Valentí Rull

QUATERNARY ECOLOGY, EVOLUTION, AND BIOGEOGRAPHY

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Abbreviations

A	Allerød
AAO	Antarctic Oscillation
AHP	African Humid Period
AMH	Anatomically Modern Humans
AO	Arctic Oscillation
AWG	Anthropocene Working Group
B	Bølling
BCE	Before Common Era
BP	Before Present
^{14}C	Carbon 14
CE	Common Era
CLAFS	Climate-Landscape-Anthropogenic Feedbacks and Synergies
DACP	Dark Ages Cold Period
DNA	DeoxyriboNucleic Acid
D–O	Dansgaard–Oeschger events
DSDP	Deep Sea Drilling Project
EBM	Energy Balance Models
EHW	Early Holocene warming
ENSO	El Niño–Southern Oscillation
ESU	Evolutionarily Significant Unit
GDGT	Glycerol Dialkyl Glycerol Tetraether
GRIP	Greenland Ice Core Project
GSSP	Global Boundary Stratotype Section and Point
GW	Global Warming
H	Heinrich events
HTM	Holocene Thermal Maximum
ICC	International Chronostratigraphic Chart
ICS	International Commission on Stratigraphy
IPCC	Intergovernmental Panel on Climate Change
ISC	International Stratigraphic Chart
IUCN	International Union for Conservation of Nature
IUGS	International Union of Geological Sciences
ka	kilo annum (kiloyear or thousand years)
LBG	Latitudinal Biodiversity Gradients
LDG	Latitudinal Diversity Gradient
LGM	Last Glacial Maximum
LIA	Little Ice Age
LUCA	Last Universal Common Ancestor
Ma	Million years before present
MCA	Medieval Climate Anomaly

MIS	Marine Isotopic Stages
MWP	Medieval Warm Period
NAO	North Atlantic Oscillation
OD	Older Dryas
ONI	Oceanic Niño Index
OtD	Oldest Dryas
PDO	Pacific Decadal Oscillation
PNV	Potential Natural Vegetation
RWP	Roman Warm Period
SMOW	Standard Mean Ocean Water
UNESCO	United Nations Educational, Scientific and Cultural Organization
SST	Sea Surface temperature
T	Termination
YD	Younger Dryas

Introduction

Aims and scope

Understanding the current world and anticipating its possible future requires knowledge of the drivers, processes, and mechanisms that have generated it. This idea results not only from scientific research but also from common sense. Whether or not we are aware of it, any explanation or reasonable prediction requires a cultural background, which is framed by our past experiences. The world as we know it has been shaped by the interaction of the components of the Earth System—the lithosphere, hydrosphere, atmosphere, biosphere, and cryosphere—during the last 2.58 million years, the geological period known as the Quaternary (Head and Gibbard, 2015). The elements necessary to build our world were already present before the Quaternary, but the processes that occurred during this period radically changed the biosphere of our planet and resulted in its current structural and functional traits. The main distinctive features of the Quaternary with respect to former geological periods are the existence of recurrent global glacial–interglacial cycles and the evolution of the genus *Homo*, two factors whose impact on the biosphere has been decisive (Ehlers and Gibbard, 2007; Goudie, 2016). Compared to the almost 4000 million years of life on Earth (Tashiro et al., 2017), the Quaternary period may seem insignificant. However, our biosphere would be completely different without the Quaternary climate changes and the inception of our species in the ecological and evolutionary scenario. Geologically, the Quaternary period is divided into two epochs: the Pleistocene, the epoch of glaciations par excellence, and the Holocene, which began 11,700 years ago with the melting of glaciers from the last glaciation (Head and Gibbard, 2015). The Holocene is the current interglacial phase, but it differs from other interglacials by its increasing human influence, which is why it has been defined as a different geological epoch after the Pleistocene (Walker et al., 2009; Roberts, 2014). However, geological, climatic, and anthropological aspects are not among the main focuses of this book, which is about ecology, evolution, and their biogeographical imprint. The main interest here is how environmental agents, especially climate changes and human activities, have shaped the biosphere and modified the physical and functional relationships among the components of the Earth System, leading to the current situation. The book is mostly focused on terrestrial and freshwater environments, a bias introduced by the background of the author. For the same reason, detailed paleoclimatic and archeological studies are beyond the scope of this book. Climate, humans, and human evolution are included but mainly as drivers of ecological and evolutionary changes.

Cyclical and directional phenomena

During the Quaternary the influences of glaciations and human evolution on the Earth System have been remarkably different. Whereas glaciations are cyclical events, which are characteristic of astronomical phenomena, human evolution is a directional and irreversible process that is inherent to biological evolution. The difference between cyclical and directional trends is fundamental and has important consequences. The great American evolutionist Stephen J. Gould noted that history in general, and evolutionary history in particular, cannot be understood without the combination of cyclical and directional phenomena (Gould, 1987). Examples of daily life are useful for understanding this reflection and introducing concepts such as predictability, irreversibility, and contingency, which will be used throughout the book. The night-and-day and seasonal cycles, which result from the rotation of the Earth and its orbit around the Sun, respectively, are the more conspicuous cyclical components of our quotidian life. These recurrent processes provide us with predictability. Day always comes after night, and spring invariably follows winter. Without this predictability, life would be very different. For example, we would be unable to reset our brain every day, know when to plant or harvest crops, or plan next summer's vacation. The main directional component is the passage of time, which inevitably accumulates without our knowledge of the future or of when and how we will die. All we know with certainty is that time passes irreversibly. This directional and irreversible component of life, which has been called the psychological arrow of time (Hawking, 1985), gives us the dose of unpredictability that we are used to and that we face with resignation. The concept of contingency, that is, the possibility of something happening or not, is intimately linked to unpredictability. For example, we can reasonably predict when we will harvest grapes. However, we cannot know if we will be healthy at that time because health depends on random (or stochastic) events occurring between now and the time of harvest. Therefore our health at the moment of harvest is a contingent circumstance.

