Closer Pacific Basin?

> If we remove the *Pacifica* hypothesis we are left to choose another causal explanation for the repeating pattern of area (floristic) relationships, and other parts of the scenario remain intact. Even if we remove some taxa, we do not change anything significant about the whole picture. But if we remove the initial transpacific area pattern, everything collapses: there is no repeating pattern from which to extrapolate and for which to build complex scenarios (Grande 1994, p 76).

As discussed in Chap. 5 for the Juan Fernández islands, the floristic relationships between the islands and the austral territories of South America call for a better explanation than a simple relationship to the current closer territory. The proposal of a Pacifica continent West of South America fits perfectly within this scheme. This old idea has been revitalized under the umbrella of vicariance biogeography (Nur and Ben-Avraham 1977, 1981; Kamp 1980; Dickins et al. 1992) (Fig. 5.10b). The hypothesis has been firmly rejected on the base of geological arguments, not based on biogeographical patterns (Cox 1990). Ocean surface maps certainly do not leave us recognizing anything like a sunken continent west of South America, but we could still question if the old land was perhaps sunken into the trench?

The formation of the Pacific plate is crucial in this sense but has still many unresolved questions. It seems that it began to form in the Mid-Jurassic at the Tongareva triple junction (Larson et al. 2002). From here, the Pacific plate expanded at the expense of the Phoenix, Farallon and Izanagi plates that surrounded it (Smith 2007). Terrane accretion on the Gondwana–Pacific margin seems to have accompanied the plate formation (Vaughan and Livermore 2005). These authors proposed a Late Triassic–Early Jurassic deformation associated with the Pangaea breakup,

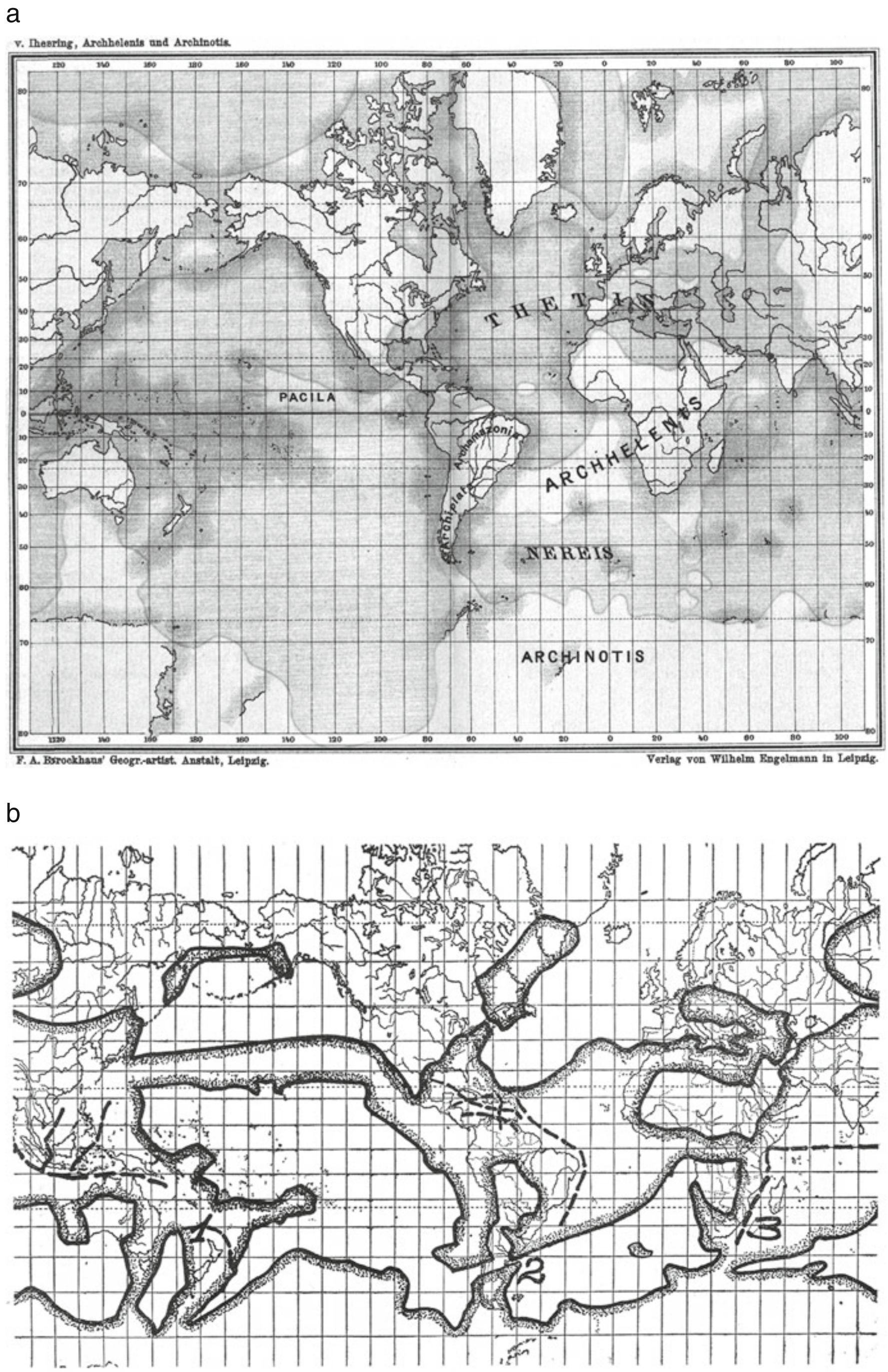

Fig. 10.3 **a** Land bridges proposed by von Ihering (1907), called *Archinotis* and *Archhelenis*; **b** land bridges proposed by Croizat (1952); *numbers* represent evolutionary "gateways"

and a mid-Cretaceous deformation. Possible effects of the last event are evident for the austral biogeography but the earlier one was probably just as important (Heads 2009).

In close relationship to the Pacifica continent hypothesis, lays the expanding Earth theory. First proposed by Lindemann (1927) and Hilgenberg (1933), it theorizes that all continents were united to form a single crust that encompassed a much smaller pre-Jurassic globe. The theory lost force during the twentieth century, in spite of being still defended by some researchers (e.g. Carey 1988; Vogel 1990). The theory was reanalysed specifically for biogeography by Shields (1998) and more recently by McCarthy (2003, 2005a,b, 2007).

McCarthy (2003) noted that the juxtaposition of New Zealand and southern Chile on expanding Earth palaeomaps provides a simple explanation (i.e. most parsimonious) for the distributions without need for additional hypotheses. According to this view, the oceanic crust did not begin forming between New Zealand and South Chile until 83.5 mya and even then the amount of Pacific Ocean crust between the two locations did not become significant for many tens of millions of years. “If the existence of Panthalassa is not assumed, then New Zealand and Chile would have remained in proximity until the Late Cretaceous and would have been separated by a narrow sealike barrier during the Eocene” (McCarthy 2003, p 1542). The close floristic relationship between the austral territories, i.e. the austral floristic realm (Chap. 4), and the persistence of numerous ancient groups in New Zealand seem to support this hypothesis. As recognized by Stevens (1997), closure of the Pacific Ocean considerably simplifies the links that occurred between New Zealand, West Antarctica and South America (Fig. 10.4).

These arguments are far from convincing traditional biogeographers, which paradoxically are rejecting the theory on the base of geologic arguments, not on the base

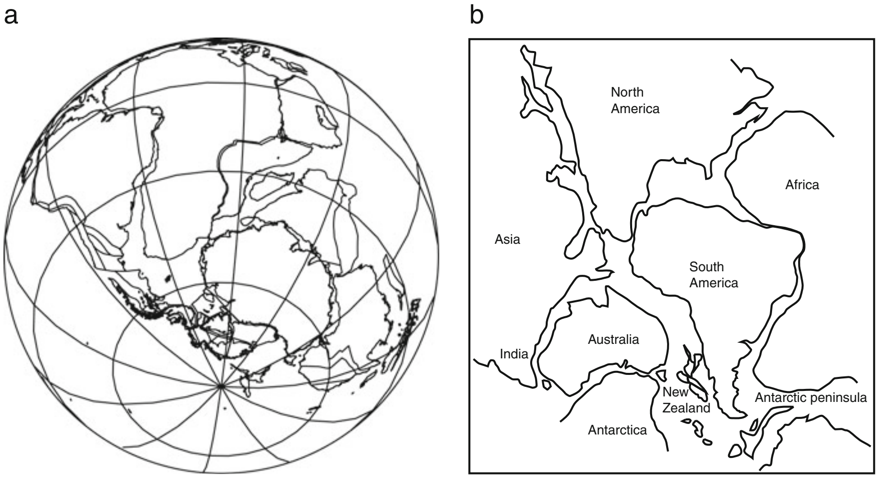

Fig. 10.4 Contrasting palaeoreconstructions: **a** the traditional model for the Late Jurassic based on the Time Trek program; **b** position of Australia and New Zealand close to South America considering a close Pacific basin (redrawn from Stevens 1997)

of biogeographical signal (Cox 1990; Briggs 2004; Ali 2006). But the theory is far from been amply rejected, as expressed by the collection of papers by the Italian geophysist G Scalera and collaborators (Scalera 2006, 2008; Scalera and Jacob 2003). Scalera (2007) proposes several methodological and theoretical aspects for gaining advance in this research field, like the development of changing-radius cartography and the reinterpretation of palaeomagnetism according to a different globe's radius at the epoch of primary magnetization. As a sign of the many challenges affecting modern biogeography, an expanding globe illustrates the cover of the book *Biogeography in a Changing World* (Ebach and Tangney 2007).

10.4.3 Three Models of Gondwana Fragmentation + One Dispersal

Not only radical views have to be considered as alternative explanations. When the model of Gondwana fragmentation has gained general acceptance, emerging views are challenging the timing of separation of the different landmasses and its implications for biogeography. As an example, most plate tectonic reconstructions assume that major continental blocks (Eurasia, Greenland, North America, South America, Africa, India, Australia and Antarctica) have separated from one another by the end of the Early Cretaceous. Hay et al. (1999) suggests this simplistic view may be incorrect, proposing instead three large continental blocks (North America-Eurasia; South America-Antarctica-India-Madagascar-Australia; and Africa) with large contiguous land areas surrounded by shallow epicontinental seas (Hay et al. 1999). Krause et al. (2006), explicitly compare two different separation scenarios for explaining the known distribution of Late Cretaceous terrestrial vertebrates from Madagascar (Fig. 10.5).

Upchurch (2008) newly proposed a practical approach for testing different models of Gondwana fragmentation with biogeographic data. Upchurch (2008) grouped the various models of Gondwanan biogeography in three alternative break-up models and one dispersal model: (a) *Samafrica model* (South America and Africa): break-up of Gondwana beginning in the Jurassic (175–140 mya), along a line from Somalia in the North to the Weddell Sea in the South; (b) *Africa-first model*: according to this vision Africa became isolated 140–120 mya whereas South America remained in contact with East Gondwana until ~80 mya; (c) *Pan-Gondwana model*: Gondwanan areas remained connected until ~80 mya and then separated almost simultaneously. The Pan-Gondwana model does not predict vicariance, because the simultaneous, rather than sequential, formation of barriers should not impose a distribution pattern on taxa and phylogenies (Upchurch 2008). These models are not necessarily exclusive.

At a more detailed scale, uncertainties persist regarding the separation of specific territories: "The time of onset of the ACC (Antarctic Circumpolar Current) is uncertain, and abundant speculation exists about its onset and effects. As knowledge of modern ocean circulation and the uses of the geological record have developed,

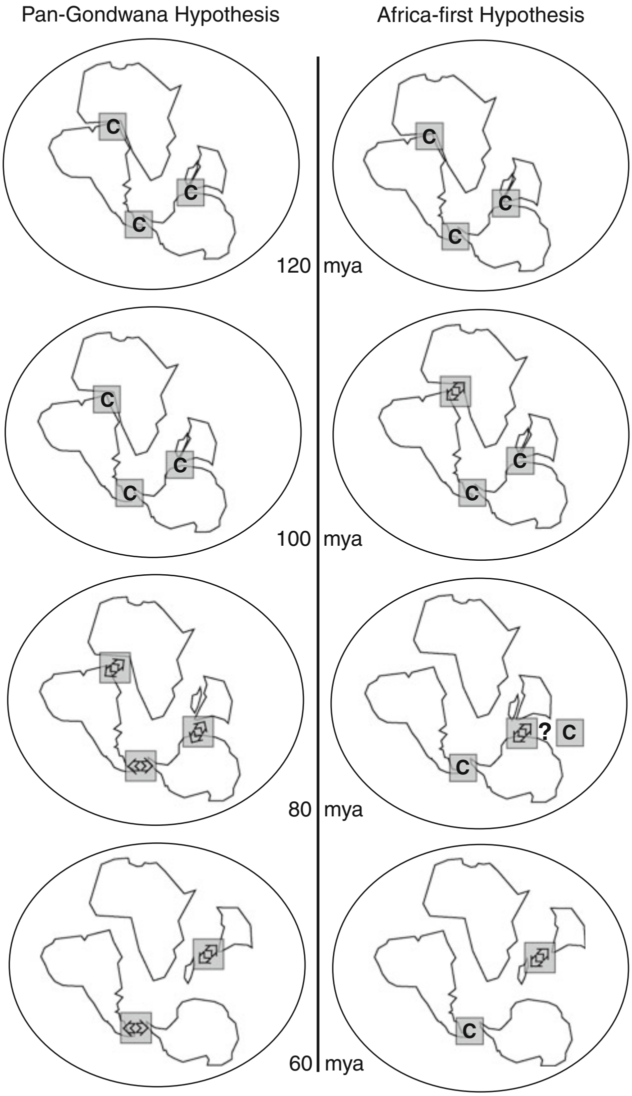

Fig. 10.5 Two different fragmentation scenarios for explaining the distribution of Late Cretaceous terrestrial vertebrates from Madagascar: *C* = connection; *arrow* = separation (adapted from Krause et al. 2006)

and as the palaeoceanographic data base has grown, so speculation has been refined, but the uncertainties in the ACC onset and subsequent variation remain significant" (Barkera and Thomas 2004) (see also Boxes 1.3 and 9.1).

Upchurch (2008) finished his discussion of the different models of Gondwanan fragmentation describing trans-oceanic long distance dispersal as a fourth biogeographical model, and he concluded that the current focus on vicariance versus dispersal is too narrow because it ignores **geodispersal** (i.e. expansion of species into areas when geographical barriers disappear), extinction, sampling errors, and palaeogeographical uncertainty (Upchurch 2008, pp 234–235).

He further emphasizes five critical points for the advancement in the field:

(1) conclusions arisen from current studies that seek to evaluate the importance of vicariance versus long-distance dispersal are dubious if they do not assess the effects of reticulation and distributional noise;
(2) palaeontological studies usually develop synthetic scenarios lacking analytical and statistically explicit methods that distinguish “genuine biogeographical patterns from distributional noise”;
(3) too often researchers tend to oversimplify biogeographical reticulation assuming that there is a single vicariance pattern caused by, and therefore congruent with, Gondwanan break-up;
(4) molecular biologists usually fail to explore (or even mention) uncertainties in palaeogeographical and palaeoclimatic reconstructions;
(5) a false impression that long-distance dispersal is the correct explanation for the distributions of organisms can appear as the consequence of sampling errors and multiple signals (Upchurch 2008, p 235).

He suggests that specialized methods (like pattern-spotting) “must be applied if an unbiased understanding of southern hemisphere biogeography is to be achieved” (Upchurch 2008, p 229). This seems to be in accordance with the more integrated and complementary programs in biogeography, like systematic biogeography (Williams and Ebach 2008), and evolutionary biogeography (Morrone 2007, 2009) (Box 10.2).

Box 10.2 Evolutionary Biogeography: Conciliating Distributions, Palaeogeographies, and Evolution

An evolutionary biogeographical analysis may involve five steps (Morrone 2007, 2009):

(1) recognition of biotic components (sets of spatio-temporally integrated taxa due to common history), through panbiogeography and methods used to identify areas of endemism;
(2) contrasting of the biotic components and identification of the vicariant events that fragmented them, through cladistic biogeography and comparative phylogeography;
(3) establishment of a hierarchic arrangement of the components in a biogeographic system of realms, regions, dominions, provinces and districts (i.e. biogeographic regionalization);

(4) identification of cenocrons (sets of taxa with similar origins and ages), dated using intraspecific phylogeography, molecular clocks and fossils; and
(5) formulation of a geobiotic scenario, that explains the evolution of the biotic components and cenocrons, integrating geological and tectonical information.

This evolutionary biogeography is a great step towards a more integrated biogeography and explicitly considers the systematic classification of areas, i.e. a systematic biogeography (cfr Williams and Ebach 2008). In the search for an even more integrative program, Parenti and Ebach (2009) propose a comparative biogeography that integrates both systematic and evolutionary biogeography.

These are good signals towards more integrated and analytical approaches in biogeography that will gain a more accurate picture from complex and mostly elusive patterns and processes in an increasingly changing and threatened global biota.

10.5 The "New Biogeography"

> . . . most of us are held captive by the notion of the world "out there", separate from us "in here." The moment we wake up to the fact that we are part of the world and engage in a conversation with her to get to know her (and ourselves) better, the captivity of a dualistic world view ends. We are freed to engage as participants in the world (Holdrege 2005).

The consideration of different scenarios for hypothesis testing is one practical solution to avoid the ad-hoc explanations that relegate biogeography as a mere descriptive discipline, usually "relegated to the interesting pay-off" in systematic studies (Upchurch 2006, p 6). "The greatest strides we can make in unlocking the mysteries and complexities of nature in this fundamentally interdisciplinary science are those from new synthesis and bold collaborations among scientists across the many descendant disciplines, long divergent but now reticulating within a strong spatial context – the **new biogeography**" (Lomolino and Heaney 2004, p 1). "We believe that the best means for advancing the frontiers of our science is to foster reintegration and reticulations among complementary research programs. The new series of synthesis –more complex, scale-variant, and multi-factorial views of how the natural world develops and diversifies – may be less appealing to some researchers, but it is likely to result in a much more realistic and more illuminating view of the complexity of nature" (Lomolino and Heaney 2004, p 2). Alas, this new biogeography will have to deal with complex science, with uncertainties, with deconstructions, all the challenges that shape the current scientific endeavour.

