Plant Geography of Chile

by

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Springer

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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. 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 2008–010, 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

Contents

Part I Geobotanical Scenario

Part II Chorology of Chilean Plants

Part III Islands Biogeography

Part IV Case Studies on Selected Families

Part V Where to from Here? Projections of Chilean Plant Geography

Abbreviations

ACC	Antarctic circumpolar current
cfr.	Refer to
Chap.	Chapter
col. sect.	Colour section
ENSO	El Niño Southern Oscillation
Fig.	Figure
GIS	Geographic information systems
K/T boundary	Cretaceous/Cenozoic boundary
m asl	Metres above sea level
mya	Million years ago
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.

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.

Chile 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 Islands Diego Ramírez and Cape Horn at 56°S (Figs. 1.1 and 1.2 (col. sect.)). The country’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).

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

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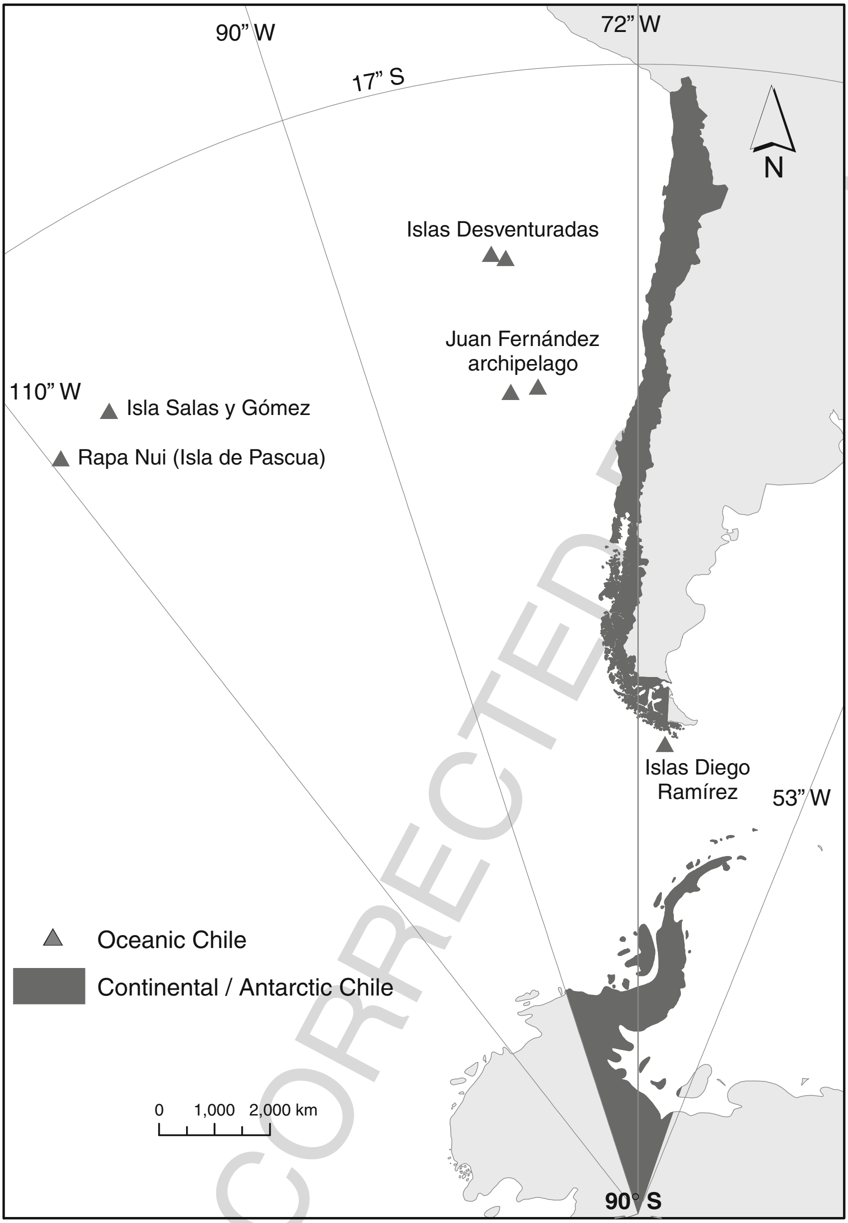

Fig. 1.1 Chile including the American continental portion, the Pacific islands, and Antarctic Peninsula. Polar stereographic projection with true scale at 71°S using ArcGIS 9. Base global map provided by ESRI Labs