In the case of the Quaternary, glacial cyclicity is also determined by astronomical mechanisms related to the rotation and orbit of the Earth (Berger, 1988). After each glaciation, characterized by global cold climates promoting the growth of large mantles of continental ice, a warmer interglacial phase occurs, when glaciers retreat until the next glaciation returns and the cycle starts again. Thus by knowing the recurrence period, glacial—interglacial alternation is predictable, albeit with some degree of uncertainty, in terms of both continuity and timing. Evolution, in contrast, is directional and lacks any specific plan or purpose due to the randomness and contingency that characterize its trends and developments, which makes it unpredictable (Mayr, 2004). This trend is known as the evolutionary arrow of time. For example, a hypothetical intelligent Jurassic observer would not have been able to anticipate that a meteorite impact would end the world of dinosaurs to pave the way for the world of mammals and, finally, for the ascent of our own species. In the case of human evolution, it would also be impossible to deduce the characteristics of current humans and their decisive influence on the planet from the traits and lifestyle of our primate ancestors. In addition, similar to the passage of years in our individual lives, evolution is irreversible since genetic modifications accumulate without the possibility of reversal. Otherwise, we would have to accept the possibility of regression to previous evolutionary states, which has never been observed in any lineage of any type of organism under natural conditions. The evolutionary arrow of time has been considered constructive, as it is defined by the generation of new life forms. By contrast, the thermodynamic arrow of time has been regarded as destructive, as it is based on the irreversible degradation of free energy into entropy (Halpern, 1990). It has been suggested that the evolutionary arrow of time is a stone in the shoe for and eventual physical theory of everything (Rull, 2012a), but this is beyond the scope of this book.

Ecology and paleoecology

The value of studying the Quaternary period to understand the present is not always recognized, especially in regard to ecology. In disciplines such as evolution or biogeography, time is implicit; without time, these disciplines would not make sense. Those who study the evolution of hominids and their historical migrations, for example, do not feel the need to justify their value to society because public interest is taken for granted due to general curiosity about the origin and evolution of our own species. In ecology, however, this is not the case. Many ecologists remain skeptical of the importance of understanding past ecosystems for understanding present ones, although they are nothing but a point in time or a snapshot of a process that started hundreds, thousands, or millions of years ago and that will continue into the future. The temporal framework of classical ecology is, at most, several decades, which prevents observing and understanding ecological processes of a larger temporal extent (Jackson, 2001). Recently, a number of ecologists have adopted a longer temporal perspective, which has led to the emergence of a new ecological branch known as long-term ecology (e.g., Müller et al., 2010). These studies are based on observation and measurement stations using the present as a starting point, with the aim of accumulating temporal data series such that future generations of ecologists will continue to do it until reaching a centennial or longer scope. Thus defined, long-term ecology is a bet for the future. Few ecologists look back in time for a longer temporal ecological perspective, including not only centuries but also millennia.

A number of paleoecologists, that is, those who study the ecology of the past (Birks and Birks, 1980), have dedicated time and effort to convincing colleagues studying the present—usually known simply as ecologists or neoecologists—of the importance of paleoecology for understanding current ecology and predicting the future (e.g., Davis, 1989; Delcourt and Delcourt, 1988, 1991; Bennett, 1997; Jackson, 2001; Bush, 2003; Anderson et al., 2006; Willis and Birks, 2006; Willis et al., 2010; Rull, 2012b; Dearing, 2013; Bradshaw and Sykes, 2014; Seddon et al., 2014; Jackson and Blois, 2016). Most of these paleoecologists consider ecology as a general discipline that includes the past, the present, and the future, not as separate entities, but as a temporal continuum of processes that must be taken into account to understand the state and functioning of the biosphere. However, in ecology, the divorce between the past and the present is obvious and is difficult to overcome. This book is written from the perspective of a former ecologist who became a paleoecologist to understand the present and attempts to contribute to the merging of the different temporal views of ecology toward a truly long-term general ecology (Rull, 2014). Several causes have been proposed to explain the divorce between the past and present in ecology. One cause is the psychological dissociation among past, present, and future, which is a characteristic of the human mind. Another important reason is that ecologists study living organisms, whereas paleoecologists analyze fossils, which leads to professional separation of a methodological nature. Another reason is the diversity of origins of scholars studying the past, from which geologists, biologists, chemists, climatologists, and professionals of other disciplines distinct from ecology converge. Finally, there is the so-called "paleo-power" that makes any discipline that uses the prefix "paleo" automatically of lesser interest for those who study the same discipline without this prefix (Rull, 2010).

Taken together, these differences create something called the "living syndrome" for the present and the "museum syndrome" for the past. The living syndrome is defined by life, dynamism, and completeness, which are characteristic of living beings, whereas the museum syndrome is defined by death, staticity, and fragmentation, which are typical characteristics of museum specimens. However, the exemplars from museums were not born that way; instead, they once exhibited the living syndrome. This is how paleoecologists see them and thus why they try to reconstruct the ecosystems of the past as living and fully functional systems, not merely as curiosities of what was and will not be again (Rull, 2010). With this mentality, we face this book, which does not consider past organisms as museum pieces but rather as the living beings that have made the existence of extant organisms and ecosystems possible. In other words, this book is not about fossils but about organisms and ecosystems, regardless of their temporal domain. Paleoecologists are not necessarily interested (albeit some maybe) in the fossils themselves but use them as the only evidence of past living organisms and communities. If possible, many paleoecologists would prefer to have a time machine to directly observe past ecosystems. However, in the absence of such a device, we prefer to rack our brains, trying to reconstruct such ecosystems and their dynamics over time based on their remains rather than to ignore that they existed at all. We believe that the effort is worthwhile, and we hope that this book will contribute to illustrating this point.

To synthesize all these considerations into one message, it is clear that there is no such thing as a biosphere of the past and another of the present but one single biosphere that has existed since the origin of life and whose continuity has been maintained over time by the same ecological and evolutionary principles. Therefore there is no ecology of the past and another of the present but a single general ecology embracing both. Thus paleoecology and ecology should be considered as two methodological approaches aimed at achieving the same objective, which is understanding the configuration and functioning of the biosphere (Rull, 2010). In the Quaternary, this concept is even more evident, as many extant species have endured a large part or even all of this period and those that evolved during it are not as different from the current ones as, for example, those of the Jurassic, when the dinosaurs populated the Earth. This results in better knowledge of the ecological requirements of the species with which we deal and provides an evident connection to the present.