The new biogeographic synthesis seems to be in tune with Goodwin’s *new biology*: “The *new* biology is biology in the form of an exact science of complex systems concerned with dynamics and emergent order. Then everything in biology changes. Instead of the metaphors of conflict, competition, selfish genes, climbing peaks in fitness landscapes, what you get is evolution as a dance. It has no goal. As Stephen Jay Gould says, it has no purpose, no progress, no sense of direction. It’s a dance through morphospace, the space of the forms of organisms” (Goodwin in Brockman 1995, p 97). In the same line is the critique of reductionist ideological biologies and the search for alternative models that respects the complexity and freedom of organisms (Rose 1997). This has certainly to do with the still insufficiently known principles of the auto-organisation of life on the base of the proposals of Varela et al. (1974), and the recent increasing developments in evolutionary biology (evo-devo) (García Azkonobieta 2005). This development is already affecting systematic problems in plant biology (e.g. Frohlich 2006), and traditionally “hard” fields like palaeobotany are beginning a concerted effort with developmental biologists to reevaluate fossils (Sanders et al. 2007; Miller 2009 onwards). Specific (and old) questions like the origin of the flower (see Box 2.4), are being approached integrating molecular phylogenetic and palaeobotanical evidence (Doyle 2008), together with early environmental constraints (Feild and Arens 2005).

According to Goodwin (2007), newer developments show signs of a return to the idealistic integral science proposed by Alexander von Humboldt (Ette 2007; Greppi 2008), inspired by a Goethean approach to science. Goethean science is only recently getting recognition (Bortoft 1996; Ebach 2005; Goodwin 2007). In contrast to the dominating mechanistic doctrine, Goethe maintained that the scientist is not a passive observer of an external universe. Rather, the scientist is involved in a reciprocal, participatory relationship with nature. Goethean science is a science of relationship, of quality and of wholeness. “And we can use this kind of science to ask questions about all forms and functions of life” (Myers 1997), as a more qualitative approach which intends to encompass the complexity of biogeographic systems and geosystems (Spedding 2003).

Lomolino and Heaney (2004) continue with optimism: “The revitalization will continue in earnest, largely through the efforts of broad-thinking scientists who no longer shy away from but embrace the complexity of nature, and who foster collaborations and conceptual reticulations in modern biogeography” (Lomolino and Heaney 2004, p 2). “We are equally confident that the current and future generations of biogeographers will continue to advance its frontiers, developing a more comprehensive understanding of, and more successful strategies for conserving, the geography of nature” (Lomolino and Heaney 2004, p 3).

The practical applications of these novel methodological and theoretical developments in comparative and evolutionary biogeography are a powerful and promising framework for a potentially rapid and coherent development of Chilean plant geography in the near future.

10.6 Coda: The Geographical Nature of Biogeography

> Between geographers and historical biogeographers there has been relatively little communication and, like Stoddart [1985], I consider this a problem. By far the majority of those publishing work with biogeographical themes are biologists. Most biology-trained biogeographers appear to have little or no familiarity with the theoretical, philosophical, and methodological literature of geography; this, at least, seems to be the only conclusion that can be drawn from the almost total absence of referral to such in their papers (Smith 1989).

Modern geographic science has intrinsically a comparative nature, since the early theoretical and empirical advances by Bernhardus Varenius, Ferdinand von Richthofen and especially Alfred Hettner (Holt-Jensen 1999). Two approaches permeate the essence of geography since its very beginning as a modern science: "chorography" (detailed description of a place), and "chorology" (interrelations among places). "The goal of the chorological point of view is to know the character of regions and places through comprehension of the existence together and interrelations among the different realms of reality" (Hettner 1927, as quoted by Hartshorne 1960, p 13) (see Chap. 4). "It was reserved for our time, to see the **comparative geography** cultivated in masterly fashion, in its widest compass, indeed in its reflex on human history, on the relations of the form of the earth to the direction of the characteristics of peoples and the progress of civilization" (Humboldt in the first volume of the *Kosmos* [1845], as quoted by Hartshorne 1939, p 230 [54]). Humboldt was referring to Carl Ritter's work *Allgemeine Vergleichende Geographie* which "has shown that the comparative geography attains thoroughness only when the whole mass of facts that have been gathered from various zones, is comprehended in one view, is placed at the disposal of the integrating *(combinierenden)* intelligence" (as quoted by Hartshorne 1939, p 230 [54]).

Current comparative biogeography (cfr Parenti and Ebach 2009) is to some extent inherited from these early developments in geography, in spite of chorology following its own line of development (see Williams 2007). "We aim to establish a *comparative biogeography*, a method or approach that incorporates systematic biogeography (biotic relationships and their classification and distribution) and evolutionary biogeography (proposal of possible mechanisms responsible for distributions). We focus first on description and application of a systematic biogeography, to demonstrate biotic area homology, and then explore mechanisms or processes that may have given rise to general patterns" (Parenti and Ebach 2009, p 47).

It seems to be that, as expected by Lomolino and Heaney (2004), the "great synthesis" will come from the "encouraging creative development and applications of the **comparative** approach..." (Lomolino and Heaney 2004, p 2).

In this sense, challenges to biogeography are the same as for geography in its intent to apprehend the complexity of geosystems. In spite of its supposed holistic nature, geography is not exempted of a tendency to specialization and reductionism, and the field is on a search towards a modern applied systems theory (Egner 2006). "General system science's concern with historic processes and the dynamic self-determined relationships between systems structure, functioning and selfcreation may be more appropriate to geographical research" (Haigh 1985).

The new discourse of science policy called “mode 2” (Gibbons et al.1994), “insists that transdisciplinarity and engagement with end users and contexts of application are necessary both to meeting major societal challenges, such as sustainability and wealth creation, and to ensuring the public relevance (and funding) of science” (Demeritt 2009).

Turning to the beginning of this last chapter, the (post)modern map of (bio)geography shows enormous challenges but at the same time tremendous opportunities. The capacity and inspiration of researchers in geography and biology will hopefully open new horizons and help reconstruct the “fragmented map” of biogeography (Box 10.3).

Box 10.3 Willi Hennig’s “Criterion of Veracity”

Willi Hennig, the great theorist behind the current cladistics paradigm, explained the “criterion of veracity” of his phylogenetic approach, with the reconstruction of a fragmented map:

> Suppose a geographer has obtained fragments of a topographic map of an unknown land. He will make every effort to reconstruct the map from the fragments. How can he succeed if the original map is unknown to him? He was not present when the map was torn up. The geographer must try to assign each fragment to its original place in the total of all the recovered fragments. He will proceed by trying to find, for a portion of a river present on one fragment of the map, the adjoining piece of the same river on another fragment. If he directs his attention to a single geographic element in his map fragments, such as rivers, he is likely to go wrong. Thus the three sections of a river, a, a′, and a″ (Fig. 10.6a) could seem to be upper, middle, and lower parts of the same river. His error becomes obvious if he considers other elements (“characters”) of his map fragments. They remain isolated; pieces of roads and railroad lines do not join up (Fig. 10.6a). But if all geographic elements are satisfactorily fitted together (Fig. 10.6b) the geographer will be convinced that the fragments have been assembled *correctly*, even though he did not know the original condition of the map (Hennig 1966, pp 130–131).

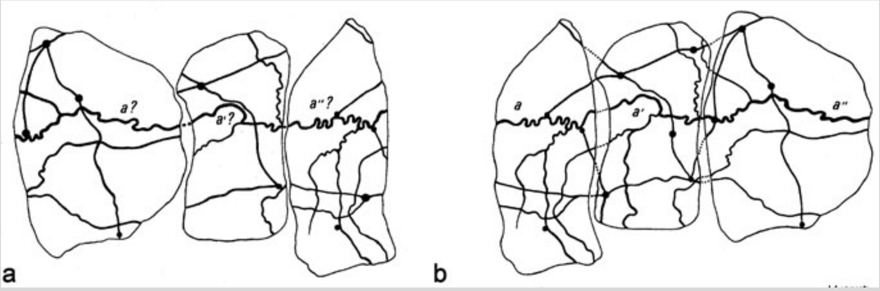

Fig. 10.6 Reconstruction of a fragmented map: **a** one possible but not correct solution; **b** voilá! the correct solution (from Hennig 1966), by permission of University of Illinois Press

All that we can do is re-collect and creatively juxtapose, experimenting with assertions and insertions of the spatial against the prevailing grain of time. In the end, the interpretation of postmodern geographies can be no more than a beginning (Soja 1989, p 2).

References

Ali JR (2006) Biogeographical and geological evidence for a smaller, completely-enclosed Pacific Basin in the Late Cretaceous: a comment. J Biogeogr 33:1670–1674

Attwell CAM, Cotterill FPD (2000) Postmodernism and African conservation science. Biodivers Conserv 9:559–577

Barkera PF, Thomas E (2004) Origin, signature and palaeoclimatic influence of the Antarctic Circumpolar Current. Earth Sci Rev 66:143–162

Bortoft H (1996) The wholeness of nature: Goethe's way of science. Floris Books, Edinburgh

Boyer SL, Giribet G (2009) Welcome back New Zealand: regional biogeography and Gondwanan origin of three endemic genera of mite harvestmen (Arachnida, Opiliones, Cyphophthalmi). J Biogeogr 36:1084–1099

Briggs JC (2004) The ultimate expanding earth hypothesis. J Biogeogr 31:855–857

Brockman J (1995) The third culture: beyond the scientific revolution. Simon and Schuster, New York, NY

Carey SW (1988) Theories of the earth and the universe: a history of dogma in the earth science. Stanford University Press, Stanford, CA

Cooper A, Cooper RA (1995) The Oligocene bottleneck and New Zealand biota: genetic record of a past environmental crisis. Proc R Soc Lond B 261:293–302

Cox CB (1990) New geological theories and old biogeographical problems. J Biogeogr 17: 117–130

Craw R (1988) Continuing the synthesis between panbiogeography, phylogenetic systematics and geology as illustrated by empirical studies on the biogeography of New Zealand and the Chatham Islands. Syst Zool 37:291–310

Crisci JV, Katinas L (2009) Darwin, historical biogeography, and the importance of overcoming binary opposites. J Biogeogr 36:1027–1032

Crisci JV, Cigliano MM, Morrone JJ, Roig-Juñent S (1991) Historical biogeography of southern South America. Syst Zool 40:152–171

Crisci JV, Katinas L, Posadas P (2003) Historical biogeography: an introduction. Harvard University Press, Cambridge, MA

Crisci JV, Sala OE, Katinas L, Posadas P (2006) Bridging historical and ecological approaches in biogeography. Aust Syst Bot 19:1–10

Croizat L (1952) Manual of phytogeography, or an account of plant dispersal throughout the world. Junk, The Hague

Croizat L (1958) Panbiogeography or an introductory synthesis of zoogeography, phytogeography, and geology; with notes on evolution, systematics, ecology, anthropology, etc. (3 vol.) Published by the author, Caracas, Venezuela

Davis CC, Bell CD, Mathews S, Donoghue MJ (2002) Laurasian migration explains Gondwanan disjunctions: evidence from Malpighiaceae. Proc Natl Acad Sci USA 99:6833–6837

Dawkins R (1998) Postmodernism disrobed. Nature 394:141–143

Dear M, Wassmansdorf G (1993) Postmodern consequences. Geogr Rev 83:321–325

Demeritt D (2009) Geography and the promise of integrative environmental research. Geoforum 40:127–129

Dickins JM, Choi DR, Yeates AT (1992) Past distribution of oceans and continents. In: Chatterjee S, Hotton N III, (eds) New concepts in global tectonics. Texas Tech. University Press, Lubbock, TX, pp 193–199

Dobson JE (1992) Spatial logic in paleogeography and the explanation of continental drift. Ann Assoc Am Geogr 82:187–206

Donoghue MJ, Moore BR (2003) Toward an integrative historical biogeography. Integr Comp Biol 43:261–270

Doyle JA (2008) Integrating molecular phylogenetic and paleobotanical evidence on origin of the flower. Int J Plant Sci 169:816–843

Ebach MC (2005) Anschauung and the archetype: the role of Goethe's delicate empiricism in comparative biology. Janus Head 8:254–270

Ebach MC, Humphries CJ (2003) Ontology of biogeography. J Biogeogr 30:959–962

Ebach MC, Humphries CJ, Williams DM (2003) Phylogenetic biogeography deconstructed. J Biogeogr 30:1285–1296

Ebach MC, Tangney RS (2007) Biogeography in a changing world. Systematics Association Special Volumes. CRC Press, Boca Raton, FL

Edgecombe GD, Giribet G (2008) A New Zealand species of the trans-Tasman centipede order Craterostigmomorpha (Arthropoda: Chilopoda) corroborated by molecular evidence. Invertebr Syst 22:1–15

Egner H (2006) Autopoiesis, form and observation – modern systems theory and its potential contribution to the integration of human and physical geography. Mitt der Österr Geogr Gesell 148:92–108

Ette O (2007) Towards world science? Humboldtian science, world concepts, and TransArea studies. In: Rehrmann N, Ramírez Sáinz L, (eds) Dos culturas en diálogo. Historia cultural de la naturaleza, la técnica y las ciencias naturales en España y América Latina. Madrid – Frankfurt am Main, Iberoamericana - Vervuert, pp. 121–150

Ezcurra C, Baccala N, Wardle P (2008) Floristic relationships among vegetation types of New Zealand and the southern Andes: Similarities and biogeographic implications. Ann Bot 101:1401–1412

Feild TS, Arens NC (2005) Form, function and environments of the early angiosperms: merging extant phylogeny and ecophysiology with fossils. New Phytol 166:383–408

Fernández-Armesto F (1997) Truth a history. Bantam Press, London

Ferré F (1997) The postmodern world. In: Meffe GK, Carroll CR, (eds) Principles of conservation biology, 2nd edn. Sinauer Associates, Sunderland, MA, pp 532–53

Frohlich MW (2006) Recommendations and goals for evo-devo research: scenarios, genetic constraint, and developmental homeostasis. Aliso 22:172–187

García Azkonobieta T (2005) Evolución, desarrollo y (auto)organización. Un estudio sobre los principios filosóficos de la evo-devo. Tesis doctoral, Universidad del País Vasco

Gibbons M, Limoges C, Nowotny H, Schwartzman S, Scott P, Trow M (1994) The new production of knowledge: the dynamics of science and research in contemporary societies. Sage, London

Gibbs G (2006) Ghosts of Gondwana: the history of life in New Zealand. Craig Potton Publishing, Nelson

Goldberg J, Trewick SA, Paterson AM (2008) Evolution of New Zealand's terrestrial fauna: a review of molecular evidence. Philos Trans R Soc B Biol Sci 363:3319–3334

Goodwin B (2007) Nature's due: healing our fragmented culture. Floris Books, Edinburgh

Grande L (1994) Repeating patterns in nature, predictability, and "impact" in science. In: Grande L, Rieppel O, (eds) Interpreting the hierarchy of nature: from systematic patterns to evolutionary process theories. Academic Press, Inc, New York, NY, pp 61–84

Greppi C (2008) A proposito di evoluzionismo e geografia. L'incontro mancato fra Humboldt e Darwin. Quad Stor 127:1–21

Griffith MP (2004) Early cactus evolution: the postmodern view. Haseltonia 10:3–11

Haigh MJ (1985) Geography and general system theory, philosophical homologies and current practice. Geoforum 16:191–203

Hall R (2002) Cenozoic geological and plate tectonic evolution of SE Asia and the SW Pacific: computer-based reconstructions, model and animations. J Asian Earth Sci 20:353–431

Hartshorne R (1939) The classical period: Humboldt and Ritter. Ann Assoc Am Geogr 29:48–84

Hartshorne R (1960) Perspective on the nature of geography. John Murray, London

Hay WW, De Conto RM, Wold CN, Wilson KM, Voigt S, Schulz M et al. (1999) Alternative global Cretaceous paleogeography. In: Barrera E, Johnson C (eds) Evolution of the Cretaceous Ocean-Climate System. GSA Special Paper 332:1–47

Heads MJ (1990) Mesozoic tectonics and the deconstruction of biogeography: a new model of Australasian biology. J Biogeogr 17:223–225

Heads M (1999) Vicariance biogeography and terrane tectonics in the South Pacific: analysis of the genus Abrotanella (Compositae). Biol J Linn Soc 67:391–432

Heads M (2002) Birds of paradise, vicariance biogeography and terrane tectonics in New Guinea. J Biogeogr 29:261–283

Heads M (2005a) The history and philosophy of panbiogeography. In: Llorente Bousquets J, Morrone JJ, (eds) Regionalización biogeográfica en Iberoamérica y tópicos afines. Las Prensas de Ciencias, Facultad de Ciencias, UNAM, México DF, pp 67–123

Heads M (2005b) Dating nodes on molecular phylogenies: a critique of molecular biogeography. Cladistics 21:62 –78

Heads M (2009) Globally basal centres of endemism: the Tasman-Coral Sea region (south-west Pacific), Latin America and Madagascar/South Africa. Biol J Linn Soc 96:222–245

Hennig W (1966) Phylogenetic systematics. University of Illinois Press, Chicago, IL

Hettner A (1927) Die Geographie, ihre Geschichte, ihr Wesen und ihre Methoden. Ferdinand Hirt, Breslau

Hilgenberg OC (1933) Vom wachsenden Erdball. Published by the author, Berlin

Holdrege C (2005) Doing Goethean science. Janus Head 8:27–52

Holt-Jensen A (1999) Geography history & concepts. A student's Guide, 3rd edn. Sage, London

Jones O (2008) Stepping from the wreckage: geography, pragmatism and anti-representational theory. Geoforum 39:1600–1612

Jones MEH, Tennyson AJD, Worthy JP, Evans SE, Worthy TH (2009) A sphenodontine (Rhynchocephalia) from the Miocene of New Zealand and palaeobiogeography of the tuatara (*Sphenodon*). Proc R Soc B 276:1385–1390