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

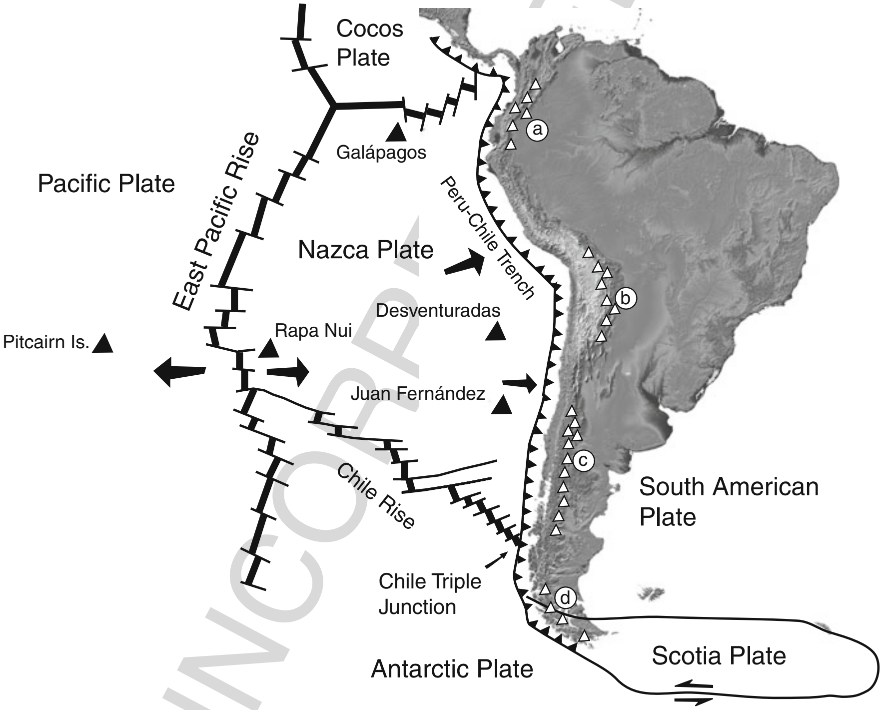

Fig. 1.3 Tectonic main features and volcanic zones of South America: **a** northern volcanic zone; **b** central volcanic zone; **c** southern volcanic zone; **d** austral volcanic zone (adapted from Orme (2007), by permission of Oxford University Press; see also Stern et al. (2007))

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).

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) (Figs. 1.3 and 1.4 (col. sect.)). 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 (Fig. 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).

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).

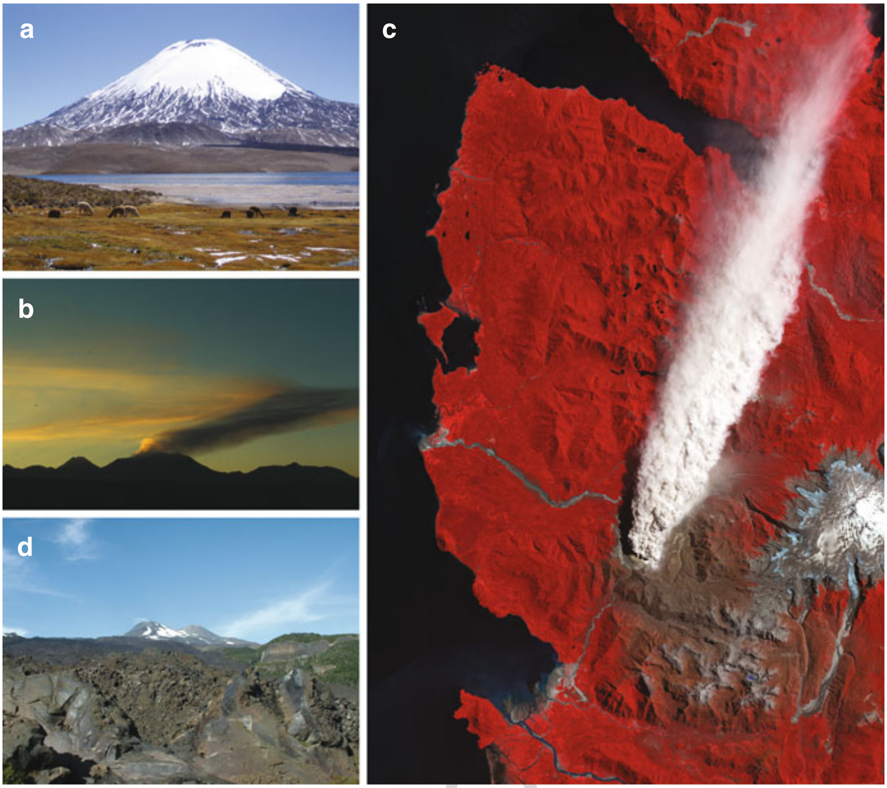

Fig. 1.4 Chilean volcanoes: **a** Parinacota volcano, 18°10′S; **b** steam expulsion of Volcán Lascar (23°20′S), on December 1996; **c** Volcán Chaitén (42°50′S), false colour Aster satellite image: plume of ash and steam advancing ca. 70 km to the north-east on January 2009; **d** lava fields around Nevados de Chillán (36°50′S) (photo credits: **a** H. Wagenseil; **b**, **d** A. Moreira-Muñoz; **c** NASA Earth Observatory (www.earthobservatory.nasa.gov))