Audience and approach

This book was written for a wide audience rather than a select group of specialized readers. Due to its content, the primary audience is obviously scientific (researchers, teachers, graduate students, and advanced undergraduate students). However, the potential audience also includes professionals from other areas and members of the general public with scientific interests, especially in relation to the origin, evolution, and future of our biosphere. Those interested in the response of organisms and ecosystems to present and future climate changes will find past analog examples that may serve as prediction models. The book is reader focused, avoids specialized jargon, and introduces more specific terms and concepts when needed. Rather than a comprehensive treatise, the book has been conceived as an introduction to the environmental and anthropogenic drivers and the ecological and evolutionary processes and mechanisms that have shaped the current world during the Quaternary period. Readers with more specialized interests in Quaternary research will find, at the end of this introduction, a list of more in-depth treatises, along with an account of the main specialized scientific journals dealing with the Quaternary. These lists are not aimed at being exhaustive, and their items have been selected according to the knowledge and preferences of the author, considering the aims and scope of this book.

This book is evidence based and provides abundant examples for the reader to evaluate material leading to ecological, evolutionary, and biogeographical inferences from the perspective of natural history, rather than experimentation or modeling (Rull, 2012c). The evidence is primary paleoecological, and the methods used to obtain it are not explained in detail. Instead, the classic literature on these methods is provided. This is a book on basic, rather than applied, science. Although it is very fashionable because it currently provides the majority of funds for scientific research, the application of Quaternary science to targets of immediate interest and, therefore, perishable matters is not treated in depth. Knowledge generation and accumulation are the most precious heritage of humanity; therefore scientific research is inherently valuable and does not need any additional or external justification (Baker, 1939). Sooner or later, all scientific knowledge is used in practical terms by society. Restricting scientific research to solving immediate problems of a sanitary, a technological, an economic or a political nature (as is currently being done) restricts the freedom and creativity of the scientist, squandering the ability of science to improve individuals, society, and the world in general (Rull, 2016). Without freedom of research, the most momentous scientific advances of recent times, such as Newton's universal law of gravitation, Darwin's biological evolution, or Einstein's relativity, would not have seen the light of day because they did not have immediate application or provide practical solutions to problems at the time of their discovery. In addition, the knowledge obtained through scientific research and its transmission across generations shapes us as individuals, fosters our freedom and free will, and makes us less susceptible to alienation and manipulation.

Book plan

The book is divided into six monographic chapters. The first chapter introduces the climatic variability of the Quaternary period and its impact on the Earth System at different levels of temporal resolution, ranging from glacial—interglacial cycles, whose frequency is tens to hundreds of thousands of years, to annual or interannual oscillations. The objective of this chapter is to provide a framework of natural environmental change suitable for understanding the biotic changes that are documented in the rest of the book. Chapter 2 analyzes biotic responses to the different types of climate change, depending on the tolerance of organisms and their ability to adapt, migrate, or modify their geographical range. This analysis is conducted at the population and species levels, with an emphasis on the biogeographical reorganizations that these species have undergone during the Quaternary. The third chapter deals with biodiversity and its changes throughout the Quaternary in relation to possible environmental drivers (tectonics, climate, topography, sea level, etc.). The objective of Chapter 3 is to test the popular and rather speculative hypothesis that glaciations result in the extinction of many species, such that the Quaternary is a period of biodiversity loss rather than diversification. Chapter 4 analyzes the dynamics of biological communities as a consequence of natural environmental changes, especially changes in climate. This chapter explains how communities change as a result of climate variability and the corresponding individual responses of species that compose them until reaching their current composition, which is most unexpected and far from definitive (if such a state even exists). The inception of our species and its consequences for the biosphere are analyzed in the fifth chapter, which emphasizes the last glacial cycle, during which humans experienced maximum growth and expanded over the whole planet, thus significantly modifying its biotic and abiotic characteristics. Human occupation has increased the complexity of organism—environment interactions by adding a new dimension, as well as the ensuing feedbacks and synergies with others. Chapter 6 discusses how the information presented in previous chapters can be used to attain informed predictions of future scenarios in the context of current and near-future climate changes. The thread of this discussion is the dilemma of whether humans will influence natural variability, thus changing the Earth System irreversibly and leading to a new geological epoch, which has been tentatively called the "Anthropocene." Finally, the epilog is a reflection on the temporal dimension of the Quaternary period as an interface between ecology and evolution, which are traditionally separated by a sharp but artificial boundary based on anthropomorphic criteria.

The chapters are organized similarly, and all of them consist of three well-differentiated parts. The first part introduces the general concepts necessary to understand everything that follows. The more educated or informed readers in each of the relevant areas may find this unnecessary, but there are two main reasons for this format. One reason is that the book should be accessible to a broad audience not necessarily versed in each of the subjects treated. We should not forget that the study of the Quaternary is intrinsically multidisciplinary. Another reason is that there are terms and concepts that may have more than one meaning, and hence, it is better to clearly specify the usage that is contemplated in this book. This is only to avoid confusion and does not mean that other possibilities are excluded. The second part of the chapters is based on specific examples of Quaternary ecological and evolutionary processes, which illustrate how the current species, communities, and biomes originated, as well as which environmental drivers were involved. In this way, the empirical nature of Quaternary research is emphasized. In addition, the readers are provided with straightforward access to factual evidence to develop their opinion on each topic and interpret the evidence according to their own criteria. Behind this is the firm conviction that scientific dissemination should rely not only on authoritative and unquestionable arguments from researchers but also on a clear exposition of how scientific knowledge is constructed, including the different points of view that may exist for each observable and measurable phenomenon. The classic works that have been paramount for the progress of Quaternary paleoecology are presented and discussed, and their respective authors are highlighted. Whenever possible, examples based on the author's own background have been included, as firsthand experience is irreplaceable and seems to be the best way to transmit what is intended. This is the only reason why self-citation is common. Each chapter ends with a summary of the main ideas that have been developed and analyzed in the form of a take-home message, rather than a repetitive summary.