Jordan GJ, Bannister JM, Mildenhall DC, Zetter R, Lee DE (2010) Fossil Ericaceae from New Zealand: deconstructing the use of fossil evidence in historical biogeography. Am J Bot 97: 59–70

Kamp PJJ (1980) Pacifica and New Zealand: proposed eastern elements in Gondwanaland's history. Nature 288:659–664

Katinas L, Morrone JJ, Crisci JV (1999) Track analysis reveals the composite nature of the Andean biota. Aust J Bot 47:111–130

Knapp M, Mudaliar R, Havell D, Wagstaff SJ, Lockhart PJ (2007) The drowning of New Zealand and the problem of *Agathis*. Syst Biol 56:862–870

Krause DW, O'Connor PM, Rogers KC, Sampson SD, Buckley GA, Rogers RR (2006) Late Cretaceous terrestrial vertebrates from Madagascar: implications for Latin American biogeography. Ann Mo Bot Gard 93:178–208

Larson RL, Pockalny RA, Viso RF, Erba E, Abrams LJ, Luyendyk BP, Stock JM, Clayton RW (2002) Mid-Cretaceous tectonic evolution of the Tongareva triple junction in the southwestern Pacific Basin. Geology 30:67–70

Lee DE, Bannister JM, Lindqvist JK (2007) Late Oligocene-Early Miocene leaf macrofossils confirm a long history of Agathis in New Zealand. N Z J Bot 45:565–578

Lindemann B (1927) Kettengebirge, kontinentale Zerspaltung und Erdexpansion. Gustav Fischer, Jena

Linder HP, Crisp MD (1995) *Nothofagus* and Pacific biogeography. Cladistics 11:5–32

Lomolino MV, Heaney LR (2004) Reticulations and reintegration of modern biogeography. In: Lomolino MV, Heaney LR, (eds) Frontiers in biogeography: new directions in the geography of nature. Sinauer, Sunderland, MA, pp 1–3

Marquet PA, Fernández M, Navarrete SA, Valdovinos C (2004) Diversity emerging: toward a deconstruction of biodiversity patterns. In: Lomolino MV, Heaney LR, (eds) Frontiers in biogeography: new directions in the geography of nature. Sinauer, Sunderland, MA, pp 191–209

McCarthy D (2003) The trans-Pacific zipper effect: disjunct sister taxa and matching geological outlines that link the Pacific margins. J Biogeogr 30:1545–1561

McCarthy D (2005a) Biogeographical and geological evidence for a smaller, completely-enclosed Pacific Basin in the Late Cretaceous. J Biogeogr 32:2161–2177

McCarthy D (2005b) Biogeography and scientific revolutions. Systematist 25:3–12

McCarthy D (2007) Are plate tectonic explanations for trans-pacific disjunctions plausible? Empirical tests of radical dispersalist theories. In: Ebach MC, Tangney RS, (eds) Biogeography in a changing world. Systematics Association special volumes. CRC Press, Boca Raton, FL, pp 171–192

McDowall RM (2008) Process and pattern in the biogeography of New Zealand – a global microcosm? J Biogeogr 35:197–212

McGlone MS (2005) Goodbye Gondwana. J Biogeogr 32:739–740

McLoughlin S (2001) The breakup history of Gondwana and its impact on pre-Cenozoic floristic provincialism. Aust J Bot 49:271–300

Michaux B, Leschen RAB (2005) East meets west: biogeology of the Campbell Plateau. Biol J Linn Soc 86:95–115

Miller JM (2009 onwards) Paleobotany of Angiosperm Origin. http://www.gigantopteroid.org/html/research.htm

Milne RI (2006) Northern Hemisphere plant disjunctions: a window on tertiary land bridges and climate change? Ann Bot 98:465–472

Morley RJ (2001) Why are there so many primitive angiosperms in the rain forests of Asia-Australasia? In: Metcalfe I, Smith JMB, et al.(eds) Faunal and floral migrations and evolution in SE Asia-Australasia. Balkema Publishers, Tokyo, pp 185–199

Morley RJ (2003) Interplate dispersal paths for megathermal angiosperms. Perspect Plant Ecol Evol Syst 6:5–20

Morrone JJ (2003) ¿Quién le teme al Darwinismo? Ciencia 54:78–88

Morrone JJ (2007) Hacia una biogeografía evolutiva. Rev Chil Hist Nat 80:509–520

Morrone JJ (2009) Evolutionary biogeography: an integrative approach with case studies. Columbia University Press, New York, NY

Morrone JJ, Crisci JV (1995) Historical biogeography: an introduction to methods. Annu Rev Ecol Syst 26:373–401

Myers N (1997) Exploring Goethean Science at Schumacher College. http://www.island.org/prescience/goethe.html

Myers AA, Giller PS, (eds) (1988) Analytical biogeography: an integrated approach to the study of animal and plant distributions. Chapman and Hall, London

Nelson G (1975) Biogeography, the vicariance paradigm, and continental drift. Syst Zool 24: 490–504

Nelson G, Ladiges PY (2001) Gondwana, vicariance biogeography and the New York School revisited. Aust J Bot 49:389–409

Nur A, Ben-Avraham Z (1977) Lost Pacifica continent. Nature 270:41–43

Nur A, Ben-Avraham Z (1981) The lost Pacifica continent: a mobilistic speculation. In: Nelson G, Rosen DE, (eds) Vicariance biogeography: a critique. Columbia University Press, New York, NY, pp 341–358

Parenti LR, Ebach MC (2009) Comparative biogeography: discovering and classifying Biogeographical patterns of a dynamic earth. University of California Press, Barkley, CA

Pole M (1994) The New Zealand flora-entirely long-distance dispersal? J Biogeogr 21:625–635

Rapalini AE (2005) The accretionary history of southern South America from the latest Proterozoic to the Late Palaeozoic: some palaeomagnetic constraints. In: Vaughan APM, Leat PT, Pankhurst RJ, (eds) Terrane processes at the margins of Gondwana, 246. Geological Society, London , 305–328, Special Publications

Renner SS (2005) Relaxed molecular clocks for dating historical plant dispersal events. Trends Plant Sci 10:550–558

Riddle BR (2005) Is biogeography emerging from its identity crisis? J Biogeogr 32:185–186

Rose S (1997) Lifelines: biology beyond determinism. Oxford University Press, Oxford

Rosen BR (1988) Biogeographic patterns: a perceptual overview. In: Myers AA, Giller P, (eds) Analytical biogeography: an integrated approach to the study of animal and plant distributions. Chapman and Hall, London, pp 23–56

Salomon M (2001) Evolutionary biogeography and speciation: essay on a synthesis. J Biogeogr 28:13–27

Sanders H, Rothwell GW, Wyatt S (2007) Paleontological context for the developmental mechanisms of evolution. Int J Plant Sci 168:719–728

Scalera G (2006) TPW and Polar Motion as due to an asymmetrical Earth expansion. In: Lavecchia G and Scalera G (eds) Frontiers in Earth Sciences: New Ideas and Interpretations. Ann Geophys 49(Supplement):483–500

Scalera G (2007) Fossils, frogs, floating islands and expanding Earth in changing-radius cartography. a comment to a discussion on Journal of Biogeography. Ann Geophys 50: 789–798

Scalera G (2008) Great and old earthquakes against great and old paradigms – paradoxes, historical roots, alternative answers. Adv Geosci 14:41–57

Scalera G, Jacob K-H, (eds) (2003) Why expanding Earth? – a book in honour of OC Hilgenberg. INGV, Rome

Sdrolias M, Müller RD, Gaina C (2003) Tectonic evolution of the southwest Pacific using constraints from backarc basins. In: Hillis RR, Müller RD (eds) Evolution and dynamics of the Australian plate. Geol Soc Aust Spec Publ 22, and Geol Soc Am Spec Pap 372: 343–359

Shields O (1998) Upper Triassic Pacific vicariance as a test of geological theories. J Biogeogr 25:203–211

Sluys R (1994) Explanations for biogeographic tracks across the Pacific Ocean: a challenge for paleogeography and historical biogeography. Prog Phys Geogr 18:42–58

Smith CH (1989) Historical biogeography: geography as evolution, evolution as geography. N Z J Zool 16:773–785

Smith AD (2007) A plate model for Jurassic to Recent intraplate volcanism in the Pacific Ocean basin. GSA Spec Pap 430:471–495

Soja EW (1989) Postmodern geographies: the reassertion of space in critical social theory. Verso, London

Spedding N (2003) Landscape and environment: biophysical processes, biophysical forms. In: Holloway SL, Rice SP, Valentine G, (eds) Key concepts in geography. SAGE, London, pp 281–303

Stevens GR (1997) The Late Jurassic ammonite fauna of New Zealand. Institute of Geological and Nuclear Sciences monograph 18 (New Zealand Geological Survey Paleontological Bulletin 74). Institute of Geological & Nuclear Sciences, Lower Hutt

Stöckler K, Daniel IL, Lockhart PJ (2002) New Zealand Kauri (*Agathis australis* (D. don) Lindl., Araucariaceae) survives Oligocene drowning. Syst Biol 51:827–832

Terribile LC, Felizola Diniz-Filho JA, Rodríguez MA, Rangel TFLVB (2009) Richness patterns, species distributions and the principle of extreme deconstruction. Glob Ecol Biogeogr 18: 123–136

Turrill WB (1953) Pioneer plan geography: the phytogeographical researches of Sir Joseph Dalton Hooker. Martinus Nijhoff, The Hague

Udvardy MDF (1981) The riddle of dispersal: dispersal theories and how they affect vicariance biogeography. In: Nelson G, Rosen DE, (eds) Vicariance biogeography: a critique. Columbia University Press, New York, NY, pp 6–29

Upchurch P (2006) What's wrong with palaeobiogeography? In: Meeting Abstracts: palaeogeography and palaeobiogeography: biodiversity in space and time, 10–13 Apr 2006, University of Cambridge, pp 5–6

Upchurch P (2008) Gondwanan break-up: legacies of a lost world? Trends Ecol Evol 23:229–236

Upchurch P, Hunn CA, Norman DB (2002) An analysis of dinosaurian biogeography: evidence for the existence of vicariance and dispersal patterns caused by geological events. Proc R Soc Lond B 269:613–621

van Steenis CGGJ (1962) The theory of land bridges in botany, with particular references to tropical plants. Blumea 11:235–542

Varela FJ, Maturana HR, Uribe R (1974) Autopoiesis: the organization of living systems, its characterization and a model. Biosystems 5:187–196

Vaughan APM, Livermore RA (2005) Episodicity of Mesozoic terrane accretion along the Pacific margin of Gondwana: implications for superplume-plate interactions. Geol Soc Lond Spec Publ 246:143–178

Vogel K (1990) The expansion of the earth – an alternative model to plate tectonics theory. In: Belousov V, (ed) Critical aspects of the plate tectonics theory, vol II. Athens, pp 19–34

von Ihering H (1907) Archhelenis und Archinotis: Gesammelte Beiträge zur Geschichte der Neotropischen Region. W. Engelmann, Leipzig

Wanntorp L, Wanntorp H-E (2003) The biogeography of Gunnera L.: vicariance and dispersal. J Biogeogr 30:979–987

Waters JM, Craw D (2006) Goodbye Gondwana? New Zealand biogeography, geology, and the problem of circularity. Syst Biol 55:351–356

Wegener A (1915) Die Entstehung der Kontinente und Ozeane. Sammlung Vieweg Nr. 23, Braunschweig

Williams DM (2007) Ernst Haeckel and Louis Agassiz: trees that bite and their geographical dimension. In: Ebach MC, Tangney RS, (eds) Biogeography in a changing world. Systematics association special volumes. CRC Press, Boca Raton, FL, pp 1–59

Williams DM, Ebach MC (2008) Foundations of systematics and biogeography. Springer, New York, NY

Wilson GDF (2008) Gondwanan groundwater: subterranean connections of Australian phreatoicidean isopods (Crustacea) to India and New Zealand. Invertebr Syst 22:301–310

Winkworth RC, Wagstaff S, Glenny D, Lockhart PJ (2002) Plant dispersal N.E.W.S. from New Zealand. Trends Ecol Evol 17:514–520

Zhou ZK, Yang XF, Yang QS (2006) Land bridge and long-distance dispersal – old views, new evidence. Chin Sci Bull 51:1030–1038

Chapter 11
Epilogue: The Juan Fernández Islands and the Long-Distance Dispersal of Utopia

As a kind of "path biographies" (cfr. Daniels and Nash 2004), ideas disperse over the globe linking concepts that seemed separate in space and time, promoting common pulses of human development. The Life and Strange Adventures of Robinson Crusoe (1719) by Daniel Defoe was a milestone in the construction of the industrial society (Laborde 2007). The ideal of humanity dominating nature, and finally the possibility of a real cohabitation between both, was the central idea of Defoe's novel and inspired the nineteenth century ideals of modernity, including Rousseau's educational ideal. "Robinson Crusoe became a primer for practical education. It was the only book Rousseau would allow the child in his educational tract Emile. ["I want him to learn in detail not from books but from things, all that must be known in such a situation; I want him to think he is Robinson himself"]" (Rousseau as quoted by Daniels and Nash 2004).

But nature remains us systematically that we are still far from dominating her. Also in Robinson Crusoe's land: the tsunami on the 27th of February 2010 erased the town of San Juan Bautista, leaving only agony and despair. The town is being reconstructed, together with the hope. This is an opportunity to rethink a new relationship with the unique biota that occupies the archipelago since millions of years. This would be a natural laboratory to rebuild and heal the relationship between nature and culture (Goodwin 2007). Since the school building does no longer exist, this is the moment to turn our eyes towards the montane forest for the cultivation of postmodern Robinsons as the "last children in the woods" (cfr. Louv 2008). Children know it better: they easily and spontaneously appreciate the wonders of nature.

> As we age, childhood becomes another country, a disputed territory of memory and meaning. Its true geography is quickly forgotten, giving away to an adult-imagined universo (Jones 2008).

There shall be somewhere still a place for Utopia. Intrinsic to humanity is the constant search for new worlds; let's revisit this time ourselves, our origin and dispersal upon this American and insular territory called Chile. The Juan Fernández Islands could be a good place for starting re-building our home for the future.

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> We commonly speak about the future, as if it is just one, which is obviously a mistake. Nothing can be foretold about the future or about the many futures whose seeds await within the womb of time, except that they will not resemble the present (J.L. Borges, my translation).

References

Daniels S, Nash C (2004) Lifepaths: geography and biography. J Hist Geogr 30:449–458

Goodwin B (2007) Nature's due: healing our fragmented culture. Floris Books, Edinburgh

Jones O (2008) True geography [] quickly forgotten, giving away to an adult-imagined universe. Approaching the otherness of childhood. Child Geogr 6:195–212

Laborde M (2007) Daniel Defoe y Jean Jacques Rousseau: con los Ojos en el Archipiélago de Juan Fernández. Rev Unive (UC) 96:76–77

Louv R (2008) Last child in the woods: saving our children from nature-deficit disorder. Algonquin Books of Chapel Hill, Chapel Hill, NC

Appendix A

Chilean native genera, ordered by floristic elements: (1) pantropical, (2) australasiatic, (3) neotropical, (4) antitropical, (5) aouth-temperate, (6) endemic, (7) cosmopolitan

Genus	Family	Order	Global distribution	Element	Track	Native spp.	Endemic spp.
Abutilon	Malvaceae	Malvales	Pantrops	1		1	0
Acacia	Fabaceae	Fabales	Tropics, Subtrop, esp Afr y Aus	1		3	0
Achyrocline	Asteraceae	Asterales	Tropics Afr, Madagascar, C Am, S Am	1		1	0
Alternanthera	Amaranthaceae	Caryophyllales	Tropics & subtrop, S Am, N Am, Aus, 1 sp Caucasus	1		2	0
Aristolochia	Aristolochiaceae	Piperales	Trop, subtrop, some in temp regions	1		2	2
Axonopus	Poaceae	Poales	Pantrops, IP	1		1	1
Bacopa	Veronicaceae	Lamiales	Trop & Subtrop, Hawaii, Madag, Aus	1		1	0
Beilschmiedia	Lauraceae	Laurales	Pantropics, Mex to S Bras, Chile, Aus, NZ, Afr, Madag	1		2	2
Boehmeria	Urticaceae	Rosales	Pantrop, JF	1		1	1
Buddleja	Scrophulariaceae	Lamiales	E Asia, tro & subtrop AM, Afr	1		3	1
Bulbostylis	Cyperaceae	Poales	Tropics & subtropics	1		1	0
Caesalpinia	Fabaceae	Fabales	Pantropics, subtropics, Arg, Madag, S Afr, Arabia	1		4	2
Calliandra	Fabaceae	Fabales	C & S Am, Afr, Madag, trop Asia	1		1	1
Carpha	Cyperaceae	Poales	Trop & S Afr, Madag, japan, New Guinea, Aus, Tasm, NZ, temp S Am	1		1	0
Centella	Apiaceae	Apiales	Pantrop to Chile, NZ, JF	1		1	0
Centipeda	Asteraceae	Asterales	Aus, NZ, New Cale, Tahiti, Chile, Madag, Mascarene Is, SE Asia	1		1	0
Cissus	Vitaceae	Vitales	Tropics incl Australia	1		1	0
Cleome	Cleomaceae	Brassicales	Tropics & subtropics, spec. Am	1		1	0
Conyza	Asteraceae	Asterales	Tropics & subtropics	1		20	15
Cordia	Boraginaceae	Unplaced	Trop & subtropics	1		1	1