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

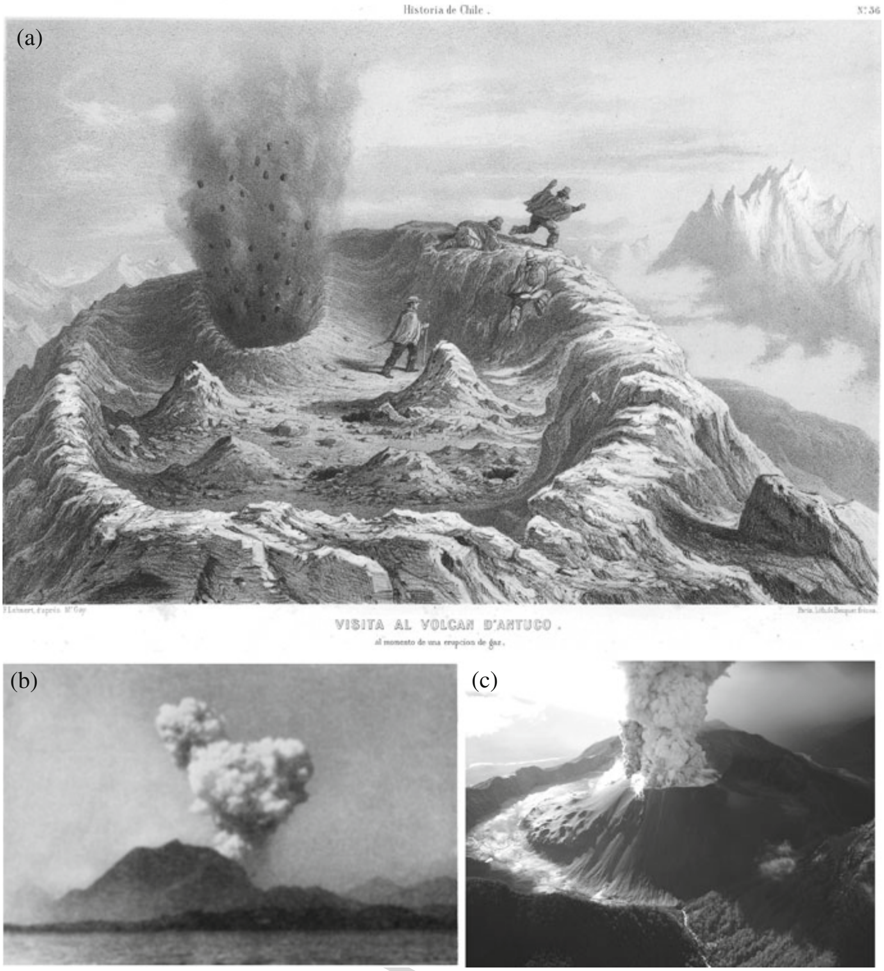

Fig. 1.5 Examples of volcanic activity in historical times: **a** ash expulsion by Volcán Antuco on the 1st March 1839, as represented in Claudio Gay's Atlas (Chap. 2); **b** eruption of Volcán Carrán in 1955 (from Illies 1959); **c** Volcán Chaitén eruption photographed on May 26, 2008 (photo by J.N. Marso, courtesy of the USGS)

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

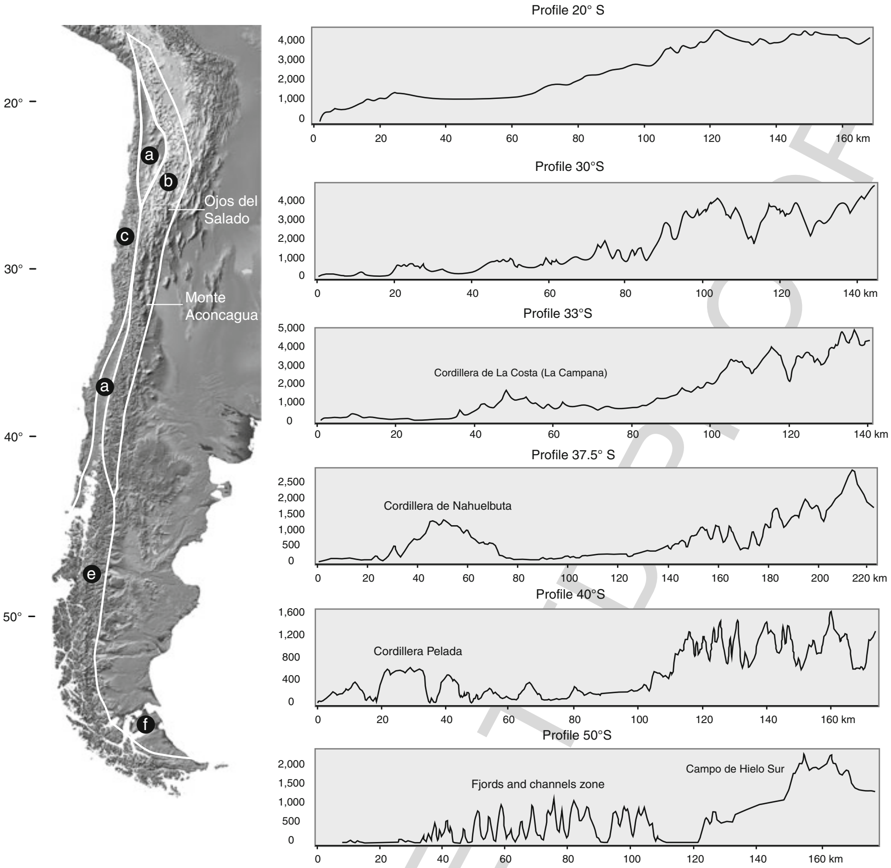

Fig. 1.6 Physiography of continental Chile, on the base of SRTM (Shuttle Radar Topography Mission) data (http://www2.jpl.nasa.gov/srtm/) (for national political limits see Fig. 1.1). Altitudinal profiles have been produced with ArcGIS 9 based on Aster GDM data (http://asterweb.jpl.nasa.gov/gdem.asp).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

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).

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. 1.8). 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).

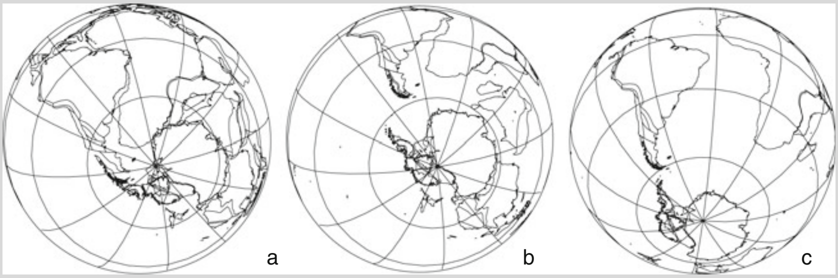

Fig. 1.7 Positions of Patagonia: **a** in the Late Carboniferous (300 mya) aggregated to the Antarctic Peninsula; **b** in the Early Cretaceous (120 mya), separated from Antarctica; **c** in the Eocene (50 mya), again close to the Antarctic Peninsula. Modeled with TimeTrek v 4.2.5, Cambridge Paleomap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

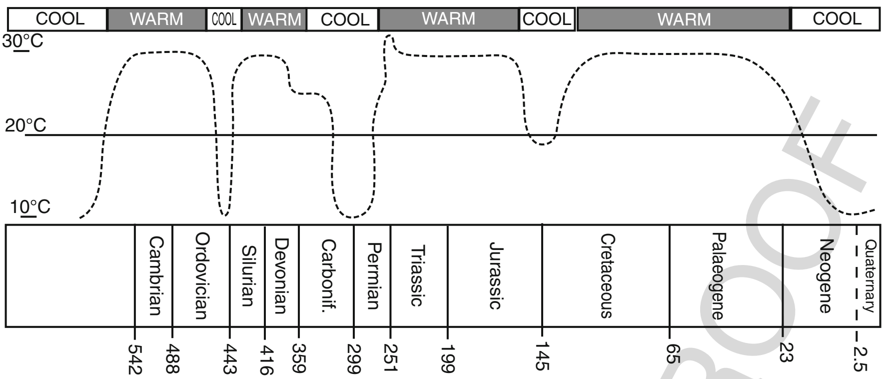

Fig. 1.8 Global climate change since the Cambrian onwards. Adapted from Frakes et al. (1992) and Scotese et al. (1999). Dates have been updated with the 2004 Geologic Time Scale (Gradstein et al. 2004)

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). AQ1 “During the 500 million years that Gondwana and its fragments existed, the ‘Earth’ 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).