References

Anderson, H.J., Bugmann, H., Dearing, J.A., Gaillard, M.-J., 2006. Linking palaeoenvironmental data and models to understand the past and to predict the future. Trends Ecol. Evol. 21, 696–704.

Baker, J.R., 1939. A counterblast to Bernalism. New Statesman Nation 18, 174–175.

Bennett, K.D., 1997. Evolution and Ecology: the Pace of Life. Cambridge University Press, Cambridge.

Berger, A., 1988. Milankovitch theory and climate. Rev. Geophys. 26, 624–657.

Birks, H.J.B., Birks, H.H., 1980. Quaternary Palaeoecology. Edward Arnold, London.

Bradshaw, R.H.W., Sykes, M.T., 2014. Ecosystem Dynamics. From the Past to the Future. Wiley-Blackwell, New York.

Bush, M.B., 2003. Ecology of a Changing Planet. Prentice Hall, Upper Saddle River.

Davis, M.B., 1989. Insights from palaeoecology on global change. Ecol. Soc. Am. Bull. 70, 222–228.

Dearing, J.A., 2013. Why Future earth needs lake sediment studies. J. Paleolimnol. 49, 537–545.

Delcourt, H.R., Delcourt, P.A., 1991. Quaternary Ecology. Chapman and Hall, London.

Delcourt, H.R., Delcourt, P.A., 1988. Quaternary landscape ecology, relevant scales in space and time. Landsc. Ecol. 2, 23–44.

Ehlers, J., Gibbard, P.L., 2007. The extent and chronology of Cenozoic global glaciation. Quat. Int. 164–165, 6–20.

Goudie, A., 2016. The Human Impact on the Natural Environment. Blackwell, Oxford.

Gould, S.J., 1987. Time's Arrow, Times Cycle. Harvard University Press, Cambridge.

Halpern, P., 1990. Time Journey: A Search for Cosmic Destiny and Meaning. McGraw-Hill, New York.

Hawking, S.W., 1985. Arrow of time in cosmology. Phys. Rev. D 32, 2489–2495.

Head, M.J., Gibbard, P., 2015. Formal subdivision of the Quaternary System/Period: past, present, and future. Quat. Int. 383, 4–35.

Jackson, S., 2001. Integrating ecological dynamics across timescales: real time, Q-time and deep time. Palaios 16, 1–2.

Jackson, S.T., Blois, J.L., 2016. Community ecology in a changing environment: perspectives from the Quaternary. Proc. Natl. Acad. Sci. U.S.A. 112, 4015–4021.

Mayr, E., 2004. What Makes Biology Unique? Cambridge University Press, Cambridge.

Müller, F., Baessler, C., Scubert, H., Klotz, S. (Eds.), 2010. Long-Term Ecological Research. Between Theory and Application. Springer, Dordrecht.

Roberts, N., 2014. The Holocene. An Environmental History. Wiley-Blackwell, Chichester.

Rull, V., 2010. Ecology and palaeoecology: two approaches, one objective. Open Ecol. J. 3, 1–5.

Rull, V., 2012a. Time, evolution and physical reductionism. EMBO Rep. 13, 181–185.

Rull, V., 2012b. Community ecology: diversity and dynamics over time. Commun. Ecol. 13, 102–116.

Rull, V., 2012c. Past natural history and ecological biodiversity modeling. Syst. Biodivers. 10, 261–265.

Rull, V., 2014. Time continuum and true long-term ecology: from theory to practice. Front. Ecol. Evol. 2, 75.

Rull, V., 2016. Free science under threat. EMBO Rep. 17, 131–135.

Seddon, A.W.R., Mackay, A.W., Baker, A.G., Birks, H.J.B., Breman, E., Buck, C.E., et al., 2014. Looking forward through the past: identification of 50 priority questions in palaeoecology. J. Ecol. 102, 156–267.

Tashiro, T., Ishida, A., Hori, M., Igisu, M., Koike, M., Méjean, P., et al., 2017. Early trace of life from 3.95 Ga sedimentary rocks in Labrador, Canada. Nature 549, 516–518.

Walker, M., Johnsen, S., Rasmussen, S.O., Popp, T., Steffensen, J.-P., Gibbard, P., et al., 2009. Formal definition and dating of the GSSP (Global Stratotype Section and Point) for the base of the Holocene using the Greenland NGRIP ice core, and selected auxiliary records. J. Quat. Sci. 24, 3–17.

Willis, K.J., Birks, H.J.B., 2006. What is natural? The need for a long-term perspective in biodiversity conservation. Science 314, 1261–1265.

Willis, K.J., Bailey, R.M., Bhagwat, S.A., Birks, H.J.B., 2010. Biodiversity baselines, thresholds and resilience: testing predictions and assumptions using palaeoecological data. Trends in Ecol. Evol. 25, 583–591.

Selected books and journals on Quaternary science

As quoted above, these lists are not exhaustive and are based on the author's own preferences, in relation to the aims and scope of the book. For this reason, books and journals specific to anthropology, archeology, and related sciences have not been included.

Books

Anderson, D.E., Goudie, A.S., Parker, A.G., 2013. Global Environments through the Quaternary. Oxford University Press, Oxford.

Bell, M., Walker, M.J.C., 2005. Late Quaternary Environmental Change. Physical and Human Perspectives. Longman, Harlow.

Bennett, K.D., 1997. Evolution and Ecology: the Pace of Life. Cambridge University Press, Cambridge.

Berglund, B.E. (Ed.), 2003. Handbook of Holocene Palaeoecology and Palaeohydrology. Blackburn, Caldwell.