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Genus	Family	Order	Global distribution	Element	Track	Native spp.	Endemic spp.
Cotula	Asteraceae	Asterales	S Afr, NZ, New Guinea, Aus, S Am	1		1	0
Cressa	Convolvulaceae	Solanales	Trop & subtrop	1		1	0
Croton	Euphorbiaceae	Malpighiales	Tropics & subtropics	1		1	1
Cryptocarya	Lauraceae	Laurales	Tropics & subtropics, Madag, S Afr, E Asia, N Australia	1		1	1
Cynodon	Poaceae	Poales	Tropics & subtropics	1		2	1
Davallia	Davalliaceae	Polypodiales	W Medit, Himal, Japan, Aus, Tahiti, Afr, Madag, IP	1		1	0
Dennstaedtia	Dennstaedtiaceae	Polypodiales	Trop to warm temp, Madag	1		1	0
Dichondra	Convolvulaceae	Solanales	Tropics & subtropics, JF	1		2	0
Dicliptera	Acanthaceae	Lamiales	Tropics & subtropics	1		1	1
Dioscorea	Dioscoreaceae	Dioscoreales	Trop, subtrop, warm-temp regions	1		36	34
Dodonaea	Sapindaceae	Sapindales	Tropics & subtrop, espec Australia	1		1	0
Drymaria	Caryophyllaceae	Caryophyllales	Pantrop	1		3	1
Elaphoglossum	Dryopteridaceae	Polypodiales	Pantrops & subtrop, Madag, IP	1		6	2
Evolvulus	Convolvulaceae	Solanales	Trops & subtrops	1		1	0
Glinus	Molluginaceae	Caryophyllales	Pantrop	1		1	0
Gomphrena	Amaranthaceae	Caryophyllales	Trop & subtrop Am, Afr, Indochina, Aus	1		2	0
Grammitis	Polypodiaceae	Polypodiales	New Guinea, Asia, Am, Aus, Madag, warm & temp, JF	1		3	0
Gunnera	Gunneraceae	Gunnerales	Am from Mexic to Chile, trop & S Afr, Madag, Malesia, Tasm, NZ, Hawaii, JF	1		11	6
Habenaria	Orchidaceae	Asparagales	Pantrop & subtrop	1		1	0
Histiopteris	Dennstaedtiaceae	Polypodiales	Pantrop, Madag	1		1	0
Hybanthus	Violaceae	Malpighiales	Trops & subtrops	1		1	0
Hypolepis	Dennstaedtiaceae	Polypodiales	Trop & subtrop, Madag	1		1	0
Ipomoea	Convolvulaceae	Solanales	Pantrop	1		1	0
Kyllinga	Cyperaceae	Poales	Pantrops	1		1	0

Genus	Family	Order	Global distribution	Element	Track	Native spp.	Endemic spp.
Leptochloa	Poaceae	Poales	Tropics & subtrop	1		1	0
Lippia	Verbenaceae	Lamiales	Am trop, many in Afr trop	1		2	1
Lobelia	Campanulaceae	Asterales	Trops & subtrops	1		5	4
Machaerina	Cyperaceae	Poales	Trops esp Australia, Hawaii, JF	1		1	1
Maytenus	Celastraceae	Celastrales	Trops & subtrops	1		4	0
Megalastrum	Dryopteridaceae	Polypodiales	Trop Am, 1 Afr to Mascarenes (no Madag), JF	1		2	1
Microlepia	Dennstaedtiaceae	Polypodiales	Paleotrop, 1 Afr, Madag, Japan, NZ, IP	1		1	0
Microsorum	Polypodiaceae	Polypodiales	Trop & warm, Madag, IP	1		1	0
Mikania	Asteraceae	Asterales	Pantrops, esp Neotrops	1		2	1
Morella	Myricaceae	Fagales	Sudam Andes Peru Ecuador, Africa, E Asia, Filipinas y Malasia	1		1	0
Nicotiana	Solanaceae	Solanales	Am, USA to Chile, Aust, New Caledonia, Namibia, JF	1		14	6
Notholaena	Pteridaceae	Polypodiales	Warm to trop Am, SW US, Mex, Madag, JF	1		1	0
Oldenlandia	Rubiaceae	Gentianales	Tropics espec Asia & Malesia, JF	1		2	1
Otholobium	Fabaceae	Fabales	E & S Afr, temp S Am	1		2	1
Passiflora	Passifloraceae	Malpighiales	Trop & subtrop Am, 1 Madag, 20 trop E Asia, Malesia, 3 Aus, NZ	1		1	0
Pellaea	Pteridaceae	Polypodiales	Trop & warm-temp, Madag	1		2	1
Pelletiera	Primulaceae	Ericales	1 subtrop S Am, 1 Macaronesia	1		1	0
Peperomia	Piperaceae	Piperales	Trop & warm esp Am, JF, Hawaii	1		7	7
Phytolacca	Phytolaccaceae	Caryophyllales	Trop & warm	1		2	1
Pilea	Urticaceae	Rosales	Trop & warm excl Australasia	1		3	2
Pilostyles	Rafflesiaceae	Malpighiales	Am US to Magallanes, Asia, 2 W Aus	1		1	0
Pityrogramma	Pteridaceae	Polypodiales	Am trop desde S US, Afr, Madag	1		1	0
Pleopeltis	Polypodiaceae	Polypodiales	Trop Am, 1 Afr-Madag, India, Sri Lanka	1		2	0
Pluchea	Asteraceae	Asterales	Pantrops	1		1	0

Genus	Family	Order	Global distribution	Element	Track	Native spp.	Endemic spp.
Podocarpus	Podocarpaceae	Pinales	Afr, Madag, Asia, Aus, Tasm, NZ, Mex, C & S Am, WI	1		2	1
Pouteria	Sapotaceae	Ericales	Trop. Am, Afr, Asia, Aus, NZ, New Caled	1		1	1
Prosopis	Fabaceae	Fabales	Trop & subtrop Am, Afr, W Asia	1		7	1
Psilotum	Psilotaceae	Psilotales	Pantrop, Hawaii, Australia, NZ, Madag, IP	1		1	1
Pycreus	Cyperaceae	Poales	Pantrops	1		3	1
Schizaea	Schizaeceae	Schizaeales	Trop & austral, N Am, Madag	1		1	0
Senna	Fabaceae	Fabales	Pantrops	1		10	7
Sigesbeckia	Asteraceae	Asterales	Pantrops	1		1	0
Spilanthes	Asteraceae	Asterales	Pantrops	1		1	0
Sticherus	Gleicheniaceae	Gleicheniales	Pantrop, Madag, JF	1		5	2
Tecoma	Bignoniaceae	Lamiales	Am tropical Arizona to Chile, 1 S Afr, Aus?	1		1	0
Thelypteris	Thelypteridaceae	Polypodiales	Trops & subtrops, Madag	1		2	0
Trichomanes	Hymenophyllaceae	Hymenophyllales	Patrop, Madag, JF	1		3	3
Trichoneura	Poaceae	Poales	Arabia, trop Afr, S US, Peru	1		1	0
Tripogon	Poaceae	Poales	Trops & subtrops	1		2	0
Triumfetta	Malvaceae	Malvales	Pantrop	1		1	0
Vittaria	Pteridaceae	Polypodiales	Pantrop, IP	1		1	0
Wedelia	Asteraceae	Asterales	Pantrops, W Australia	1		1	0
Wolffiella	Araceae	Alismatales	Trop & warm Am, 1 S Afr	1		1	0
Fagara	Rutaceae	Sapindales	Am, Afr, Asia, JF	1		2	2
Alonsoa	Scrophulariaceae	Lamiales	Trop Am Mexico, C Am, Chile, Bol, 2 sp S Afr	1		2	1
Amphibromus	Poaceae	Poales	Aus, NZ, S Am	2	AUS	1	0
Aristotelia	Elaeocarpaceae	Oxalidales	E Aus, Tasman, NZ, Arg, Chile	2	AUS	1	0
Azorella	Apiaceae	Apiales	Andes to temp S Am, Malvinas, Antarctic Islands	2	AUS	17	2

Genus	Family	Order	Global distribution	Element	Track	Native spp.	Endemic spp.
Berberidopsis	Berberidopsidaceae	Berberidopsidales	B. beckleri en Aus: Queensland & New S Wales, B. corallina: Chile	2	AUS	1	1
Cortaderia	Poaceae	Poales	S Am, 4 NZ, 1 New Guinea	2	AUS	6	0
Discaria	Rhamnaceae	Rosales	Aus, NZ, S Am	2	AUS	2	0
Donatia	Stylidiaceae	Asterales	Tasman, NZ, subantarctic S Am	2	AUS	1	0
Eucryphia	Cunoniaceae	Oxalidales	SE Aus, Tasm, Chile	2	AUS	2	1
Fuchsia	Onagraceae	Myrtales	C & S Am, NZ, Tahiti	2	AUS	2	1
Griselinia	Griseliniaceae	Apiales	NZ, Chile, Paraguay, S Brasil	2	AUS	5	3
Haloragis	Haloragaceae	Saxifragales	Aus, N. Caled, NZ, Rapa, JF	2	AUS	2	2
Heterozostera	Zosteraceae	Alismatales	Coastal temp Aus, Tasm, N Chile	2	AUS	1	0
Jovellana	Calceolariaceae	Lamiales	NZ, Chile	2	AUS	3	3
Laurelia	Atherospermataceae	Laurales	NZ & Chile	2	AUS	1	1
Lepidothamnus	Podocarpaceae	Pinales	2 NZ, 1 S Chile/Arg	2	AUS	1	0
Lomatia	Proteaceae	Proteales	Aus, Tas, S Am	2	AUS	3	0
Luzuriaga	Luzuriagaceae	Liliales	1 NZ, 3 Chile, Arg to T Fuego	2	AUS	3	1
Maireana	Amaranthaceae	Caryophyllales	Australia, Chile	2	AUS	1	0
Marsippospermum	Juncaceae	Poales	NZ, S S Am, Tfuego, Falkland	2	AUS	3	0
Orites	Proteaceae	Proteales	6 temp E Aus, 3 Andes S Am	2	AUS	1	0
Ourisia	Veronicaceae	Lamiales	Tasm, NZ, Andes S Am	2	AUS	11	3
Phyllachne	Stylidiaceae	Asterales	Tasm, NZ, temp S Am	2	AUS	1	0
Prumnopitys	Podocarpaceae	Pinales	Costa Rica to Chile, New Caled, NZ, E Aus	2	AUS	1	0
Raukaua	Araliaceae	Apiales	Tasm, NZ, Chile	2	AUS	2	1
Rostkovia	Juncaceae	Poales	NZ, S S Am, Tfuego, Falkland	2	AUS	1	0
Rytidosperma	Poaceae	Poales	Australia, NZ, Arg, Chile, IP	2	AUS	6	2
Schizeilema	Apiaceae	Apiales	11 NZ, 1 Aus, 1 S S Am	2	AUS	1	0
Selliera	Goodeniaceae	Asterales	Aus, NZ, Chile	2	AUS	1	0
Tetrachondra	Tetrachondraceae	Lamiales	1 NZ, 1 Patagonia, Tfuego	2	AUS	1	0
Trichocline	Asteraceae	Asterales	S Am, 1 W Aus	2	AUS	5	2

Genus	Family	Order	Global distribution	Element	Track	Native spp.	Endemic spp.
Ficinia	Cyperaceae	Poales	Cape Region S Afr, 1 subantarctic circumpolar	2	C-AUS	1	0
Nertera	Rubiaceae	Gentianales	Madag, SE Asia, Malesia, Aus, NZ, Hawaii, S Am, JF	2	C-AUS	1	0
Rumohra	Dryopteridaceae	Polypodiales	Circumaustral, J Fernandez, Madag	2	C-AUS	2	1
Wahlenbergia	Campanulaceae	Asterales	Circumaustral	2	C-AUS	6	5
Abrotanella	Asteraceae	Asterales	New Guinea, Aus, Tasmania, NZ, SAm (TFuego), JF, Falkland Is.	2	TPAC	6	3
Apodasmia	Restionaceae	Poales	SE Asia, Malesia, New Guinea, Aus, Tasm, NZ, Chile, Arg	2	TPAC	1	1
Araucaria	Araucariaceae	Pinales	New Guinea, Aus, New Caledonia, S Chile, SE Brasil	2	TPAC	1	0
Arthropteris	Tectarinaceae	Polypodiales	New Guinea, NZ, Juan Fernandez, Madag	2	TPAC	1	1
Astelia	Asteliaceae	Asparagales	Masc, New Guinea, Aus, NZ, Polinesia, Chile	2	TPAC	1	0
Caldcluvia	Cunoniaceae	Oxalidales	Philippines, Sulawesi, Moluccas, New Guinea, trp Aus, S Chile Arg	2	TPAC	1	0
Citronella	Cardiopteridaceae	Aquifoliales	Malesia, E Aus, New Cale, Fiji, Samoa, C & trop S Am	2	TPAC	1	1
Colobanthus	Caryophyllaceae	Caryophyllales	S Pacific, Aus, NZ, temp S Am, Ecuador	2	TPAC	3	0
Coprosma	Rubiaceae	Gentianales	E Malesia, Aus, NZ, Pacific, JF, 12 sp Hawaii	2	TPAC	2	2
Dicksonia	Dicksoniaceae	Cyatheales	Trop Am, Malesia, New Guinea, Aus, New Caled, NZ	2	TPAC	2	2
Doodia	Blechnaceae	Polypodiales	Australia, NZ, Pacific islands, Hawaii, N Guinea, IP	2	TPAC	1	0
Gaimardia	Centrolepidaceae	Poales	New Guinea, NZ, Tasmania, TFuego, Falkland	2	TPAC	1	0
Gevuina	Proteaceae	Proteales	New Guinea, Aus, Chile, Arg	2	TPAC	1	0
Hebe	Veronicaceae	Lamiales	New Guinea, Aus, Tasm, NZ, temp S Am, Falkland	2	TPAC	2	0

Genus	Family	Order	Global distribution	Element	Track	Native spp.	Endemic spp.
Lagenophora	Asteraceae	Asterales	SE Asia, Malesia, Australia, Tasmania, NZ, C & S Am, JF, Falkland, Tristan da Cunha.	2	TPAC	3	0
Leptinella	Asteraceae	Asterales	New Guinea, Aus, NZ, Subantarctic Is, S Am	2	TPAC	1	0
Leptostigma	Rubiaceae	Gentianales	SE Asia, NZ, W S Am	2	TPAC	1	1
Libertia	Iridaceae	Asparagales	New Guinea, E Aus, NZ, Andes S Am, JF	2	TPAC	6	5
Muehlenbeckia	Polygonaceae	Caryophyllales	New Guinea, Aus, Tasm, NZ, W S Am	2	TPAC	2	0
Nothofagus	Nothofagaceae	Fagales	New Guinea, Aus, Tasm, NZ, New Caled, temp S Am	2	TPAC	10	4
Oreobolus	Cyperaceae	Poales	Malesia, Aus, Tasm, NZ, Hawaii, JF, trop & temp Am, Chile, Tfuego, Falkland	2	TPAC	1	0
Oreomyrrhis	Apiaceae	Apiales	E Asia, Borneo, N Guinea, SE Aus, NZ, Mex, C Am, Andes, Tfuego, Falkland	2	TPAC	1	0
Santalum	Santalaceae	Santalales	Indomalasia to Aus, Hawaii, JF (ex)	2	TPAC	1	1
Uncinia	Cyperaceae	Poales	Malesia, Pacific, Aus, SE Asia, C & S Am, JF	2	TPAC	18	7
Acantholippia	Verbenaceae	Lamiales	Arid S Am, Arg, Chile, Bol	3	C-AND	3	1
Anatherostipa	Poaceae	Poales	Arg, Bol, Chile, Ecuador, Peru	3	C-AND	4	1
Andeimalva	Malvaceae	Malvales	Chile, Peru, Bol	3	C-AND	1	1
Anthochloa	Poaceae	Poales	Andes Chile Peru	3	C-AND	1	0
Aphyllocladus	Asteraceae	Asterales	Andes S Bolivia, N Chile, NW Arg	3	C-AND	1	1
Arachnitis	Corsiaceae	Liliales	Chile, Arg, Bol	3	C-AND	1	0
Argylia	Bignoniaceae	Lamiales	S Peru, N C Chile & Arg, A. uspallatensis S Bol	3	C-AND	11	8
Balbisia	Vivianiaceae	Geraniales	Peru, Bol, Chile, Arg	3	C-AND	4	2
Browningia	Cactaceae	Caryophyllales	Peru, Bol, Chile, Paraguay	3	C-AND	1	0
Chaetanthera	Asteraceae	Asterales	S Peru, Bol, Chile, Arg	3	C-AND	38	16
Chersodoma	Asteraceae	Asterales	S Peru, Bol, Chile, Arg	3	C-AND	3	0
Clinanthus	Amaryllidaceae	Asparagales	Perú, Chile	3	C-AND	1	0
Corryocactus	Cactaceae	Caryophyllales	Bol, S Peru, N Chile	3	C-AND	1	0