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).

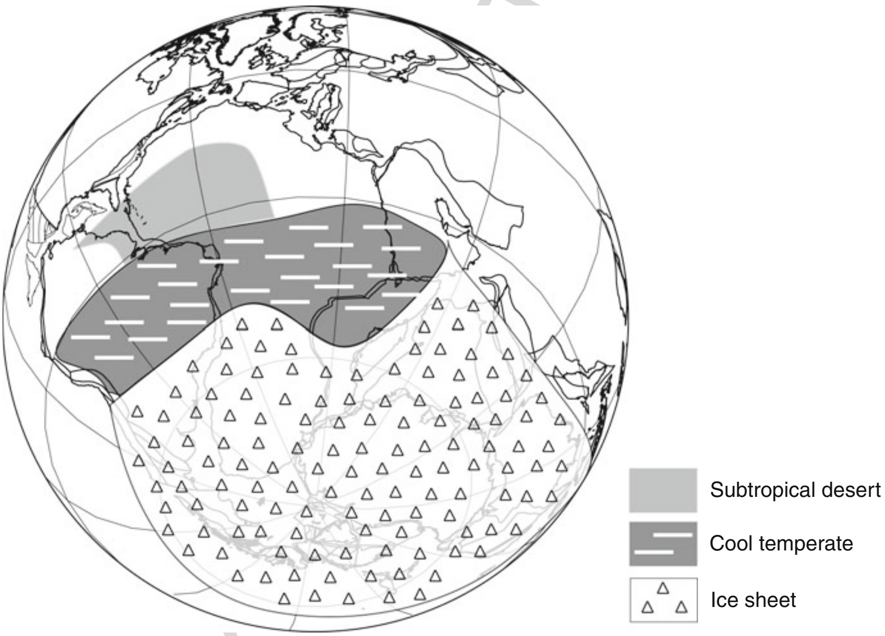

Fig. 1.9 Late Carboniferous biomes (adapted from Willis and McElwain (2002) on a TimeTrek 4.2.5 model, Cambridge Paleomap Services)

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 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).

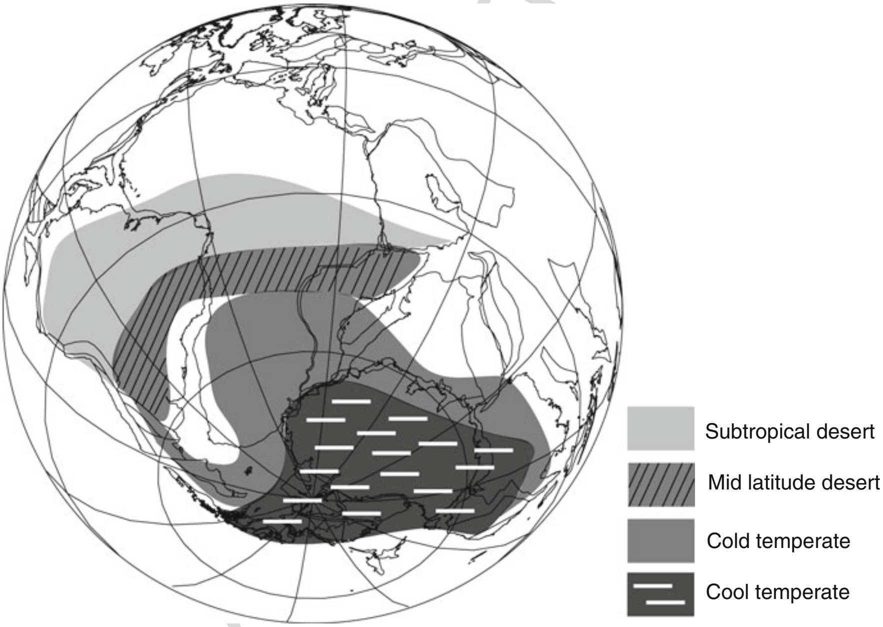

Fig. 1.10 Middle Permian biomes (adapted from Willis and McElwain (2002) on a TimeTrek 4.2.5 model, Cambridge Paleomap Services)

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, bennetittes, 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 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)

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 (Smith et al. 1994), or as late as the Palaeocene (Hay et al. 1999) or Eocene (Brundin 1988)" (Orme 2007, p 10) (see Box 9.1). The TimeTrek model shows indeed a much earlier separation of South America and Antarctica at around 130 mya (Early Cretaceous) (Fig. 1.8).