Birks, H.J.B., Birks, H.H., 1980. Quaternary Palaeoecology. Edward Arnold, London.
Birks, H.J.B., Lotter, A.F., Juggins, S., Smol, J.P. (Eds.), 2012. Tracking Environmental Change Using Lake Sediments. Vol. 5: Data Handling and Numerical Techniques. Kluwer, Dordrecht.
Bradely, R.S., 2015. Paleoclimatology. Reconstructing Climates of the Quaternary. Elsevier-Academic Press, Oxford.
Cronin, T.H., 2009. Paleoclimates. Understanding Climate Change Past and Present. Columbia University Press, New York.
Dawson, A.G., 1996. Ice Age Earth. Late Quaternary Geology and Climate. Routledge, London.
Delcourt, H.R., Delcourt, P.A., 1991. Quaternary Ecology. Chapman and Hall, London.
Ehlers, J., Gibbard, P.L., Hughes, P.D. (Eds.), 2015. Quaternary Glaciations – Extent and Chronology. Elsevier, Amsterdam.
Elias, S. (Ed.), 2013. Encyclopedia of Quaternary Science. Elsevier, Amsterdam.
Flint, R.F., 1971. Glacial and Quaternary Geology. Wiley, New York.
Goudie, A., 2006. The Human Impact on the Natural Environment. Blackwell, Oxford.
Huntley, B., Birks, H.J.B., 1983. An Atlas of Past and Present Pollen Maps for Europe: 0–13,000 Years Ago. Cambridge University Press, Cambridge.
Last, W.M., Smol, J.P. (Eds.), 2001. Tracking Environmental Change Using Lake Sediments. Vol. 1: Basin Analysis, Coring, and Chronological Techniques. Kluwer, Dordrecht.
Last, W.M., Smol, J.P. (Eds.), 2001. Tracking Environmental Change Using Lake Sediments. Vol. 2: Physical and Geochemical Methods. Kluwer, Dordrecht.
Lowe, J.J., Walker, M.J.C., 2014. Reconstructing Quaternary Environments. Routledge, London.
Martin, P.S., Klein, R.G. (Eds.), 1984. Quaternary Extinctions. A Prehistoric Revolution. University of Arizona Press, Tucson.
Pielou, E.C., 1979. Biogeography. John Wiley and Sons, New York.
Roberts, N., 2014. The Holocene. An Environmental History. Wiley-Blackwell, Chichester.
Smol, J.P., Birks, H.J.B., Last, W.M. (Eds.), 2001. Tracking Environmental Change Using Lake Sediments. Vol. 3: Terrestrial, Algal, and Siliceous Indicators. Kluwer, Dordrecht.
Smol, J.P., Birks, H.J.B., Last, W.M. (Eds.), 2001. Tracking Environmental Change Using Lake Sediments. Vol. 4: Zoological Indicators. Kluwer, Dordrecht.
Walker, M., 2005. Quaternary Dating Methods. Wiley, Chichester.

Journals

Classic journals

Annual Review of Earth and Planetary Sciences (Annual Reviews)
Anthropocene (Elsevier)
Boreas (Wiley)
Climatic Change (Springer)
Earth and Planetary Science Letters (Elsevier)
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Journal of Paleolimnology (Springer)

Journal of Quaternary Science (Wiley)
Nature Climate Change (Nature)
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Nature Geoscience (Nature)
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Elementa: Science of the Anthropocene (University of California Press)
Frontiers in Earth Science (Frontiers Media)
Frontiers in Ecology and Evolution (Frontiers Media)
Open Quaternary (Ubiquity Press)
Quaternary (MDPI)

CHAPTER ONE

Climate: continuous variability and its impact on the Earth System

Contents

Earth's poles were not always covered with ice. Phases of warmer climate, when our planet was similar to a greenhouse and had no polar ice caps (greenhouse Earth), have alternated with phases of generally lower temperatures, in which—similar to today—Earth looked similar to an old fridge that has not been defrosted for a long time: the poles were overwhelmed with huge, thick masses of ice (icehouse Earth). The Cenozoic, the era in which we currently live, which started approximately 66 million years ago with the extinction of the dinosaurs, started with a greenhouse phase that lasted from its beginning until the end of the Eocene, approximately 34 million years ago (Prothero et al., 2003). This greenhouse phase was then followed by an icehouse phase, in force until the present day (Fig. 1.1). The beginning of this last phase was marked by the accumulation of ice over Antarctica (South Pole) approximately 34 million years ago (Ma). The icehouse phase became gradually more intense during the

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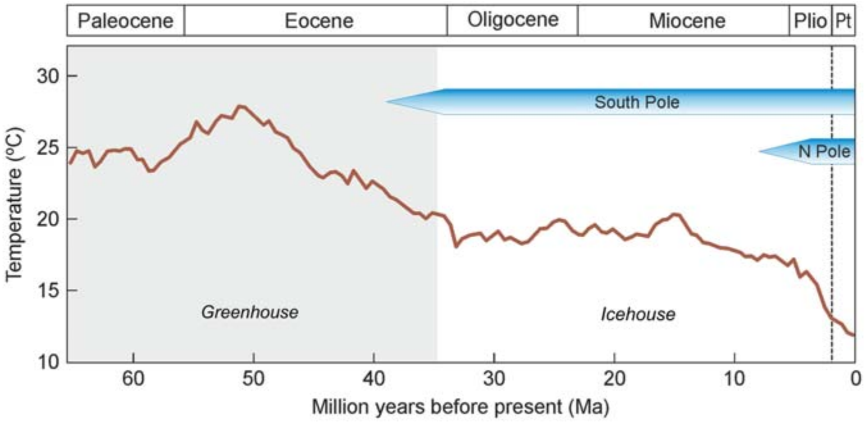

Figure 1.1 Variations in the average surface temperature on Earth during the Cenozoic. Blue bars represent phases of polar ice accumulation. *Plio*, Pliocene; *Pt*, Pleistocene. *Redrawn and modified from Hansen et al. (2013).*

Miocene–Pliocene transition (~5 Ma), when ice accumulation also started at the North Pole. This eventually resulted in the present situation, which is the coldest phase of the Cenozoic and among the coldest phases in Earth's history (Fig. 1.1). An interesting detail is that the warmest phase took place during the Eocene (~50 Ma), when global temperatures were approximately 12°C higher than they are today, which makes the slightly more than half a degree temperature increase of the last centuries appear quite modest. It is important to make a distinction between icehouse phases and glaciations, on the one hand, and greenhouse phases and interglacials, on the other. An icehouse phase may last for tens of millions of years and is marked by the continuous presence of polar ice caps. A glaciation, however, takes place over only tens of thousands of years and is defined by the expansion of polar ice masses at lower latitudes. The same difference in temporal scale exists between a greenhouse phase and an interglacial phase, but with an additional particularity: the poles are not frozen during greenhouse phases, while they are during interglacial phases (as can be witnessed in the Holocene, the interglacial in which we live). The Quaternary is part of an icehouse phase, that is, a phase in which the poles are covered with permanent ice caps, but these ice caps have recurrently expanded during glaciations and retracted during interglacials.