Genus	Family	Order	Global distribution	Element	Track	Native spp.	Endemic spp.
Cristaria	Malvaceae	Malvales	Chile, Arg, Bol, Perú, ID	3	C-AND	19	16
Cumulopuntia	Cactaceae	Caryophyllales	Bol, S Peru, N Chile	3	C-AND	2	0
Dielsiochloa	Poaceae	Poales	Peru, Bol, Arg, Chile	3	C-AND	1	0
Domeykoa	Apiaceae	Apiales	Peru Chile	3	C-AND	2	2
Eccremocarpus	Bignoniaceae	Lamiales	Peru, Chile, Arg	3	C-AND	1	0
Eremocharis	Apiaceae	Apiales	Andes Chile Peru	3	C-AND	1	1
Eremodraba	Brassicaceae	Brassicales	Andes Chile Peru	3	C-AND	1	0
Fabiana	Solanaceae	Solanales	S Peru, Bol, Chile, Arg	3	C-AND	8	1
Haageocereus	Cactaceae	Caryophyllales	Peru, Chile	3	C-AND	2	1
Haplopappus	Asteraceae	Asterales	S Am Chile, Arg, Peru	3	C-AND	54	42
Haplorhus	Anacardiaceae	Sapindales	Chile, Peru	3	C-AND	1	0
Helogyne	Asteraceae	Asterales	Peru, Chile, Bol, Arg	3	C-AND	2	1
Islaya	Cactaceae	Caryophyllales	Peru, Chile	3	C-AND	4	3
Junellia	Verbenaceae	Lamiales	Peru, Bol, Chile, Arg	3	C-AND	24	5
Kageneckia	Rosaceae	Rosales	Chile, Peru, Bolivia, Arg	3	C-AND	2	2
Laennecia	Asteraceae	Asterales	Bol, Arg, Chile	3	C-AND	1	0
Lampaya	Verbenaceae	Lamiales	Bol, Chile, Arg	3	C-AND	2	1
Lepidoceras	Santalaceae	Santalales	S Peru, Chile	3	C-AND	1	1
Leucheria	Asteraceae	Asterales	Peru, Bol, Arg, Chile	3	C-AND	42	16
Loasa	Loasaceae	Cornales	Chile, Arg, 1 sp coastal Peru	3	C-AND	31	18
Lobivia	Cactaceae	Caryophyllales	Andes Peru, Bol, Chile, Arg	3	C-AND	2	0
Lophopappus	Asteraceae	Asterales	Peru, Bol, Chile, Arg	3	C-AND	3	1
Maihueniopsis	Cactaceae	Caryophyllales	Andes Peru, Bol, Chile, Arg	3	C-AND	13	9
Malesherbia	Malesherbiaceae	Malpighiales	Andes Peru, Chile, Arg	3	C-AND	16	13
Mastigostyla	Iridaceae	Asparagales	Peru, Arg	3	C-AND	1	0
Mathewsia	Brassicaceae	Brassicales	Peru, Chile	3	C-AND	5	5
Mniodes	Asteraceae	Asterales	Peru, Chile	3	C-AND	2	0
Montiopsis	Portulacaceae	Caryophyllales	Chile, Argentina, Bolivia y Perú	3	C-AND	18	5

Genus	Family	Order	Global distribution	Element	Track	Native spp.	Endemic spp.
Moschopsis	Calyceraceae	Asterales	Perú, Chile, Arg, Patagonia	3	C-AND	5	0
Mostacillastrum	Brassicaceae	Brassicales	S Peru, Bol, Chile, Arg	3	C-AND	8	1
Nardophyllum	Asteraceae	Asterales	Arg, Chile	3	C-AND	4	2
Nassauvia	Asteraceae	Asterales	Bol, Arg, Chile, Falklands	3	C-AND	23	3
Neowerdermannia	Cactaceae	Caryophyllales	Peru, Bol, Chile, Arg	3	C-AND	1	1
Neuontobothrys	Brassicaceae	Brassicales	S Peru, Chile, Arg	3	C-AND	8	3
Nicandra	Solanaceae	Solanales	Peru, Arg, Chile	3	C-AND	1	0
Nolana	Solanaceae	Solanales	Peru to Chile, Galapagos	3	C-AND	44	40
Ocyroe	Asteraceae	Asterales	Bol, Arg, Chile	3	C-AND	1	0
Oreocereus	Cactaceae	Caryophyllales	Andes Peru, Bol, Chile, Arg	3	C-AND	4	1
Oxychloë	Juncaceae	Poales	Andes S Am	3	C-AND	3	0
Oziroe	Asparagaceae	Asparagales	Chile, Arg, Perú, Bol, Paraguay	3	C-AND	4	1
Pachylaena	Asteraceae	Asterales	Andes N Chile Arg	3	C-AND	1	0
Palaua	Malvaceae	Malvales	Coastal Peru and Chile	3	C-AND	4	2
Parastrephia	Asteraceae	Asterales	Andes Bol, Chile, Perú, Arg	3	C-AND	3	0
Pasithea	Xanthorrhoeaceae	Asparagales	Peru, Chile	3	C-AND	1	0
Patosia	Juncaceae	Poales	Andes Chile Arg Bol	3	C-AND	1	0
Pennellia	Brassicaceae	Brassicales	Andes Peru, Chile, Arg, Bol	3	C-AND	2	0
Philibertia	Apocynaceae	Gentianales	Andes Perú, Chile, Bolivia, Argentina	3	C-AND	2	0
Phylloscirpus	Cyperaceae	Poales	Arg, Chile, Bol	3	C-AND	3	0
Pitraea	Verbenaceae	Lamiales	S Am, Chile, Peru, Arg	3	C-AND	1	0
Plazia	Asteraceae	Asterales	Peru, Bol, Arg, Chile	3	C-AND	2	1
Polyachyrus	Asteraceae	Asterales	Peru, Chile	3	C-AND	7	4
Proustia	Asteraceae	Asterales	Bol, Chile, Arg, Peru	3	C-AND	3	2
Pycnophyllum	Caryophyllaceae	Caryophyllales	Andes Peru, Chile, Arg, Bol	3	C-AND	5	0
Quinchamalium	Santalaceae	Santalales	Andes Bol, Chile, Perú, Arg	3	C-AND	14	13
Salpichroa	Solanaceae	Solanales	S Am: Ecuad, Peru, Bol, Bra, Parag, Uru, Chile, Arg	3	C-AND	2	0

Genus	Family	Order	Global distribution	Element	Track	Native spp.	Endemic spp.
Stangea	Valerianaceae	Dipsacales	Arg,Chil,Perú	3	C-AND	1	0
Tetraglochin	Rosaceae	Rosales	Arg, Chil, Perú	3	C-AND	3	0
Trichocereus	Cactaceae	Caryophyllales	Chile, Arg, S Peru	3	C-AND	7	6
Tunilla	Cactaceae	Caryophyllales	Andes Peru, Bol, Chile, Arg	3	C-AND	2	0
Urmenetea	Asteraceae	Asterales	N Chile, NW Arg	3	C-AND	1	0
Urocarpidium	Malvaceae	Malvales	Perú, Chile	3	C-AND	1	0
Weberbauera	Brassicaceae	Brassicales	Andes Peru, Chile, Arg, Bol	3	C-AND	6	3
Zameioscirpus	Cyperaceae	Poales	Arg, Chile, Bol	3	C-AND	3	0
Aa	Orchidaceae	Asparagales	Andes Colombia to Argentina	3	W-AND	1	0
Aristeguietia	Asteraceae	Asterales	Colombia, Ecuador, Peru, Chile	3	W-AND	1	1
Blepharocalyx	Myrtaceae	Myrtales	Trop & subtro S Am, WI	3	W-AND	1	1
Bulnesia	Zygophyllaceae	Zygophyllales	S Am: Venezuela Colombia disjunct to Chile-Arg, Brazil	3	W-AND	1	1
Chuquiraga	Asteraceae	Asterales	Andes S Am, Patagonia	3	W-AND	5	2
Cremolobus	Brassicaceae	Brassicales	Andes Colombia to Chile	3	W-AND	1	0
Cuatrecasasiella	Asteraceae	Asterales	Ecuador, Peru, Chile, Arg	3	W-AND	1	0
Desfontainia	Desfontainiaceae	Bruniales	Costa Rica to Cape Horn	3	W-AND	1	0
Diplostephium	Asteraceae	Asterales	Trop Andes from Colombia to Bol & N Chile, 1 sp Costa Rica	3	W-AND	2	0
Distichia	Juncaceae	Poales	Andes S Am	3	W-AND	2	0
Dunalia	Solanaceae	Solanales	Andes Colombia to Argentina	3	W-AND	1	0
Dysopsis	Euphorbiaceae	Malpighiales	Andes Costa Rica, Ecuador, Chile, Arg, JF	3	W-AND	2	1
Escallonia	Escalloniaceae	Escalloniales	Andes S Am, SE Brasil, JF	3	W-AND	14	6
Eudema	Brassicaceae	Brassicales	Andes Ecuador to Arg	3	W-AND	3	0
Exodeconus	Solanaceae	Solanales	S Am, Peru, Ecuador, Galapagos, N Chile	3	W-AND	3	0
Geoffroea	Fabaceae	Fabales	S Am from Colombia & Venez to Arg, Brazil	3	W-AND	1	0
Llagunoa	Sapindaceae	Sapindales	Andean trop S Am	3	W-AND	1	1
Luciliocline	Asteraceae	Asterales	Andes S Am, Venezuela to Peru, Chile, Arg	3	W-AND	3	0

Genus	Family	Order	Global distribution	Element	Track	Native spp.	Endemic spp.
Mutisia	Asteraceae	Asterales	Andes Colombia to Chile, Arg, Parag, SE Brasil, Urug	3	W-AND	23	11
Myrcianthes	Myrtaceae	Myrtales	Trop Am, Andes, Brazil, WI	3	W-AND	1	1
Myrteola	Myrtaceae	Myrtales	Colombia to Chile, JF, Brazil	3	W-AND	1	0
Nototriche	Malvaceae	Malvales	Ecuador, Peru, Bol, Chile, Arg	3	W-AND	24	6
Ombrophytum	Balanophoraceae	Santalales	Peru, W Brasil, N Arg, Chile	3	W-AND	1	0
Perezia	Asteraceae	Asterales	Andes from Colombia to Chile, SE Brazil	3	W-AND	20	1
Polylepis	Rosaceae	Rosales	Andes Venezuela to Arg, Chile	3	W-AND	2	0
Polypsecadium	Brassicaceae	Brassicales	Colombia to Chile/Arg	3	W-AND	3	2
Tristerix	Loranthaceae	Santalales	Andes Colombia to Chile	3	W-AND	3	1
Werneria	Asteraceae	Asterales	Andes Ecuador to Chile	3	W-AND	8	1
Xenophyllum	Asteraceae	Asterales	Andes Colombia to N Arg, Chile	3	W-AND	5	0
Adesmia	Fabaceae	Fabales	Peru, Chile, Arg, S Brasil, TFuego	3	S-AMZ	130	85
Alstroemeria	Alstroemeriaceae	Liliales	Chile, S Brasil, Perú, Arg	3	S-AMZ	35	26
Arjona	Santalaceae	Santalales	Temp S Am, Brazil	3	S-AMZ	3	0
Azara	Salicaceae	Malpighiales	8 temp Chile-Arg, s subtrop NW Arg, Bol, SE Bra, Uruguay, JF	3	S-AMZ	8	5
Blumenbachia	Loasaceae	Cornales	Brasil, Uruguay, Paraguay, Argentina, Chile	3	S-AMZ	3	0
Boopis	Calyceraceae	Asterales	Andes, Arg, S Brasil	3	S-AMZ	7	2
Brachystele	Orchidaceae	Asparagales	Trop Am esp. Brasil	3	S-AMZ	1	0
Caiophora	Loasaceae	Cornales	Peru, Bol, Arg, Chile, 1 sp Urug, Bras, Ecuad	3	S-AMZ	5	0
Calotheca	Poaceae	Poales	Arg, Bras, Chile, Uruguay	3	S-AMZ	1	0
Calycera	Calyceraceae	Asterales	Temp S Am, Brazil	3	S-AMZ	7	4
Chevreulia	Asteraceae	Asterales	S Brasil, Bol, Paraguay, Urug, Chile, N C Arg, Falkland	3	S-AMZ	4	0
Chloraea	Orchidaceae	Asparagales	Andes Chile Perú, Arg, Brazil	3	S-AMZ	32	18
Ciclospermum	Apiaceae	Apiales	Arg, Bol, Brasil, Chile, Paraguay, Uruguay	3	S-AMZ	2	0
Cliococca	Linaceae	Malpighiales	Brasil, Uruguay, Paraguay, Argentina, Chile	3	S-AMZ	1	0

Genus	Family	Order	Global distribution	Element	Track	Native spp.	Endemic spp.
Codonorchis	Orchidaceae	Asparagales	S trop & temp S Am, Brazil	3	S-AMZ	1	0
Colletia	Rhamnaceae	Rosales	Subtrop & temp S Am, Brazil, JF	3	S-AMZ	3	2
Colliguaja	Euphorbiaceae	Malpighiales	Temp S Am, S Brasil	3	S-AMZ	3	2
Crinodendron	Elaeocarpaceae	Oxalidales	Bol, N Arg, C Chile, Brasil	3	S-AMZ	2	2
Dasyphyllum	Asteraceae	Asterales	Chile, Andes, SE Brazil	3	S-AMZ	2	1
Deuterocohnia	Bromeliaceae	Poales	Peru, Bol, SW Bra, N Chile, N Arg	3	S-AMZ	1	1
Facelis	Asteraceae	Asterales	S Brasil, Peru, Bol, Paraguay, Urug, Chile, Arg	3	S-AMZ	2	0
Herbertia	Iridaceae	Asparagales	Temp S Am, Chile, Brazil	3	S-AMZ	1	0
Herreria	Asparagaceae	Asparagales	Brasil, Uru, Parag, Arg, Chile	3	S-AMZ	1	1
Jaborosa	Solanaceae	Solanales	Temp S Am. S Peru, Bol, Bras, Parag, Chile, Arg, Uru	3	S-AMZ	11	1
Ligaria	Loranthaceae	Santalales	C Peru, E Bol, C Chile, Urug, n Arg, S Brasil	3	S-AMZ	1	0
Lithrea	Anacardiaceae	Sapindales	S Am: Arg, Bol, Paraguay, SE Brazil, Chile.	3	S-AMZ	1	1
Lucilia	Asteraceae	Asterales	Andes S Am, Chile, Arg, Peru	3	S-AMZ	3	1
Margyricarpus	Rosaceae	Rosales	S Andes to Chile, JF, Brazil	3	S-AMZ	2	1
Micropsis	Asteraceae	Asterales	Brazil, Arg, Urug, Chile	3	S-AMZ	1	1
Myrceugenia	Myrtaceae	Myrtales	Chile, Arg, SE Brasil, JF	3	S-AMZ	14	10
Noticastrum	Asteraceae	Asterales	Peru, Bol, Chile, Arg, Ecuador, Brazil	3	S-AMZ	5	4
Ophryosporus	Asteraceae	Asterales	Trop & subtrop S Am, Brazil	3	S-AMZ	8	3
Picrosia	Asteraceae	Asterales	Subtrop S Am, Chile, Peru, Arg, Brazil	3	S-AMZ	1	0
Pleurophora	Lythraceae	Myrtales	S Am, Brazil	3	S-AMZ	3	3
Quillaja	Quillajaceae	Fabales	Temp S Am, Arg, Chile, Brazil	3	S-AMZ	1	1
Rhodophiala	Amaryllidaceae	Asparagales	Chile, Arg, Bol, Bras	3	S-AMZ	27	24
Rhombolytrum	Poaceae	Poales	S Brasil, Urug, Chile	3	S-AMZ	1	1
Skytanthus	Apocynaceae	Gentianales	Brasil, Chile	3	S-AMZ	1	1
Tessaria	Asteraceae	Asterales	S Am, Brazil	3	S-AMZ	1	0
Tweedia	Apocynaceae	Gentianales	Bol, Uru, Chile, Arg	3	S-AMZ	3	3
Viviania	Vivianiaceae	Geraniales	S Brasil, Chile, Arg	3	S-AMZ	3	1

Genus	Family	Order	Global distribution	Element	Track	Native spp.	Endemic spp.
Cruckshanksia	Rubiaceae	Gentianales	Chile, Arg	3	C-AND	7	4
Gymnophyton	Apiaceae	Apiales	Andes Chile Arg	3	C-AND	5	5
Kurzamra	Lamiaceae	Lamiales	Chile/Arg	3	C-AND	1	0
Lenzia	Portulacaceae	Caryophyllales	Chile Arg	3	C-AND	1	0
Monttea	Veronicaceae	Lamiales	Chile 1, Arg. 2	3	C-AND	1	1
Pyrrhocactus	Cactaceae	Caryophyllales	Arg, Chile	3	C-AND	20	20
Reyesia	Solanaceae	Solanales	Chile Arg	3	C-AND	4	3
Schizopetalon	Brassicaceae	Brassicales	C N Chile, Arg	3	C-AND	10	9
Mulguraea	Verbenaceae	Lamiales	Chile, Arg, Peru	3	C-AND	2	1
Werdermannia	Brassicaceae	Brassicales	N Chile, Arg	3	C-AND	3	3
Ageratina	Asteraceae	Asterales	E USA, C & W S Am, West Indies	3	W-NT	1	0
Aloysia	Verbenaceae	Lamiales	Am: SW US to Chile & Arg	3	W-NT	1	1
Ambrosia	Asteraceae	Asterales	Canada, Mexico, S Am, West Indies	3	W-NT	1	0
Antidaphne	Santalaceae	Santalales	W trop SA: S Mexico, S & S Am	3	W-NT	1	1
Argemone	Papaveraceae	Ranunculales	N & S AM, WI, Hawaii	3	W-NT	4	2
Argyrochosma	Pteridaceae	Polypodiales	Trop Am, USA to Chile	3	W-NT	2	1
Asteriscium	Apiaceae	Apiales	Mexico to Patagonia	3	W-NT	4	4
Astrolepis	Pteridaceae	Polypodiales	Trop Am, USA to Chile	3	W-NT	1	0
Baccharis	Asteraceae	Asterales	Trop AM, W N Am, esp S Am	3	W-NT	40	11
Bomarea	Alstroemeriaceae	Liliales	Mex to trop Am	3	W-NT	3	1
Bouteloua	Poaceae	Poales	Am from Canada to Argentina	3	W-NT	1	0
Bowlesia	Apiaceae	Apiales	N & S Am, B. incana S US	3	W-NT	7	3
Calandrinia	Portulacaceae	Caryophyllales	Am W USA to Chile	3	W-NT	10	2
Calceolaria	Calceolariaceae	Lamiales	AM from Mex to TFuego	3	W-NT	59	45
Calydorea	Iridaceae	Asparagales	Trop & Subtrop Am	3	W-NT	1	1
Cestrum	Solanaceae	Solanales	Trop Am, esp Brasil & Andes	3	W-NT	1	0
Chaptalia	Asteraceae	Asterales	Trop & subtrop Am, S USA	3	W-NT	1	0
Chusquea	Poaceae	Poales	C & S Am, WI, JF	3	W-NT	10	7