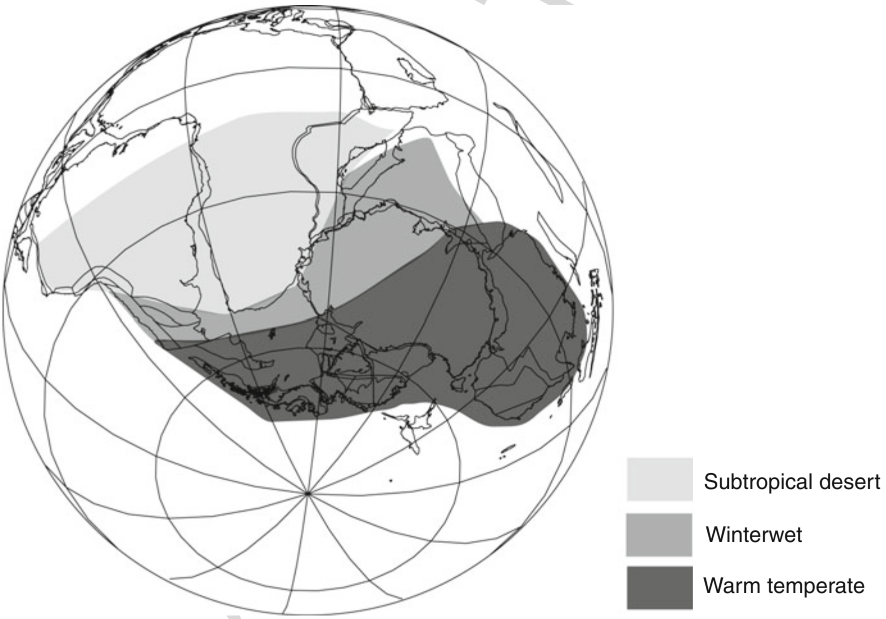

Fig. 1.11 Early Jurassic biomes (adapted from Willis and McElwain (2002) on a TimeTrek 4.2.5 model, Cambridge Paleomap Services)

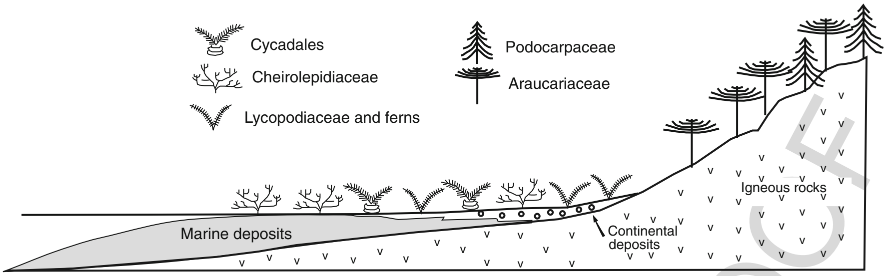

Fig. 1.12 Palaeoenvironmental reconstruction of middle Jurassic flora from Neuquén, Argentina (adapted from Quattrocchio et al. 2007)

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 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. It is but possible that transient small ice-caps 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), 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

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)	

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).

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)

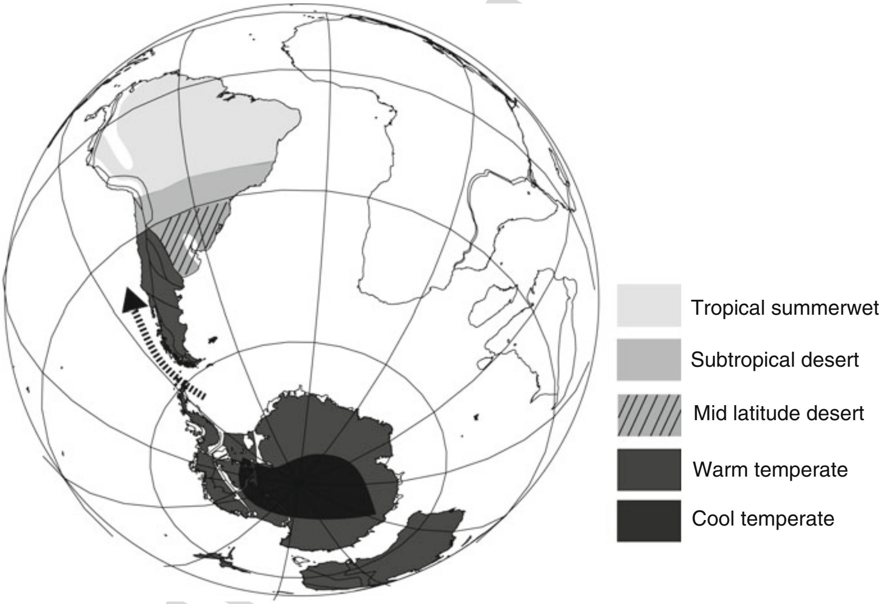

Fig. 1.14 Late Cretaceous biomes; *arrow* shows northernmost expansion of *Nothofagus* (see text) (adapted from Willis and McElwain (2002) on a TimeTrek 4.2.5 model, Cambridge Paleomap Services)

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).

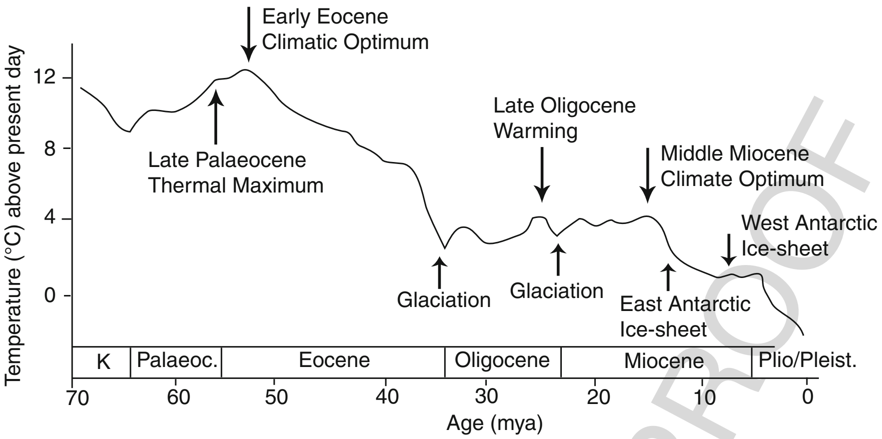

Fig. 1.15 Global climatic fluctuations during the Cenozoic, based on global deep-sea oxygen and carbon isotope records (adapted from Zachos et al. 2001)