After establishing the general paleoclimatic context, we will analyze the nature of the climatic changes of the Quaternary in detail and at different scales of resolution. This will allow us to demonstrate the considerable variability of the climate over time, especially in the period we live in. By different scales of resolution, we refer to the different time intervals in which climatic changes take place. For example, we are all aware of the existence of daily temperature oscillations, and we also know that they become more intensive the farther we are from the equator. We are also able to perceive, and even measure, seasonal meteorological changes throughout the year, or the variations in given parameters (such as rainfall) from one year to another (i.e., interannual variation) that lead to the occurrence of wet and dry years. Older generations can even notice climatic trends that take place over a lifetime, just as we remember how winters used to be colder when we were kids. As it takes some decades to observe these trends, we call them decadal changes. Thus there are four types of climatic variations (daily, yearly, interannual, and decadal) that we can distinguish within the scale of a human lifetime or, in other words, that we can observe based on our own experience alone. Other changes of lower frequency take more than one lifetime to occur, so we need historical measurements and documentary records to discover them; these are called centennial changes. As the frequency of climatic changes decreases, we need to go farther back in time to recognize them until we reach the limit set by a lack of historical meteorological observations. At that point, paleoclimatology comes into play.

1.1 Some notions of paleoclimatology

The beginning of history is traditionally set by the appearance of written sources. Anything that happened before that is considered prehistory, and understanding it requires different types of evidence, such as archaeological finds (e.g., bones, stone or metal tools, and cave paintings). The same is true for climate change. Historical meteorological measurements—also called instrumental measurements, given that they were carried out using instruments specifically built for that purpose—allow us to observe centennial changes at most, but changes that took place over millennia (millennial changes) are beyond their reach. The scientific discipline that studies climatic changes happening before the age of instrumental measurements is called paleoclimatology and uses indirect indicators called proxies. These proxies can be discovered in so-called paleoclimatic archives, notably sediments accumulated orderly over time that make it possible to reconstruct the climatic history of a given place. By comparing these archives in the proper geographical context, we can determine if a climate change or trend is of local scale (meaning that it took place only at the studied location) or of a regional, continental, or global magnitude. The most commonly used—although not the only—paleoclimatic archives are lake and marine sediments, polar ice, and tree rings. Determining the age of these sediments by means of dating methods such as the carbon-14 (^{14}C) or radiocarbon method and others (Walker, 2005) allows us to establish the time interval covered by each archive and the ages of their different stratigraphic units and paleoclimatic events. The reader is referred to classical books on paleoclimatology such as Anderson et al. (2007), Bradley (2015), and Cronin (2009) for more detailed information.

1.1.1 Paleoclimatic proxies

Proxies are physicochemical or biological entities or parameters whose presence/absence and/or abundance are directly related to particular climatic settings or variables. Extensive accounts of the most used proxies and the paleoclimatic information they provide can be found elsewhere (Last and Smol, 2001a,b; Smol et al., 2001a,b; Amstrong and Brasier, 2005; Birks et al., 2012). Here, we will provide some examples useful for a general understanding of how paleoclimatic reconstruction works. One example of a physicochemical proxy is the titanium content in marine sediments, which is a function of precipitation (Boyle, 2001). Titanium is found in continental rocks, and its minerals are mobilized by the weathering of these rocks. The presence of titanium in marine sediments is secondary and is an indicator of terrigenous material that has been transported from the continent via the fluvial system that discharges into the sea. The titanium content increases with increasing intensity of continental erosion, which is a function of the river flow rate, which in turn depends on the overall rainfall received by the river basin in question. If the titanium supply of, for example, 6000 years ago is higher than that of 3000 years ago, we can infer that the amount of rainfall on the source continent was higher 6000 years ago than 3000 years ago. We call this approach qualitative or relative estimation since it is based on a comparison. By the calibration of the proxy, however, it would also be possible to obtain a quantitative estimate. The most commonly used calibration method involves modern analogs, which in this case would mean titanium measurements in contemporary sediments together with rainfall data for the corresponding sedimentary basins. By this method, we would obtain so-called transfer functions, which are mathematical expressions—usually linear regressions—that allow us to translate titanium values into rainfall values. For our earlier example, this kind of calibration would make it possible to infer that the rainfall 6000 years ago was, for example, 1200 mm per year, while 3000 years ago, it reached a value of only 500 mm per year. A thorough account of physicochemical proxies is provided by Last and Smol (2001b).

A typical biological proxy is the presence and/or abundance of microfossils of organisms that are especially sensitive to climatic conditions. For example, several species of so-called nonbiting flies, or chironomids, which undergo larval development in lakes, are stenothermic organisms, which means that they can tolerate only a very narrow range of ambient temperatures (Section 2.1.1). The opposite case is that of eurytherm organisms, which can live and develop under a much wider temperature range. The first group represents an excellent paleoclimatic proxy, while the second one is quite the opposite. When they die, these insects end up in sediments, and some of their parts—especially the head capsules and the mandibles—are preserved for thousands of years. Based on these features, the organisms can be identified to the species level, enabling us to determine if they were stenothermic species or not and, if so, which temperature range they preferred. The proportions of warm- and cool-climate species, if properly calibrated by modern analogs, provide us with quantitative paleotemperature reconstructions (Walker, 2001). These kinds of proxies are also known as paleothermometers. A comprehensive account of biological proxies used in paleoclimatic reconstruction of terrestrial environments can be found in Smol et al. (2001a,b). Statistical tools for calibration and other quantitative paleoclimatic inferences can be found in Birks et al. (2012). Another type of biological proxy is biomarkers, whose paleoclimatic utility is growing fast due to the recent development of molecular analytical techniques. Common paleoclimatic biomarkers are, for example, alkenones or glycerol dialkyl glycerol tetraethers that are produced by specific bacterial and phytoplankton taxa and can be used as paleothermometers. The hydrogen isotopic composition of plant leaf waxes is also commonly used to infer paleoprecipitation values. Castañeda and Schouten (2011) provide a review of the main features and paleoenvironmental usefulness of molecular biomarkers.