Genus	Family	Order	Global distribution	Element	Track	Native spp.	Endemic spp.
Coreopsis	Asteraceae	Asterales	N & S Am	3	W-NT	1	1
Dalea	Fabaceae	Fabales	Am, Canada to Arg	3	W-NT	3	2
Dichanthelium	Poaceae	Poales	Toda America	3	W-NT	1	0
Drimys	Winteraceae	Canellales	Mexico, C & S Am, JF	3	W-NT	3	2
Echinodorus	Alismataceae	Alismatales	USA to Argentina and Chile	3	W-NT	1	0
Elodea	Hydrocharitaceae	Alismatales	Am temp	3	W-NT	1	0
Erechtites	Asteraceae	Asterales	N & S Am	3	W-NT	1	1
Fuertesimalva	Malvaceae	Malvales	Mexico, C Andes, Galapagos, ID	3	W-NT	3	1
Gamochaeta	Asteraceae	Asterales	N & S Am, Brazil, JF	3	W-NT	24	10
Grabowskia	Solanaceae	Solanales	Mexico, Galapagos, temp S Am	3	W-NT	1	0
Greigia	Bromeliaceae	Poales	C & S Am, JF	3	W-NT	4	4
Grindelia	Asteraceae	Asterales	W N Am & S Am, Brazil	3	W-NT	3	0
Habranthus	Amaryllidaceae	Asparagales	USA, Mexico to Argentina and Chile	3	W-NT	1	0
Helenium	Asteraceae	Asterales	W N Am, Mexico, C America, Andes	3	W-NT	7	6
Heterosperma	Asteraceae	Asterales	SW USA, Mexico, C Am, Peru, Arg, Chile	3	W-NT	2	0
Jarava	Poaceae	Poales	Arg, Bol, Chile, Colombia, CosRica, Ecuador, El Salvador, Guatemala, Mexico, Peru, USA, Uruguay, Venezuela	3	W-NT	19	1
Krameria	Krameriaceae	Zygophyllales	SW US, Mexico, Ecuador, Chile, Arg, Brazil	3	W-NT	2	1
Lachemilla	Rosaceae	Rosales	Mexico to Andes Chile Arg	3	W-NT	3	0
Lepechinia	Lamiaceae	Lamiales	California, Andes, Mexico to S Brasil, Arg, Chile	3	W-NT	3	3
Lophosoria	Dicksoniaceae	Cyatheales	Trop Am	3	W-NT	1	0
Mecardonia	Veronicaceae	Lamiales	Am S US to Arg	3	W-NT	1	0
Mentzelia	Loasaceae	Cornales	SW Nam, WI, Canada, neotropics to Chile, Arg	3	W-NT	3	1
Monnina	Polygalaceae	Fabales	Am SW US to Chile	3	W-NT	2	2

Genus	Family	Order	Global distribution	Element	Track	Native spp.	Endemic spp.
Nama	Boraginaceae	Unplaced	N Am from California, Mex, C Am to Brasil, WI, Hawaii	3	W-NT	2	0
Nasa	Loasaceae	Cornales	Colombia, Ecuador, Peru, few in Chile, Bolivia, Venezuela and C Am (to S Mexico).	3	W-NT	1	0
Nassella	Poaceae	Poales	C & S Am	3	W-NT	28	11
Nierembergia	Solanaceae	Solanales	Mex to Arg, Bras	3	W-NT	1	0
Nothoscordum	Alliaceae	Asparagales	Am	3	W-NT	5	3
Oenothera	Onagraceae	Myrtales	Temp & subtrop N C & S Am	3	W-NT	14	3
Olsynium	Iridaceae	Asparagales	Andean and temp S Am and NW N Am	3	W-NT	10	3
Piptochaetium	Poaceae	Poales	Am US to Arg, JF	3	W-NT	7	3
Puya	Bromeliaceae	Poales	C & S Am, Brazil	3	W-NT	8	8
Rostraria	Poaceae	Poales	Arg, Caribe, Chil, Mexico, Peru, USA,Urug	3	W-NT	1	0
Schinus	Anacardiaceae	Sapindales	Mexico to Arg	3	W-NT	11	4
Schkuhria	Asteraceae	Asterales	Trop & subtrop Am	3	W-NT	2	0
Sisyrinchium	Iridaceae	Asparagales	N, C & S Am	3	W-NT	18	10
Stenandrium	Acanthaceae	Lamiales	S US to C Chile	3	W-NT	1	0
Stevia	Asteraceae	Asterales	S US to Chile	3	W-NT	2	1
Tagetes	Asteraceae	Asterales	N & S Am	3	W-NT	3	0
Tillandsia	Bromeliaceae	Poales	Trop & subtrop Am, WI	3	W-NT	5	1
Trixis	Asteraceae	Asterales	SW N Am to Chile	3	W-NT	1	0
Tropaeolum	Tropaeolaceae	Brassicales	Mexico to Chile	3	W-NT	18	15
Ugni	Myrtaceae	Myrtales	Am from Mex to Chile, JF	3	W-NT	3	2
Vasconcellea	Caricaceae	Brassicales	Mexico to N Arg & S Brasil	3	W-NT	1	1
Verbesina	Asteraceae	Asterales	Trop & subtrop Am, WI	3	W-NT	3	1
Viguiera	Asteraceae	Asterales	Trop & subtrop Am, WI	3	W-NT	4	2
Villanova	Asteraceae	Asterales	Mex to Chile	3	W-NT	2	1
Agalinis	Orobanchaceae	Lamiales	Trop, warm C & S Am, USA	4	ANT-P	2	1
Agoseris	Asteraceae	Asterales	9 sp W N Am, Mexico, 2 sp Chile, Arg	4	ANT-P	2	1

Genus	Family	Order	Global distribution	Element	Track	Native spp.	Endemic spp.
Allionia	Nyctaginaceae	Caryophyllales	SW & C US, Mexico to Chile & Arg	4	ANT-P	1	0
Amblyopappus	Asteraceae	Asterales	Calif, NW Mexico, Chile	4	ANT-P	1	0
Amphiscirpus	Cyperaceae	Poales	Canada, USA, Arg, Chile	4	ANT-P	1	0
Amsinckia	Boraginaceae	Unplaced	W US, W temp S Am	4	ANT-P	2	0
Bahia	Asteraceae	Asterales	SW US, Mex, Chile	4	ANT-P	1	1
Blennosperma	Asteraceae	Asterales	2 California, 1 Chile	4	ANT-P	1	1
Bromidium	Poaceae	Poales	S US & subtrop S Am	4	ANT-P	2	1
Bryantiella	Polemoniaceae	Ericales	W N Am, Chile	4	ANT-P	1	0
Camissonia	Onagraceae	Myrtales	W N Am, Mex, S Am temp	4	ANT-P	1	0
Cardionema	Caryophyllaceae	Caryophyllales	W N Am to Chile	4	ANT-P	3	1
Chascolytrum	Poaceae	Poales	Central & S Am, USA	4	ANT-P	1	0
Chiropetalum	Euphorbiaceae	Malpighiales	Mexico 2, Peru, S Bras, Arg, Chile	4	ANT-P	4	3
Chorizanthe	Polygonaceae	Caryophyllales	Arid & semiarid W Am, Chile	4	ANT-P	13	12
Cistanthe	Portulacaceae	Caryophyllales	N Am, Calif, Arizona, N México & S Am, Peru, Bol, Arg, Chile	4	ANT-P	24	15
Clarkia	Onagraceae	Myrtales	N Am spec. California, 1 sp Chile/Arg	4	ANT-P	1	0
Collomia	Polemoniaceae	Ericales	W N Am, Bol to Patagonia	4	ANT-P	1	0
Cryptantha	Boraginaceae	Unplaced	W US, W temp S Am	4	ANT-P	40	31
Dissanthelium	Poaceae	Poales	Peru, Chile, Bol to California	4	ANT-P	1	0
Downingia	Campanulaceae	Asterales	W N Am, 1 Chile	4	ANT-P	1	0
Encelia	Asteraceae	Asterales	SW USA, Mexico, Chile, Peru, Galapagos	4	ANT-P	1	0
Errazurizia	Fabaceae	Fabales	SW US, Mex, 1 sp Chile	4	ANT-P	1	1
Flourensia	Asteraceae	Asterales	SW USA, Mexico, Peru, Chile, Arg	4	ANT-P	1	1
Gayophytum	Onagraceae	Myrtales	Temp W N Am & W S Am	4	ANT-P	2	0
Gilia	Polemoniaceae	Ericales	W N Am & S Am	4	ANT-P	3	0
Glandularia	Verbenaceae	Lamiales	Disjunct N Am S Am	4	ANT-P	12	3
Gutierrezia	Asteraceae	Asterales	W N Am & South S Am	4	ANT-P	6	5
Hoffmannseggia	Fabaceae	Fabales	25 SW US, Chile, Arg	4	ANT-P	8	0

Genus	Family	Order	Global distribution	Element	Track	Native spp.	Endemic spp.
Ipomopsis	Polemoniaceae	Ericales	W N Am & Florida, 1 Chile Arg	4	ANT-P	1	0
Larrea	Zygophyllaceae	Zygophyllales	SW N Am, S Am	4	ANT-P	2	0
Lastarriaea	Polygonaceae	Caryophyllales	California, Chile	4	ANT-P	1	1
Lasthenia	Asteraceae	Asterales	SW US, Chile-Arg	4	ANT-P	1	0
Legenere	Campanulaceae	Asterales	1 Calif, 1 Chile	4	ANT-P	1	0
Leptosiphon	Polemoniaceae	Ericales	W N Am, Chile	4	ANT-P	1	1
Lepuropetalon	Celastraceae	Celastrales	SE USA, Mexico, Chile, Arg Uruguay	4	ANT-P	1	0
Lilaea	Juncaginaceae	Alismatales	Pacific Am Canada to Chile	4	ANT-P	1	0
Madia	Asteraceae	Asterales	W N Am, Chile-Arg	4	ANT-P	2	1
Malacothrix	Asteraceae	Asterales	W N Am, Chile	4	ANT-P	1	0
Mancoa	Brassicaceae	Brassicales	Mexico, Andes Peru, Bol, Arg, Chile	4	ANT-P	1	0
Microsteris	Polemoniaceae	Ericales	W N Am & S Am	4	ANT-P	1	0
Munroa	Poaceae	Poales	1 W US, 4 SW S Am	4	ANT-P	3	0
Navarretia	Polemoniaceae	Ericales	W N Am, Chile, Arg	4	ANT-P	1	0
Nitrophila	Amaranthaceae	Caryophyllales	US, Mex, Chile, Arg	4	ANT-P	1	1
Oxytheca	Polygonaceae	Caryophyllales	W N Am, Chile, Arg	4	ANT-P	1	0
Pectocarya	Boraginaceae	Unplaced	W N Am, S Am	4	ANT-P	3	1
Perityle	Asteraceae	Asterales	SW N Am, C Am, 1 Chile Peru	4	ANT-P	1	0
Phacelia	Boraginaceae	Unplaced	W N Am, S Am	4	ANT-P	6	0
Podagrostis	Poaceae	Poales	Arg, Chile, Canadá, USA	4	ANT-P	1	0
Porlieria	Zygophyllaceae	Zygophyllales	S USA, Mexico, S Am	4	ANT-P	1	1
Psilocarphus	Asteraceae	Asterales	W US, temp S Am	4	ANT-P	2	0
Sphaeralcea	Malvaceae	Malvales	W N Am, Mex, S Am	4	ANT-P	2	1
Symphyotrichum	Asteraceae	Asterales	N Am, Mexico, S Am	4	ANT-P	4	0
Tarasa	Malvaceae	Malvales	Mexico (2), disjunct to Peru, Chile, Arg	4	ANT-P	10	4
Tigridia	Iridaceae	Asparagales	Mex, Guatemala disjunct to Peru, Chile, Bol, Brazil	4	ANT-P	1	0
Tiquilia	Boraginaceae	Unplaced	Arid N & S Am	4	ANT-P	5	1

Genus	Family	Order	Global distribution	Element	Track	Native spp.	Endemic spp.
Tropidocarpum	Brassicaceae	Brassicales	California, Chile	4	ANT-P	1	1
Vahlodea	Poaceae	Poales	Arg, Chile, Canadá, USA	4	ANT-P	1	0
Distichlis	Poaceae	Poales	Am from Canada to Argentina, 1 sp Australia	4	C-PAC	3	0
Flaveria	Asteraceae	Asterales	W N Am, Mexico, S Am, 1 sp Aus	4	C-PAC	1	0
Gaultheria	Ericaceae	Ericales	E & SE Asia, Malesia, Aus, NZ, N, C, S Am, WI, JF	4	C-PAC	10	1
Gochnatia	Asteraceae	Asterales	Trop & Subtrop Am, S USA, SE Asia	4	C-PAC	1	1
Lilaeopsis	Apiaceae	Apiales	Am Canada to TFuego, Aus, NZ	4	C-PAC	1	0
Microseris	Asteraceae	Asterales	W N Am, 1 Chile, 1 Aus, NZ	4	C-PAC	1	0
Plagiobothrys	Boraginaceae	Unplaced	W N Am, South Am, E Asia, Aus	4	C-PAC	17	11
Sicyos	Cucurbitaceae	Cucurbitales	Aus, Tasm, NZ, Hawaii, N & S Am, ID	4	C-PAC	1	0
Soliva	Asteraceae	Asterales	S Am, N Am, Aus	4	C-PAC	2	0
Acaena	Rosaceae	Rosales	S Afr (1), New Guinea, Aus, Tasmania, NZ, subantarctic Is, Polynesia, Hawaii, California to SA, JF	4	C-PAC	19	2
Carpobrotus	Aizoaceae	Caryophyllales	S Afr, Aus, Tasman, NZ, Calif, Chile	4	C-PAC	1	0
Weinmannia	Cunoniaceae	Oxalidales	Madag, Australasia, Mex, C & S Am	4	C-PAC	1	0
Adenocaulon	Asteraceae	Asterales	W NA, Mexico, Hawaii, Guatemala, Chile, Arg, Himalayas, E Asia	4	W-ANT	1	0
Agrostis	Poaceae	Poales	Temp & warm regions, montane tropics, JF, IP	4	W-ANT	22	4
Alopecurus	Poaceae	Poales	Warm temp & subtrop regions & montane tropics	4	W-ANT	6	2
Amelichloa	Poaceae	Poales	S Am, Mexico	4	W-ANT	2	0
Anaphalis	Asteraceae	Asterales	Asia, North and South America	4	W-ANT	1	1
Androsace	Primulaceae	Ericales	N Hemisphere, China, few sp SA (TFuego)	4	W-ANT	1	0
Anemone	Ranunculaceae	Ranunculales	Euras, Sumatra, S & E Afr, NZ, A multifida disj N Am to Chile	4	W-ANT	7	3
Antennaria	Asteraceae	Asterales	Arctic & temp Euras, Andes S Am	4	W-ANT	1	0

Genus	Family	Order	Global distribution	Element	Track	Native spp.	Endemic spp.
Arenaria	Caryophyllaceae	Caryophyllales	America, temp Eurasia, N Afr	4	W-ANT	7	3
Armeria	Plumbaginaceae	Caryophyllales	SAm Andes to Tfuego, Euro, Russia	4	W-ANT	1	0
Artemisia	Asteraceae	Asterales	Temp Eurasia & W N Am, S Afr, S Am, Pacific Is	4	W-ANT	2	0
Astragalus	Fabaceae	Fabales	N Am, Andes, temp Eurasia, montane trop Afr	4	W-ANT	49	23
Bartsia	Orobanchaceae	Lamiales	Circumboreal, Eur, Medit, Afr, Andes	4	W-ANT	3	1
Berberis	Berberidaceae	Ranunculales	Euras, N Afr, N & S AM	4	W-ANT	19	11
Botrychium	Ophioglossaceae	Ophioglossales	Temp, polar, trop montane	4	W-ANT	2	0
Bromus	Poaceae	Poales	Eurasia, N & S Afr, montane trop Asia, Am, JF	4	W-ANT	10	0
Caltha	Ranunculaceae	Ranunculales	Arctic & temp N Hemis, NZ, temp S AM	4	W-ANT	3	0
Cardamine	Brassicaceae	Brassicales	Cosmop, temp N hemis & montane tropics, JF	4	W-ANT	15	4
Castilleja	Orobanchaceae	Lamiales	Euras, E N Am, C & S Am	4	W-ANT	3	0
Catabrosa	Poaceae	Poales	Temp Eurasia, N Am, Chile	4	W-ANT	2	0
Chrysosplenium	Saxifragaceae	Saxifragales	N & temp S Am, Euro, N Afr, Asia,	4	W-ANT	2	0
Cicendia	Gentianaceae	Gentianales	1 Euro & Medit, 1 Calif, W S Am	4	W-ANT	1	0
Cryptogramma	Pteridaceae	Polypodiales	Temperate N & S	4	W-ANT	1	0
Cystopteris	Woodsiaceae	Polypodiales	Temp & warm regions, montane tropics	4	W-ANT	1	0
Danthonia	Poaceae	Poales	N & S Am, Euro, Caucasus	4	W-ANT	4	2
Deschampsia	Poaceae	Poales	Temp & cool, espec N Euro, montane tropics	4	W-ANT	15	3
Descurainia	Brassicaceae	Brassicales	S Am, N Am, Canary Is.	4	W-ANT	12	4
Draba	Brassicaceae	Brassicales	Arctic & temp n Hemis, Asia, montane C & S Am	4	W-ANT	8	1
Elatine	Elatinaceae	Malpighiales	Temp, trop & subtrop regions	4	W-ANT	1	0
Empetrum	Ericaceae	Ericales	N temp & Arctic, Europa, S Andes, Falkland, JF	4	W-ANT	1	0
Ephedra	Ephedraceae	Ephedrales	Eurasia, AM	4	W-ANT	7	2
Epilobium	Onagraceae	Myrtales	Temp Euro, N Am, arctic, montane trop	4	W-ANT	12	2
Erigeron	Asteraceae	Asterales	Eurasia, N & S Am, Aus, JF	4	W-ANT	17	8