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* 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 (col. sect.)). 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 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

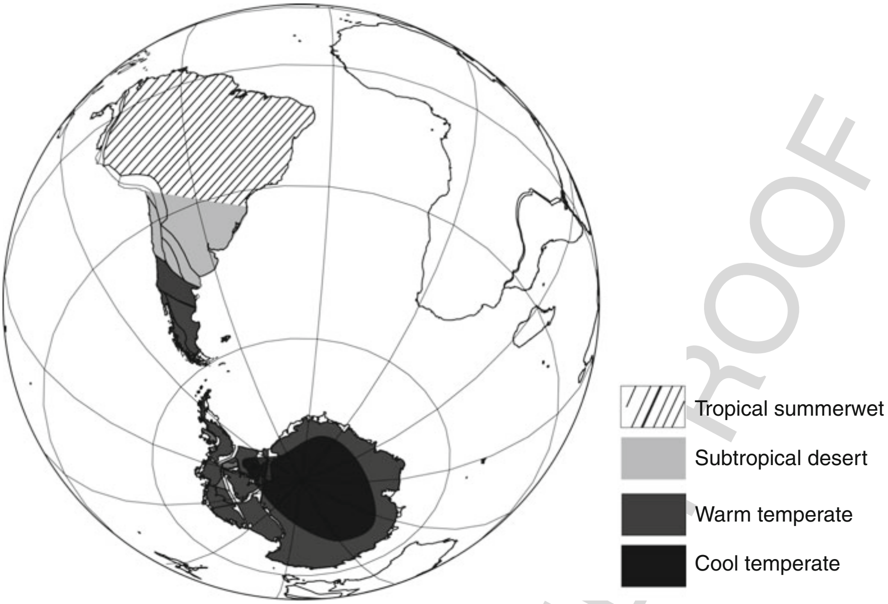

Fig. 1.16 Early Eocene biomes (adapted from Willis and McElwain (2002) on a TimeTrek 4.2.5 model, Cambridge Paleomap Services)

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 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

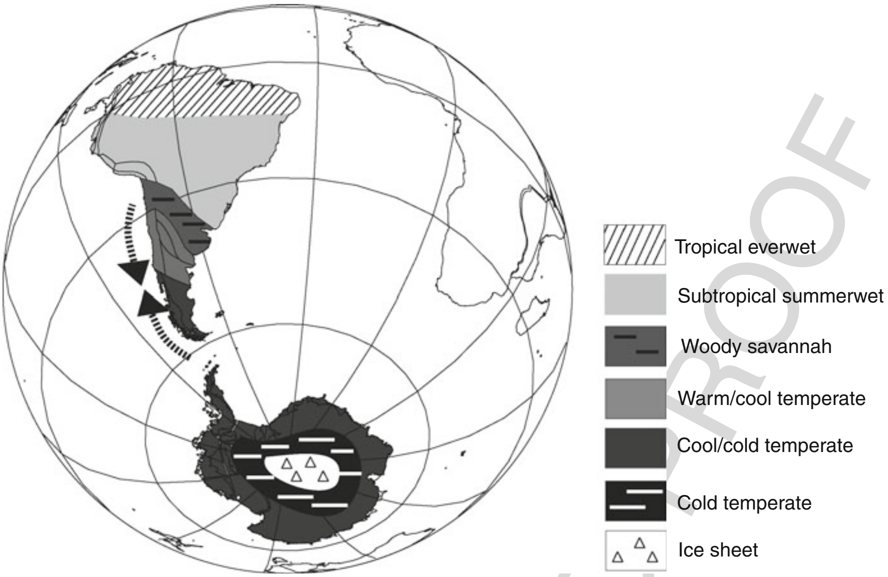

Fig. 1.17 Early Oligocene biomes; arrows show mixture of tropical and austral floras (adapted from Willis and McElwain (2002) on a TimeTrek 4.2.5 model, Cambridge Paleomap Services)

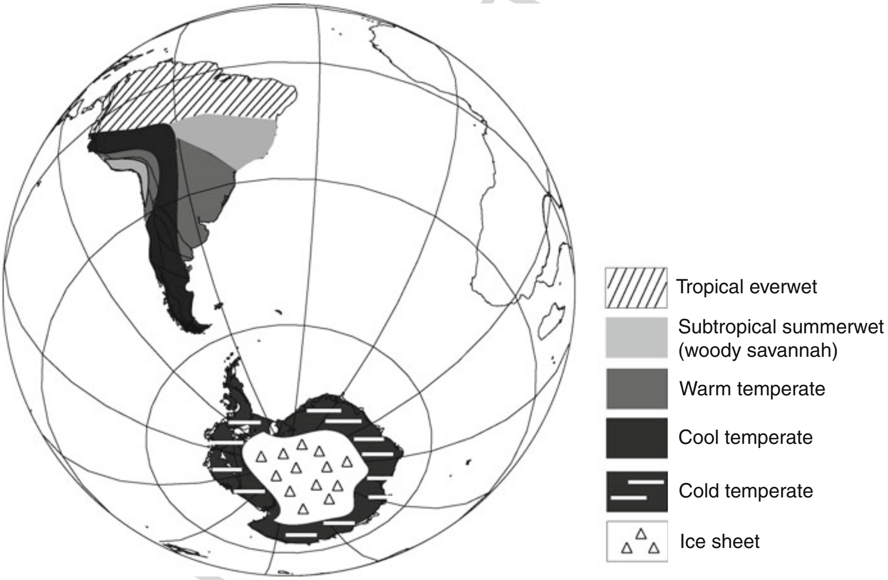

Fig. 1.18 Miocene biomes (adapted from Willis and McElwain (2002) on a TimeTrek 4.2.5 model, Cambridge Paleomap Services)

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 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) 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*,