1.1.2 The oxygen isotopic ratio

The stable isotopic composition of selected elements—usually carbon, nitrogen, and oxygen—is widely used for paleoenvironmental reconstruction (Ito, 2001; Wolfe et al., 2001; Talbot, 2001). Here, we discuss in more depth the case of oxygen isotopic composition, one of the most typical paleoclimatological proxies, to help us understand many of the graphs that we usually see in the literature (including this chapter) and the paleoclimatic trends that they are meant to convey. Stable isotopes of oxygen are usually measured in archives such as polar ice or marine sediments but can also be recorded in coral growth rings or in limestone cave stalactites. As is well known, a water molecule is composed of two hydrogen atoms and one oxygen atom. However, these elements, as many others, have more than one type of atom, called isotopes. The isotopes are distinguished from one other based on the number of neutrons they contain within their nucleus and, as a consequence, the differences in their atomic weights. Some isotopes are radioactive and disintegrate in a couple of seconds, while others are stable and remain unchanged. In the case of oxygen, the stable isotopes are ^{16}O (8 protons and 8 neutrons), ^{17}O (8 protons and 9 neutrons), and ^{18}O (8 protons and 10 neutrons). The first one is predominant as it is contained in 99.76% of water molecules. It is followed by ^{18}O (0.20%) and, lastly, ^{17}O (0.04%). The oxygen isotopes that interest us most are the lightest and heaviest ones (^{16}O and ^{18}O, respectively) and, more precisely, the $^{18}O:^{16}O$ isotope ratio that defines the parameter known as $\delta^{18}O$:

$$\delta^{18}O = \left[\frac{^{18}O:^{16}O_{sample}}{^{18}O:^{16}O_{reference}} - 1\right] \times 1000\ ‰$$

The reference isotopic ratio is that of Standard Mean Ocean Water (SMOW), which is the well-mixed seawater found at depths of 200–500 m. Variations in $\delta^{18}O$ in marine sediments and polar ice caps allow us to reconstruct the climate of the past. But what is the mechanism behind all this?

For SMOW, $\delta^{18}O = 0‰$. Positive values of this variable indicate waters that are enriched in ^{18}O, while negative values indicate enrichment in ^{16}O. The key processes to understanding oxygen isotope dynamics in water—a process known as isotope fractionation—are evaporation and condensation. When ocean water evaporates, molecules containing the lighter oxygen isotope (^{16}O) tend to evaporate more easily; thus atmospheric water has negative $\delta^{18}O$ values. When this water travels toward the poles, it cools down and condenses to form precipitation. As the heaviest isotope (^{18}O) condenses before the others, the atmospheric water becomes increasingly depleted in this isotope. This means that the $\delta^{18}O$ values of atmospheric water become increasingly negative en route to the poles (Fig. 1.2). As a result, the precipitation that falls over the poles is highly enriched in ^{16}O, so polar ice can be regarded as a reservoir of water rich in this isotope, whereas oceanic water is enriched in ^{18}O. For this reason, paleoclimatic estimation based on oxygen isotope fractionation depends on the paleoclimatic archive we are dealing with, either polar ice or marine sediments.

In polar ice the $\delta^{18}O$ value decreases with increasing amounts of ice accumulated at the poles, which is to say that it decreases with increasing amounts of ^{16}O retained there. Therefore the most negative values are recorded during glaciations, when the polar ice caps expand toward the equator. By contrast, during interglacial phases, when the climate is warmer and there is less ice at the poles, this value is higher, although still negative, as the frozen polar waters continue to be enriched in ^{16}O. In these polar archives, the oxygen isotope composition is measured directly in air bubbles trapped in the ice. The situation is different, though, if marine sediments are used as paleoclimatic archives. In this case, during glaciation, ocean water is enriched in ^{18}O isotopes due to the increased ^{16}O proportion of the polar ice. This also means that the $\delta^{18}O$ values of seawater are positive and become increasingly larger with growing polar ice caps. During interglacial

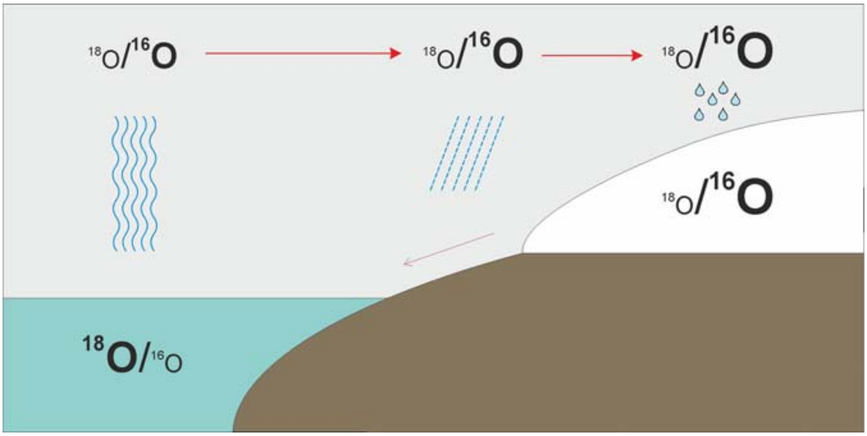

Figure 1.2 Schematic representation of oxygen isotope fractionation in water during the water cycle. Isotope enrichment is emphasized by large bold lettering.

phases the $\delta^{18}O$ values of ocean water decrease but continue to be positive since ocean water is still enriched in ^{18}O. In marine sediments, oxygen isotopes are measured in the calcium carbonate ($CaCO_3$) of fossilized shells of marine organisms (typically foraminifers). The isotope composition of these shells is identical to that of seawater of the same age since the organisms use the oxygen of the water they inhabited to build their exoskeletons. In summary, $\delta^{18}O$ is a proxy used to establish the amount of ice accumulated on the Earth's surface at any given time in history.