Genus	Family	Order	Global distribution	Element	Track	Native spp.	Endemic spp.
Euphrasia	Orobanchaceae	Lamiales	Temp N Hemishp, Euro, Middle Asia, Australia, NZ, temp S Am, JF	4	W-ANT	16	12
Fagonia	Zygophyllaceae	Zygophyllales	Medit, Euro, SW Asia, NE Afr, SW N Am, Peru, Chile	4	W-ANT	1	0
Gentiana	Gentianaceae	Gentianales	Euro, NW Afr, Asia, E Aus, Am	4	W-ANT	1	0
Glycyrrhiza	Fabaceae	Fabales	Eurasia, Aus, N Am & temp S Am	4	W-ANT	1	0
Halerpestes	Ranunculaceae	Ranunculales	Temperate Asia, N & S Am	4	W-ANT	2	0
Hieracium	Asteraceae	Asterales	Temp regions & montane tropics, excl Australasia	4	W-ANT	4	0
Hippuris	Veronicaceae	Lamiales	Circumboreal, S Am, Australia	4	W-ANT	1	0
Hordeum	Poaceae	Poales	Temp & subtrop regs, montane tropics	4	W-ANT	9	1
Hydrangea	Hydrangeaceae	Cornales	Himalayas, Asia, Philippines, N, C Am, Andes to Chile	4	W-ANT	1	0
Hypochaeris	Asteraceae	Asterales	Temp S Am, Eurasia Medit, N Afr	4	W-ANT	31	17
Isolepis	Cyperaceae	Poales	Cape Region S Afr, Australasia, S Am, north temperate	4	W-ANT	4	0
Lathyrus	Fabaceae	Fabales	Temp N hemis, Medit, montane tropics, E Afr, S Am	4	W-ANT	13	3
Leymus	Poaceae	Poales	Temp regs	4	W-ANT	1	0
Limonium	Plumbaginaceae	Caryophyllales	N temperate, circumboreal, austral	4	W-ANT	1	1
Littorella	Veronicaceae	Lamiales	1 N Am, 1 S Am, 1 Euro	4	W-ANT	1	0
Lupinus	Fabaceae	Fabales	N & S Am, Medit, montane trops, E Afr	4	W-ANT	6	2
Malvella	Malvaceae	Malvales	3 sp W USA, Mexico, 1 sp Peru to Uruguay, 1 sp. Medit	4	W-ANT	1	0
Melica	Poaceae	Poales	Temp regs & montane trops	4	W-ANT	8	7
Minuartia	Caryophyllaceae	Caryophyllales	Arctic & temp regions, Mexico, Ethiopia, Himalayas, Chile	4	W-ANT	1	1
Mirabilis	Nyctaginaceae	Caryophyllales	Am trop, Himal, China	4	W-ANT	5	3

Genus	Family	Order	Global distribution	Element	Track	Native spp.	Endemic spp.
Muhlenbergia	Poaceae	Poales	Temp & subtrop Am, Asia	4	W-ANT	3	0
Myosotis	Boraginaceae	Unplaced	Eurasia, montane trops, S Afr, N Guinea, Aus, NZ	4	W-ANT	2	0
Myosurus	Ranunculaceae	Ranunculales	Temp regs hemis N & S, M apetalus disj N Am	4	W-ANT	2	0
Noccaea	Brassicaceae	Brassicales	N temp, few S Am	4	W-ANT	1	0
Osmorhiza	Apiaceae	Apiales	N Am, E Asia, temp S Am	4	W-ANT	4	0
Paronychia	Caryophyllaceae	Caryophyllales	North temperate, austral	4	W-ANT	6	3
Pennisetum	Poaceae	Poales	Trop & temp regs	4	W-ANT	1	0
Persea	Lauraceae	Laurales	Trops & subtrops Am & Asia, Macaronesia	4	W-ANT	1	0
Phalaris	Poaceae	Poales	Temperate Eurasia, America	4	W-ANT	2	1
Phleum	Poaceae	Poales	Temperate Eurasia, America	4	W-ANT	1	0
Pinguicula	Lentibulariaceae	Lamiales	Am, Medit, circumboreal	4	W-ANT	2	0
Poa	Poaceae	Poales	Temp & cold & montane trops	4	W-ANT	42	7
Polemonium	Polemoniaceae	Ericales	Temp Eurasia, N Am, Chile	4	W-ANT	1	0
Potentilla	Rosaceae	Rosales	N & S Am, temp Euras	4	W-ANT	1	0
Primula	Primulaceae	Ericales	N Hemisp, trop Asia, temp S Am	4	W-ANT	1	0
Rhamnus	Rhamnaceae	Rosales	N Hemisp, S Afr, S Am	4	W-ANT	1	1
Ribes	Grossulariaceae	Saxifragales	N Hemis, N Afr, S Am Canada to Tfuego	4	W-ANT	11	6
Salix	Salicaceae	Malpighiales	Arctic temp, few in trops, temp S Am, 1 S Afr	4	W-ANT	1	0
Saxifraga	Saxifragaceae	Saxifragales	N temp, Eurasia, W N Am, Andes S Am	4	W-ANT	1	0
Solidago	Asteraceae	Asterales	Eurasia, N Am, Mexico, 1 S Am	4	W-ANT	2	0
Spartina	Poaceae	Poales	Am, W Euro, NW Afr	4	W-ANT	1	0
Spergula	Caryophyllaceae	Caryophyllales	Europe, Patagonia	4	W-ANT	4	1
Stemodia	Veronicaceae	Lamiales	Trops and Subtrops, Madag	4	W-ANT	1	0
Taraxacum	Asteraceae	Asterales	Temp N Hemis & temp S Am, NZ, JF	4	W-ANT	3	1
Tetragonia	Aizoaceae	Caryophyllales	N & S Afr, SE Asia, Aus, Tasm, NZ, Polinesia, Peru, Chile	4	W-ANT	8	7
Trifolium	Fabaceae	Fabales	Temp & subtrop exc Aus	4	W-ANT	10	5

Genus	Family	Order	Global distribution	Element	Track	Native spp.	Endemic spp.
Triglochin	Juncaginaceae	Alismatales	N temperate, circumboreal, austral	4	W-ANT	3	0
Triodanis	Campanulaceae	Asterales	N Am, Mex, Guatem, Medit	4	W-ANT	1	0
Valeriana	Valerianaceae	Dipsacales	N temp Eurasia, S Afr, Andes	4	W-ANT	44	21
Verbena	Verbenaceae	Lamiales	Temp & trop Am, few OW	4	W-ANT	10	4
Vicia	Fabaceae	Fabales	Temp N Hemis, Medit, few trop Afr, S Am, Hawaii	4	W-ANT	19	12
Woodsia	Woodsiaceae	Polypodiales	Temp & cool temp Eurasia, Afr, Am, exc Aus	4	W-ANT	1	0
Menodora	Oleaceae	Lamiales	Trop & subtrop Am, S Afr	4		1	1
Acrisione	Asteraceae	Asterales	Central Chile, Arg	5		2	1
Aextoxicon	Aextoxicaceae	Berberidopsidales	Chile, Arg	5		1	0
Amomyrtus	Myrtaceae	Myrtales	Temp S Am: Arg, Chile	5		2	1
Anarthrophyllum	Fabaceae	Fabales	Andes Chile Arg	5		6	2
Asteranthera	Gesneriaceae	Lamiales	Chile, Arg	5		1	0
Austrocactus	Cactaceae	Caryophyllales	Arg, Chile	5		3	1
Austrocedrus	Cupressaceae	Pinales	Arg, Chile	5		1	0
Barneoudia	Ranunculaceae	Ranunculales	Arg, Chile	5		3	0
Belloa	Asteraceae	Asterales	Andes S Arg, Chile	5		1	0
Benthamiella	Solanaceae	Solanales	S Chile-Arg, Patagonia	5		4	0
Bipinnula	Orchidaceae	Asparagales	Temp S Am: Chile, Arg	5		4	4
Bolax	Apiaceae	Apiales	Temp SA	5		2	0
Boquila	Lardizabalaceae	Ranunculales	Arg, Chile	5		1	0
Brachyclados	Asteraceae	Asterales	Temp Chile, Arg	5		1	0
Callianthemoides	Ranunculaceae	Ranunculales	Arg, Chile	5		1	0
Campsidium	Bignoniaceae	Lamiales	Arg, Chile: C. valdivianum	5		1	0
Chiliotrichum	Asteraceae	Asterales	S Andes Chile, Argentina	5		2	0
Combera	Solanaceae	Solanales	Andes Chile Arg	5		2	1
Corynabutilon	Malvaceae	Malvales	Chile, Arg	5		7	6
Diostea	Verbenaceae	Lamiales	Temperate S Am, Arg, Chile	5		1	0

Genus	Family	Order	Global distribution	Element	Track	Native spp.	Endemic spp.
Diplolepis	Apocynaceae	Gentianales	Chile, Arg	5		6	3
Diposis	Apiaceae	Apiales	temp S Am	5		1	1
Doniophyton	Asteraceae	Asterales	Andes Chile Arg	5		2	0
Drapetes	Thymelaeaceae	Malvales	temp S Am	5		1	0
Elytropus	Apocynaceae	Gentianales	Chile, Arg	5		1	0
Embothrium	Proteaceae	Proteales	Chile y Argentina, 1 spp.	5		1	0
Eriachaenium	Asteraceae	Asterales	Tierra del Fuego	5		1	0
Famatina	Amaryllidaceae	Asparagales	Chile, Arg	5		2	2
Fitzroya	Cupressaceae	Pinales	Chile Arg	5		1	0
Fonkia	Veronicaceae	Lamiales	Chile, Arg	5		1	0
Gamocarpha	Calyceraceae	Asterales	Temp S Am	5		6	2
Gamochaetopsis	Asteraceae	Asterales	S Arg, Chile	5		1	0
Gavilea	Orchidaceae	Asparagales	Temp S Am, JF	5		12	6
Gilliesia	Alliaceae	Asparagales	Chile, Arg	5		4	3
Guindilia	Sapindaceae	Sapindales	Chile Arg	5		1	0
Hamadryas	Ranunculaceae	Ranunculales	Antarctic S Am	5		4	0
Huanaca	Apiaceae	Apiales	Chile, Arg	5		4	0
Hymenoglossum	Hymenophyllaceae	Hymenophyllales	Chile, Arg	5		1	0
Lardizabala	Lardizabalaceae	Ranunculales	Chile and adjacent Argentina	5		1	1
Laretia	Apiaceae	Apiales	Chile, Argentina	5		1	0
Laureliopsis	Atherospermataceae	Laurales	Chile Arg	5		1	0
Lebetanthus	Ericaceae	Ericales	Patagonia	5		1	0
Lecanophora	Malvaceae	Malvales	Arg, Chile	5		1	0
Lepidophyllum	Asteraceae	Asterales	Patagonia Chile-Arg	5		1	0
Leptophyllochloa	Poaceae	Poales	Arg Chile, JF	5		1	0
Luma	Myrtaceae	Myrtales	Chile Arg	5		2	1
Macrachaenium	Asteraceae	Asterales	Patagonia & TFuego	5		1	0
Maihuenia	Cactaceae	Caryophyllales	Arg, Chile	5		2	0

Genus	Family	Order	Global distribution	Element	Track	Native spp.	Endemic spp.
Melosperma	Veronicaceae	Lamiales	Chile, Arg	5		2	0
Menonvillea	Brassicaceae	Brassicales	Chile, Arg	5		19	13
Misodendrum	Misodendraceae	Santalales	S Am, south of 33	5		8	1
Mitraria	Gesneriaceae	Lamiales	Chile, Arg	5		1	0
Mulinum	Apiaceae	Apiales	S Andes	5		5	1
Myoschilos	Santalaceae	Santalales	Chile, Arg	5		1	0
Nanodea	Santalaceae	Santalales	Temp S Am	5		1	0
Nastanthus	Calyceraceae	Asterales	Chile, Arg, Falkland Is.	5		5	1
Notopappus	Asteraceae	Asterales	Chile Arg	5		4	0
Ochetophila	Rhamnaceae	Rosales	Chile, Arg	5		2	0
Odontorrhynchus	Orchidaceae	Asparagales	Temp S Am: Chile, Arg	5		4	4
Onuris	Brassicaceae	Brassicales	Chile, Patagonia	5		5	0
Oreopolus	Rubiaceae	Gentianales	Chile, Arg, Patagonia	5		1	0
Ortachne	Poaceae	Poales	Arg, Chile	5		2	0
Ovidia	Thymelaeaceae	Malvales	temp S Am	5		1	0
Philesia	Philesiaceae	Liliales	Chile, Arg	5		1	0
Philippiella	Caryophyllaceae	Caryophyllales	Patagonia Chile-Arg.	5		1	0
Phycella	Amaryllidaceae	Asparagales	Chile, Arg	5		6	5
Pilgerodendron	Cupressaceae	Pinales	Chile Arg	5		1	0
Pozoa	Apiaceae	Apiales	Andes Chile Arg	5		2	0
Pterocactus	Cactaceae	Caryophyllales	Patagonia Arg, Chile	5		2	0
Relchela	Poaceae	Poales	Chile Arg	5		1	0
Retanilla	Rhamnaceae	Rosales	Chile, Arg	5		3	3
Rhaphithamnus	Verbenaceae	Lamiales	Chile, Arg, JF	5		2	1
Salpiglossis	Solanaceae	Solanales	Chile, Arg	5		2	1
Sarcodraba	Brassicaceae	Brassicales	Chile, Arg	5		1	0
Saxegothaea	Podocarpaceae	Pinales	Chile, Arg	5		1	0
Saxifragella	Saxifragaceae	Saxifragales	Antarctic S Am	5		1	0

Genus	Family	Order	Global distribution	Element	Track	Native spp.	Endemic spp.
Saxifragodes	Saxifragaceae	Saxifragales	Tfuego	5		1	0
Schizanthus	Solanaceae	Solanales	Chile, Arg	5		12	10
Serpyllopsis	Hymenophyllaceae	Hymenophyllales	Chile, Arg	5		1	0
Solaria	Alliaceae	Asparagales	Chile, Arg	5		1	0
Solenomelus	Iridaceae	Asparagales	Chile, Arg	5		2	1
Synammia	Polypodiaceae	Polypodiales	Arg, Chile, JF	5		3	2
Tapeinia	Iridaceae	Asparagales	Chile, Arg	5		1	0
Tepualia	Myrtaceae	Myrtales	Chile, Arg	5		1	0
Tetroncium	Juncaginaceae	Alismatales	Temp S Am, Magallanes	5		1	0
Tribeles	Escalloniaceae	Escalloniales	Chile & TFuego	5		1	0
Trichopetalum	Asparagaceae	Asparagales	Chile, Arg	5		1	1
Triptilion	Asteraceae	Asterales	Chile, Arg	5		7	5
Tristagma	Alliaceae	Asparagales	Chile, Arg, Uru	5		6	5
Xerodraba	Brassicaceae	Brassicales	S Arg, Chile	5		2	0
Zoellnerallium	Alliaceae	Asparagales	Chile, Arg	5		2	1
Adenopeltis	Euphorbiaceae	Malpighiales	Chile	6		1	1
Anisomeria	Phytolaccaceae	Caryophyllales	Chile	6		2	2
Araeoandra	Vivianiaceae	Geraniales	Chile	6		1	1
Avellanita	Euphorbiaceae	Malpighiales	Chile	6		1	1
Bakerolimon	Plumbaginaceae	Caryophyllales	Chile	6		1	1
Balsamocarpon	Fabaceae	Fabales	Chile	6		1	1
Bridgesia	Sapindaceae	Sapindales	Chile	6		1	1
Calopappus	Asteraceae	Asterales	Chile	6		1	1
Cissarobryon	Vivianiaceae	Geraniales	Chile	6		1	1
Conanthera	Tecophilaeaceae	Asparagales	Chile	6		5	5
Copiapoa	Cactaceae	Caryophyllales	N Chile	6		22	22
Cyphocarpus	Campanulaceae	Asterales	Chile	6		3	3
Desmaria	Loranthaceae	Santalales	Chile	6		1	1

Genus	Family	Order	Global distribution	Element	Track	Native spp.	Endemic spp.
Dinemagonum	Malpighiaceae	Malpighiales	Chile	6		1	1
Dinemandra	Malpighiaceae	Malpighiales	Chile	6		1	1
Epipetrum	Dioscoreaceae	Dioscoreales	Chile	6		3	3
Ercilla	Phytolaccaceae	Caryophyllales	Chile	6		2	2
Eriosyce	Cactaceae	Caryophyllales	Chile	6		5	5
Eulychnia	Cactaceae	Caryophyllales	Chile	6		6	6
Fascicularia	Bromeliaceae	Poales	Chile	6		1	1
Francoa	Francoaceae	Geraniales	Chile	6		1	1
Gethyum	Alliaceae	Asparagales	Chile	6		2	2
Gomortega	Gomortegaceae	Laurales	Chile	6		1	1
Guynesomia	Asteraceae	Asterales	Chile	6		1	1
Gymnachne	Poaceae	Poales	Chile	6		1	1
Gypothamnium	Asteraceae	Asterales	N Chile	6		1	1
Hollermayera	Brassicaceae	Brassicales	Chile	6		1	1
Homalocarpus	Apiaceae	Apiales	Chile	6		6	6
Huidobria	Loasaceae	Cornales	Chile	6		2	2
Ivania	Brassicaceae	Brassicales	N Chile	6		1	1
Jubaea	Arecaceae	Arecales	Chile	6		1	1
Lapageria	Philesiaceae	Liliales	Chile	6		1	1
Latua	Solanaceae	Solanales	Chile	6		1	1
Legrandia	Myrtaceae	Myrtales	Chile	6		1	1
Leontochir	Alstroemeriaceae	Liliales	Chile	6		1	1
Leptocarpha	Asteraceae	Asterales	Chile	6		1	1
Leucocoryne	Alliaceae	Asparagales	Chile	6		14	14
Leunisia	Asteraceae	Asterales	C Chile	6		1	1
Marticorenia	Asteraceae	Asterales	Chile	6		1	1
Metharme	Zygophyllaceae	Zygophyllales	N Chile	6		1	1
Microphyes	Caryophyllaceae	Caryophyllales	Chile	6		3	3