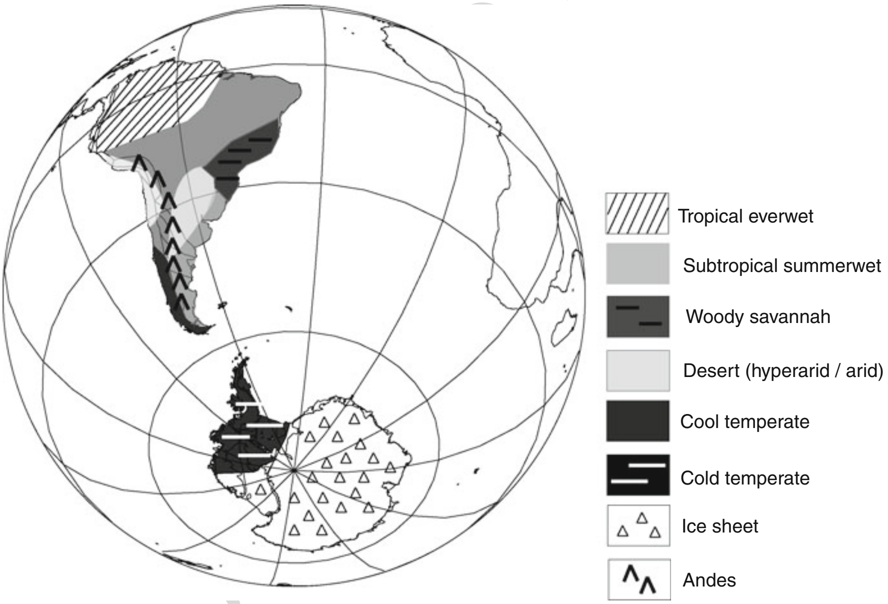

Fig. 1.19 Pliocene biomes (adapted from Dowsett et al. (1999) and Haywood et al. (2002), on a TimeTrek 4.2.5 model, Cambridge Paleomap Services)

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.

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 treelines to lower in altitude (Villagrán et al. 1998; Heusser 2003). Vegetation close 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. 9.7). 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

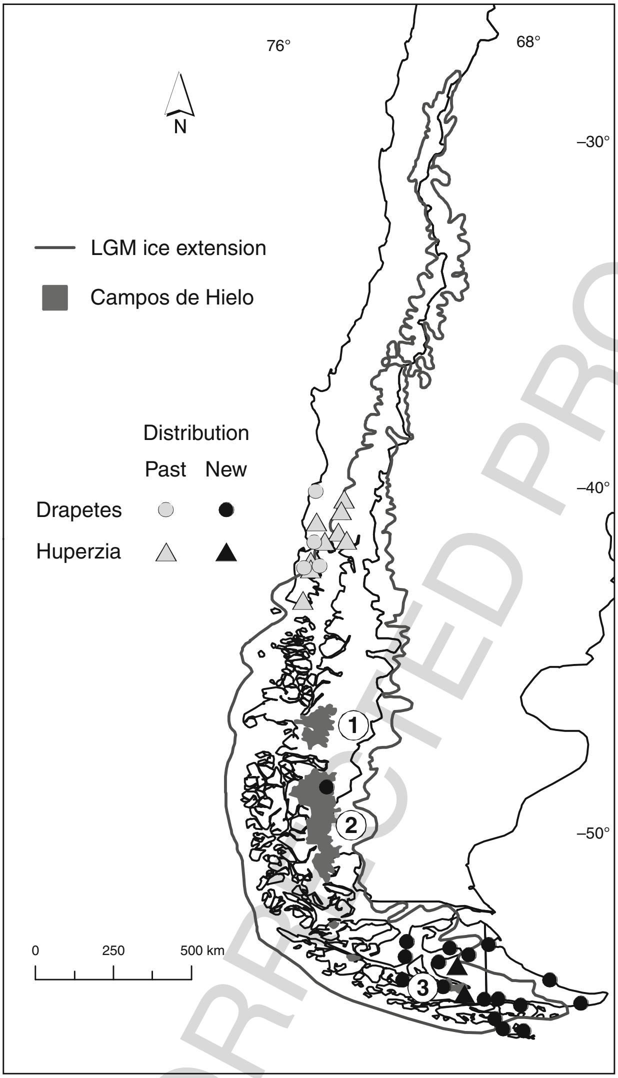

Fig. 1.20 Maximal extension of the last cycle of the Llanquihue glaciation (after Denton et al. 1999; Heusser 2003). Remnants of the Pleistocene glaciations: (1) Campo de Hielo Patagónico Norte, (2) Campo de Hielo Patagónico Sur, (3) Cordillera de Darwin. Also shown is the past and current distribution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

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 (see maps in Sect. 2.2). 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 ice-caps 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). 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

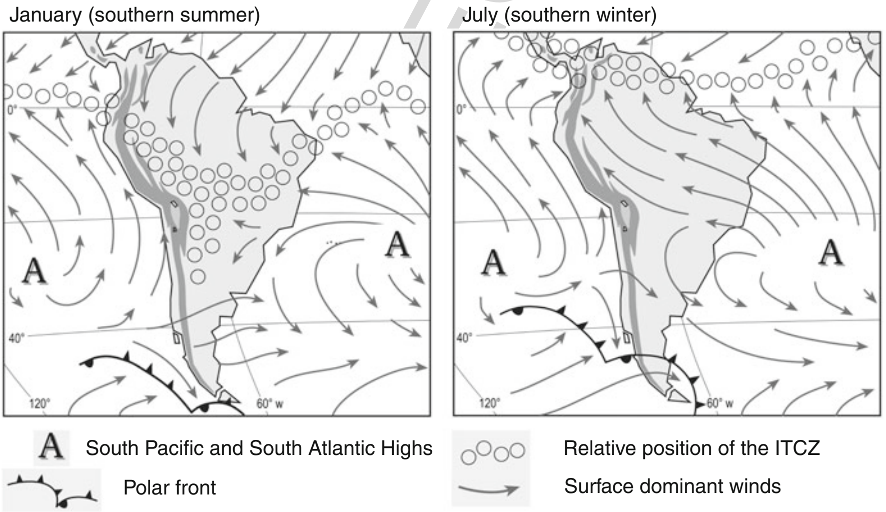

Fig. 1.21 Atmospheric circulation over South America. Note the yearly N–S displacement of the Intertropical Convergence Zone (ITCZ) (adapted from Emck et al. 2006)

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.