Genus	Family	Order	Global distribution	Element	Track	Native spp.	Endemic spp.
Miersia	Alliaceae	Asparagales	Chile	6		4	4
Miqueliopuntia	Cactaceae	Caryophyllales	Chile	6		1	1
Moscharia	Asteraceae	Asterales	Chile	6		2	2
Neoporteria	Cactaceae	Caryophyllales	Chile	6		6	6
Notanthera	Loranthaceae	Santalales	Chile temperate, JF	6		1	1
Ochagavia	Bromeliaceae	Poales	Chile, JF	6		4	4
Oxyphyllum	Asteraceae	Asterales	N Chile	6		1	1
Peumus	Monimiaceae	Laurales	Chile	6		1	1
Phrodus	Solanaceae	Solanales	Chile (Atacama & Coquimbo)	6		1	1
Pintoa	Zygophyllaceae	Zygophyllales	Chile	6		1	1
Pitavia	Rutaceae	Sapindales	Chile	6		1	1
Placea	Amaryllidaceae	Asparagales	Chile	6		5	5
Pleocarphus	Asteraceae	Asterales	N Chile	6		1	1
Podanthus	Asteraceae	Asterales	Chile	6		2	2
Reicheella	Caryophyllaceae	Caryophyllales	Chile	6		1	1
Sarmienta	Gesneriaceae	Lamiales	Chile	6		1	1
Scyphanthus	Loasaceae	Cornales	Chile	6		1	1
Speea	Alliaceae	Asparagales	Chile	6		1	1
Tecophilaea	Tecophilaeaceae	Asparagales	Chile	6		2	2
Tetilla	Francoaceae	Geraniales	Chile	6		1	1
Thelocephala	Cactaceae	Caryophyllales	Chile	6		6	6
Traubia	Amaryllidaceae	Asparagales	Chile	6		1	1
Trevoa	Rhamnaceae	Rosales	Chile	6		1	1
Valdivia	Escalloniaceae	Escalloniales	Chile	6		1	1
Vestia	Solanaceae	Solanales	Chile	6		1	1
Zephyra	Tecophilaeaceae	Asparagales	Chile	6		1	1
Centaurodendron	Asteraceae	Asterales	JF	6		2	2
Cuminia	Lamiaceae	Lamiales	JF	6		1	1

Genus	Family	Order	Global distribution	Element	Track	Native spp.	Endemic spp.
Dendroseris	Asteraceae	Asterales	JF	6		11	11
Juania	Arecaceae	Arecales	JF	6		1	1
Lactoris	Lactoridaceae	Piperales	JF	6		1	1
Lycapsus	Asteraceae	Asterales	Desventuradas Islands (Chile)	6		1	1
Margyracaena	Rosaceae	Rosales	JF	6		1	1
Megalachne	Poaceae	Poales	JF	6		2	2
Nesocaryum	Boraginaceae	Unplaced	Desventuradas Islands (Chile)	6		1	1
Podophorus	Poaceae	Poales	JF	6		1	1
Robinsonia	Asteraceae	Asterales	JF	6		8	8
Sanctambrosia	Caryophyllaceae	Caryophyllales	Desventuradas Islands (Chile)	6		1	1
Selkirkia	Boraginaceae	Unplaced	JF	6		1	1
Thamnoseris	Asteraceae	Asterales	Desventuradas Islands (Chile)	6		1	1
Thyrsopteris	Thyrsopteridaceae	Cyatheales	JF	6		1	1
Yunquea	Asteraceae	Asterales	JF	6		1	1
Adiantum	Pteridaceae	Polypodiales	Cosmop, esp Neotrops, Madag	7		5	3
Amaranthus	Amaranthaceae	Caryophyllales	Subtrop & temp, Euro, S Am, N Am, 16 sp Russia,	7		2	1
Anagallis	Primulaceae	Ericales	Euro, Russia, N & S Afr, Madag, W Asia, Himalayas, N Aus, 2 sp. S Am	7		1	0
Anthoxanthum	Poaceae	Poales	Temp & warm Eurasia, N Afr, montane tropics	7		7	2
Aphanes	Rosaceae	Rosales	Am, Euro, Medit, Ethiop, Australia, Caucasus	7		3	2
Apium	Apiaceae	Apiales	Euro, Medit, N & S Afr, Madag, W & E Asia, Malesia, Aus, N, C & S Am, JF, IP	7		5	3
Aristida	Poaceae	Poales	N Am, Medit, temp Asia, tropics & subtropics	7		3	0
Asplenium	Aspleniaceae	Polypodiales	Subcosmop, Madag, JF	7		10	3
Atriplex	Amaranthaceae	Caryophyllales	Cosmop, Eurasia, Aus, ID	7		21	15
Azolla	Salviniaceae	Salviniales	Trop & warm, Euro, Asia, Madag, Tristan da Cunha, Hawaii	7		1	0

Genus	Family	Order	Global distribution	Element	Track	Native spp.	Endemic spp.
Bidens	Asteraceae	Asterales	Cosmop, mostly Am	7		2	0
Blechnum	Blechnaceae	Polypodiales	Subcosmop, Madag, JF	7		13	6
Bothriochloa	Poaceae	Poales	Temp & subtrop, montane tropics	7		2	0
Callitriche	Veronicaceae	Lamiales	Cosmop	7		6	1
Calystegia	Convolvulaceae	Solanales	Cosmop, temp & trop hemis N & S, JF	7		2	0
Carex	Cyperaceae	Poales	Cosmop, JF	7		67	16
Cenchrus	Poaceae	Poales	Temp & subtrop, montane tropics	7		3	0
Centaurea	Asteraceae	Asterales	Eurasia, N China, N & tro Afr, Aus, NZ, N Am	7		7	7
Centaurium	Gentianaceae	Gentianales	Cosmop exc trop & S Afr, N hemisp 1 ext. to Aus, 1 to Chile	7		1	0
Cerastium	Caryophyllaceae	Caryophyllales	Cosmop	7		1	0
Ceratophyllum	Ceratophyllaceae	Ceratophyllales	Cosmop	7		1	0
Cheilanthes	Pteridaceae	Polypodiales	Cosmop, esp Neotrops & S Afr, Madag	7		9	0
Chenopodium	Amaranthaceae	Caryophyllales	Cosmop, JF, ID	7		16	4
Chloris	Poaceae	Poales	Cosmop	7		2	0
Clinopodium	Lamiaceae	Lamiales	Temp & subtrop, Medit	7		4	2
Convolvulus	Convolvulaceae	Solanales	Cosmop esp. temp, trop & subtrops	7		6	1
Coriaria	Coriariaceae	Cucurbitales	Mex to Chile, W Medit, Himal to Japan, New Guinea, NZ. C ruscifolia disj NZ	7		1	0
Corrigiola	Caryophyllaceae	Caryophyllales	S Am Andes Colom to Chile, Euro, Medit, Afr, Madag	7		3	3
Crassula	Crassulaceae	Saxifragales	Cosmop, Euro, A & S Afr, Madag, Aus, Am	7		7	1
Cuscuta	Convolvulaceae	Solanales	Cosmop	7		11	5
Cynanchum	Apocynaceae	Gentianales	Trops & subtrops	7		4	2
Cynoglossum	Boraginaceae	Unplaced	Temp & subtrop reg	7		1	1
Cyperus	Cyperaceae	Poales	Trop, subtrop, temp regions, JF	7		14	3

Genus	Family	Order	Global distribution	Element	Track	Native spp.	Endemic spp.
Daucus	Apiaceae	Apiales	Euro, Medit, SW & S Asia, trop Afr. Aus, NZ, & Am	7		2	0
Deyeuxia	Poaceae	Poales	Temp & subtrop reg & montane tropics	7		22	0
Digitaria	Poaceae	Poales	Temp & subtrop reg & montane tropics	7		2	0
Diplazium	Woodsiaceae	Polypodiales	Cosmop, IP	7		1	0
Drosera	Droseraceae	Caryophyllales	Cosmop, espec Aus, Tasm & NZ	7		1	0
Dryopteris	Dryopteridaceae	Polypodiales	Cosmop, IP	7		1	0
Eleocharis	Cyperaceae	Poales	Cosmop, JF	7		18	1
Elymus	Poaceae	Poales	Temp & subtrop, montane tropics	7		4	0
Enneapogon	Poaceae	Poales	Temp Eurasia, Am, trop & subtrop	7		1	0
Equisetum	Equisetaceae	Equisetales	Almost cosmop, Madag	7		2	0
Eragrostis	Poaceae	Poales	Temp & trop, ID	7		8	2
Eriochloa	Poaceae	Poales	Temp & subtrop	7		1	0
Erodium	Geraniaceae	Geraniales	Cosmop	7		1	0
Eryngium	Apiaceae	Apiales	Trop & temp, Eurasia, Am, Afr, Malesia, Aus, JF	7		15	13
Euphorbia	Euphorbiaceae	Malpighiales	Subcosmop	7		23	16
Festuca	Poaceae	Poales	Cosmop	7		25	5
Frankenia	Frankeniaceae	Caryophyllales	Temp Euro, Afr, Aus, Am, ID	7		6	1
Galium	Rubiaceae	Gentianales	Cosmop, JF	7		20	9
Gentianella	Gentianaceae	Gentianales	Eurasia, NW Afr, N, C & S Am, Aus, NZ	7		5	2
Geranium	Geraniaceae	Geraniales	Cosmop, espec tem regs & tropic montane	7		5	1
Geum	Rosaceae	Rosales	Arctic & temp regions	7		7	4
Glyceria	Poaceae	Poales	Temp & subtrop, montane tropics	7		1	0
Gnaphalium	Asteraceae	Asterales	Cosmop	7		27	14
Gratiola	Veronicaceae	Lamiales	Temp & subtrop, montane tropics	7		1	0
Heliotropium	Boraginaceae	Unplaced	Temp, subtrop, trop regs, arid	7		22	16
Huperzia	Lycopodiaceae	Lycopodiales	Subcosmop, Madag	7		2	0

Genus	Family	Order	Global distribution	Element	Track	Native spp.	Endemic spp.
Hydrocotyle	Apiaceae	Apiales	Cosmop	7		8	1
Hymenophyllum	Hymenophyllaceae	Hymenophyllales	Trop & S temp, Euro, Japan, Madag, JF	7		19	3
Hypericum	Hypericaceae	Malpighiales	Temp regs, montane tropics	7		2	1
Imperata	Poaceae	Poales	Trop, subtrop & temp regions	7		2	1
Isoetes	Isoetaceae	Isoetales	Cosmop, Madag	7		3	0
Juncus	Juncaceae	Poales	Cosmop, JF, IP	7		22	2
Koeleria	Poaceae	Poales	Temp & subtrops, montane trops	7		3	0
Landoltia	Araceae	Alismatales	Cosmop	7		1	0
Lemna	Araceae	Alismatales	Cosmop	7		3	0
Lepidium	Brassicaceae	Brassicales	Cosmop, ID	7		25	14
Limosella	Scrophulariaceae	Lamiales	Cosmop, Madag	7		1	0
Lindernia	Linderniaceae	Lamiales	Trops, subtrops, temp, Madag	7		1	0
Linum	Linaceae	Malpighiales	Temp & subtrops	7		5	4
Ludwigia	Onagraceae	Myrtales	Cosmop	7		4	0
Luzula	Juncaceae	Poales	Cosmop, JF	7		7	1
Lycium	Solanaceae	Solanales	N Am, tem S Am, Eurasia, S Afr, Aus, IP	7		11	2
Lycopodium	Lycopodiaceae	Lycopodiales	Trop & temp	7		6	0
Lysimachia	Primulaceae	Ericales	Cosmop	7		1	0
Marsilea	Marsileaceae	Salviniales	Trop & temp, Madag	7		1	0
Mimulus	Phrymaceae	Lamiales	Am, S Afr, Madag, E Asia, JF	7		7	2
Montia	Portulacaceae	Caryophyllales	Temp Eurasia, Medit, montane tropics, Afr, A Aus, A & S Am,	7		1	0
Myriophyllum	Haloragaceae	Saxifragales	Subcosmop	7		2	0
Ophioglossum	Ophioglossaceae	Ophioglossales	Subcosmop, Madag, JF	7		5	1
Orobanche	Orobanchaceae	Lamiales	Temp, subtrop, N Hemis	7		2	1
Oxalis	Oxalidaceae	Oxalidales	Cosmop	7		53	26
Panicum	Poaceae	Poales	Temp, subtrop, trop regs	7		3	0
Parietaria	Urticaceae	Rosales	Subcosmop, JF, ID	7		1	0

Genus	Family	Order	Global distribution	Element	Track	Native spp.	Endemic spp.
Paspalum	Poaceae	Poales	Temp & trop regs, IP	7		8	0
Phragmites	Poaceae	Poales	Cosmop	7		1	0
Pilularia	Marsileaceae	Salviniales	Euro, Aus, NZ, Ethiopia, W S Am	7		1	0
Plantago	Veronicaceae	Lamiales	Cosmop, JF, ID	7		23	8
Pleurosorus	Aspleniaceae	Polypodiales	España, Marruecos, Aus, Tasm, NZ, Chile, Arg	7		1	0
Plumbago	Plumbaginaceae	Caryophyllales	Trop & warm-temp regs	7		1	0
Polycarpon	Caryophyllaceae	Caryophyllales	Cosmop	7		1	1
Polygala	Polygalaceae	Fabales	Subcosmop	7		7	2
Polygonum	Polygonaceae	Caryophyllales	Cosmop	7		5	2
Polypogon	Poaceae	Poales	Cosmop	7		8	1
Polystichum	Dryopteridaceae	Polypodiales	Cosmop, Madag, IP	7		6	2
Portulaca	Portulacaceae	Caryophyllales	Trop, subtrop & temp regions	7		1	0
Potamogeton	Potamogetonaceae	Alismatales	Cosmop	7		7	0
Pteris	Pteridaceae	Polypodiales	Cosmop, Madag, JF	7		3	2
Puccinellia	Poaceae	Poales	N temp: Asia, N Am, S temp: S Afr, Aus, S Am	7		8	0
Ranunculus	Ranunculaceae	Ranunculales	Cosmop, R acaulis disj NZ, Falkland, R bonariensis disj N Am S Am	7		18	1
Rhynchospora	Cyperaceae	Poales	Cosmp	7		1	0
Rorippa	Brassicaceae	Brassicales	Cosmop	7		3	1
Rubus	Rosaceae	Rosales	Cosmop, JF	7		2	0
Rumex	Polygonaceae	Caryophyllales	Cosmop	7		10	3
Ruppia	Ruppiaceae	Alismatales	Cosmop	7		2	0
Sagina	Caryophyllaceae	Caryophyllales	Temp N Hemis, E Afr, Asia, N Guinea, Aus, NZ, Andes	7		2	0
Sagittaria	Alismataceae	Alismatales	Cosmop	7		2	0
Salvia	Lamiaceae	Lamiales	Cosmop	7		5	0
Samolus	Primulaceae	Ericales	Cosmop, IP	7		3	1

Genus	Family	Order	Global distribution	Element	Track	Native spp.	Endemic spp.
Sanicula	Apiaceae	Apiales	Subcosmop, exc Aus & NZ	7		2	0
Sarcocornia	Amaranthaceae	Caryophyllales	Eurasia, S Afr (15), Aus, Tasm, NZ, N & S Am (8), JF	7		4	0
Schoenoplectus	Cyperaceae	Poales	Cosmp	7		3	0
Schoenus	Cyperaceae	Poales	Subcosmop	7		4	0
Scirpus	Cyperaceae	Poales	North temperate, austral, JF, IP	7		5	3
Scutellaria	Lamiaceae	Lamiales	Cosmop	7		3	1
Senecio	Asteraceae	Asterales	Cosmop	7		224	103
Setaria	Poaceae	Poales	Trop, subtrop & temp regions	7		1	0
Silene	Caryophyllaceae	Caryophyllales	Temp N hemis, Medit, S Afr	7		8	0
Solanum	Solanaceae	Solanales	Subcosmop, JF, ID, IP	7		44	19
Sophora	Fabaceae	Fabales	Trop & most N temp, JF, IP	7		5	4
Spergularia	Caryophyllaceae	Caryophyllales	Cosmop, JF, ID	7		10	9
Sporobolus	Poaceae	Poales	Am, Asia, Afr, 1 Euro	7		2	0
Stachys	Lamiaceae	Lamiales	Trop, subtrop, temp regions exc. Australasia	7		11	9
Stellaria	Caryophyllaceae	Caryophyllales	Cosmop	7		9	4
Stipa	Poaceae	Poales	Temp N Hemis, montane trops, IP	7		1	0
Stuckenia	Potamogetonaceae	Alismatales	Subcosmop	7		3	0
Suaeda	Amaranthaceae	Caryophyllales	Cosmop, ID	7		5	2
Teucrium	Lamiaceae	Lamiales	Cosmop	7		2	2
Trisetum	Poaceae	Poales	Cold & temp, montane tropics, JF	7		15	2

Genus	Family	Order	Global distribution	Element	Track	Native spp.	Endemic spp.
Typha	Typhaceae	Poales	Cosmop	7		2	0
Urtica	Urticaceae	Rosales	Subcosmop, temperate	7		10	4
Utricularia	Lentibulariaceae	Lamiales	Cosmop	7		1	0
Veronica	Veronicaceae	Lamiales	Cosmop	7		1	0
Viola	Violaceae	Malpighiales	Cosmop	7		72	50
Vulpia	Poaceae	Poales	N & S Am, Euro, N Afr, M Asia	7		3	0
Wolffia	Araceae	Alismatales	Cosmop, warm temperate and tropical regions	7		1	0
Zannichellia	Potamogetonaceae	Alismatales	Cosmop	7		1	0

Tracks: Austral-antarctic (AUS), Tropical Pacific (TPAC), Circum-austral (C-AUS), Wide Neotropical (W-NT), Wide Andean (W-AND), Central Andean (C-AND), South-Amazonian (S-AMZ), Wide antitropical (W-ANT), Antitropical Pacific (ANT-P), Circum-Pacific track (C-PAC).
Islands: Juan Fernández (JF), Isla de Pascua (IP), Islas Desventuradas (ID).

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