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, 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.

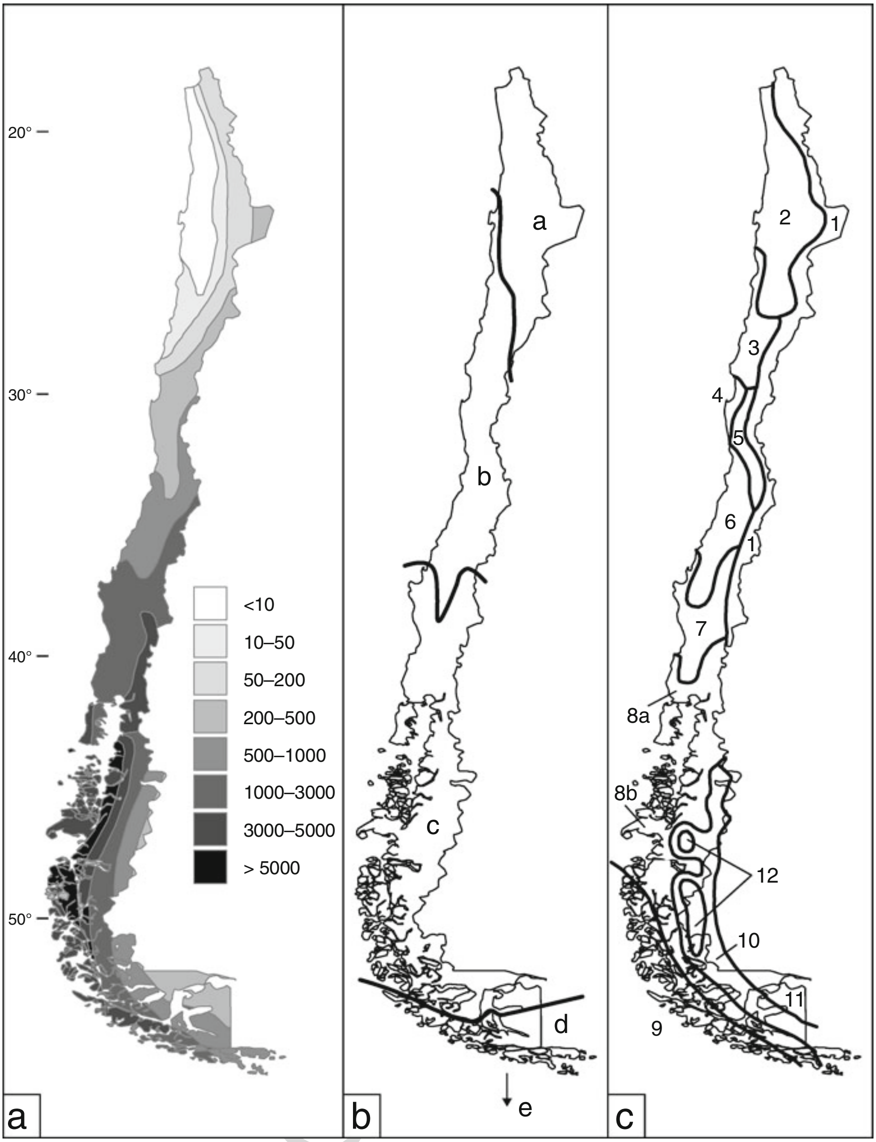

Fig. 1.22 **a** Annual precipitation, based on Schmithüsen (1956) updated with current available data; **b** five Chilean macro-bioclimates (adapted from Luebert and Pliscoff 2006); **c** distribution of vegetation formations according Schmithüsen (1956): *1*= Andean vegetation; *2*= desert core; *3*= 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

(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.

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 (col. sect.)).

(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 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 (col. sect.)).

(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).

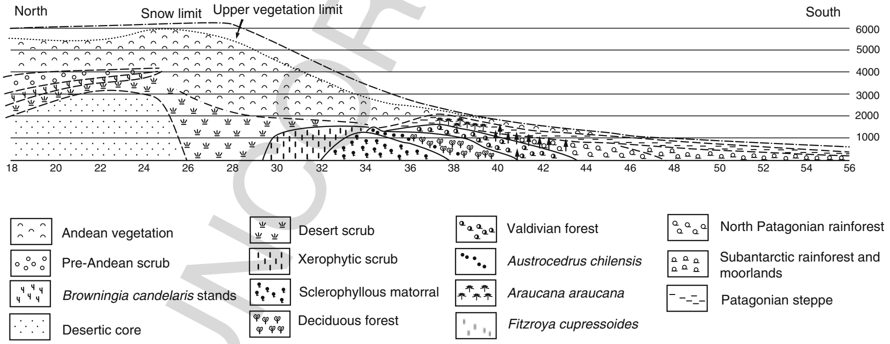

Fig. 1.23 Distribution of vegetation formations along the altitudinal profile according Schmithüsen (1956)

Fig. 1.24 Chilean vegetation: **a** high-Andean vegetation, *Azorella compacta* at Parinacota (18°30′S); **b** high-Andean vegetation, vegas de Zapaleri, limit to Bolivia at 22°50′S; **c** *Puya coerulea*, characteristic of the xeric matorral at Cerro La Campana (33°S); **d** slerophyllous 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

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. 2.20). 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 chilensisP. 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 (col. sect.)), *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 *Pilgerodendrum 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).

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Chapter 1

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