Calibration, that is, transformation of $\delta^{18}O$ values into paleotemperatures, is usually carried out using modern-analog training sets. However, a clear and direct relationship between these two parameters exists only under certain conditions. In areas where yearly average temperatures are lower than 15°C, paleotemperatures may be estimated using a simple transfer function (Fig. 1.3). Therefore $\delta^{18}O$ may be used directly as a paleothermometer. In other areas, especially in the tropics, $\delta^{18}O$ may be a function not only of temperature but also of rainfall. Therefore local or regional calibrations may be required to unravel the influence of either temperature or precipitation on $\delta^{18}O$ values.

1.2 Quaternary climatic variability

The paleoclimatic methods described previously make it possible to reconstruct the climatic variability that prevailed during the Quaternary at time scales with different resolutions: from glacial cycles, in general, to the climatic changes of the last millennium. Hereafter, we will briefly summarize the existing information at various levels: (1) the complete Quaternary, at a resolution of millions of years; (2) the last four glaciations, at a resolution of hundreds of thousands of years; (3) the last glaciation, at a resolution of tens of thousands of years; (4) the following deglaciation, at a resolution of thousands of years (millennial); and (5) the last two millennia, at a resolution of centuries (centennial). This will give us an idea of the continuity and complexity of climate variability that the Earth System has endured during the last ~2.6 million years. It will also serve as an introduction to the subsequent analysis of the consequences that this climate variability has had for the biosphere in general and for different organisms and ecosystems in particular.

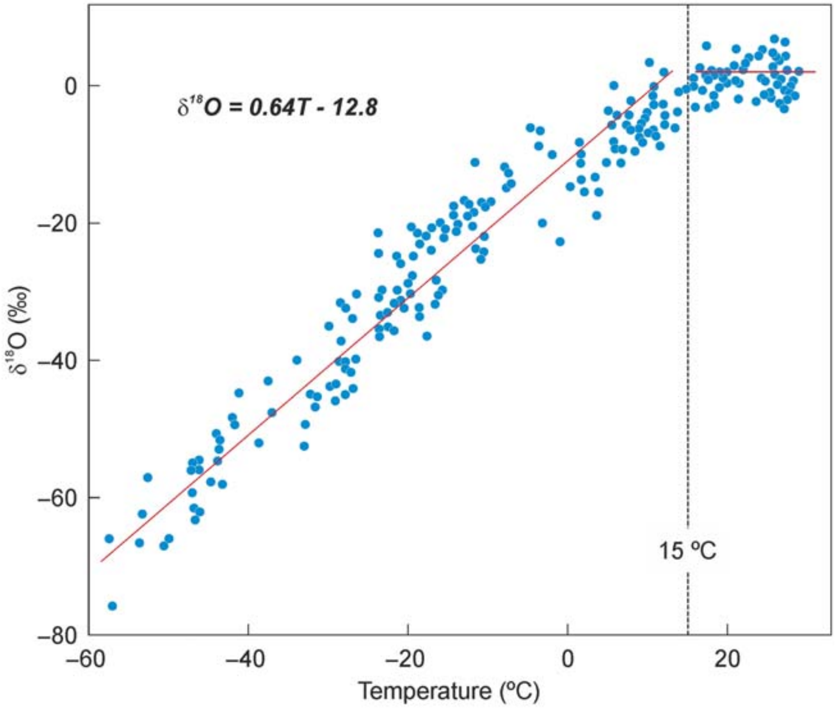

Figure 1.3 Modern relationship between the $\delta^{18}O$ of rainwater and the mean annual temperature at different points on the planet. At temperatures below 15°C the relationship is linear, and the temperature can be calculated from $\delta^{18}O$ with the aid of the transfer function shown in the upper left corner (*T*—temperature). Above 15°C the relationship becomes nonlinear because the isotopic composition is also affected by other factors, for example, precipitation. *Redrawn and modified from Jouzel et al. (1994).*

1.2.1 Glacial–interglacial cycles

Less than half a century ago, glaciologists were convinced that there had been four glaciations in the Quaternary, which in Europe, and more precisely in the Alps, which were known (in chronological order) as Günz, Mindel, Riss, and Würm. Their equivalents in North America were Nebraska, Kansas, Illinois, and Wisconsin, respectively. This view was based on geomorphological studies of landform changes caused by glacial erosion and sedimentation (Flint, 1971). The situation, however, underwent a radical change after the 1960s with the study of marine sediments obtained by deep ocean floor drilling using technologies similar to those used in oil and gas exploration. Using proxies such as oxygen isotopes in foraminifera shells and chronological correlations of paleoclimatic events worldwide, it was possible to establish the sequence of global glacial–interglacial cycles that took place since the beginning of the Quaternary. More than 100 climatic oscillations, called Marine Isotope Stages (MISs), were identified correlatively (Cohen and Gibbard, 2011). Each of them received an identification number, with even numbers used to indicate cold intervals and odd numbers, to signal warm intervals (Fig. 1.4). More than 40 of the cold MISs are considered real glaciations, which means that glacial–interglacial cycles occurred at least 40 times during the Pleistocene. These cycles had a clear periodicity of 41,000 years (41 ka) until 800,000 years before present (ka BP) and then changed to a periodicity of 100,000 years (100 ka) (Raymo, 1994). This relatively stable periodicity was due to astronomical causes.

At a small observation scale, Earth's rotation and orbital revolution around the Sun have a relatively constant period, but if we increase the observation scale to millions of years, we find that there are variations in these movements and that they are usually of a cyclical nature. These are the orbital cycles, also called Milankovitch cycles in honor of the Serbian astronomer Milutin Milanković, who described and characterized them in the 1920s. Milankovitch developed mathematical models to estimate long-term variations in solar energy reaching the Earth, depending on rotation and orbital parameters, and their influence on global climatic events such as glaciations and interglacials. Initially, this theory lacked empirical support and was criticized, but further deep-sea drilling provided the needed paleoclimatic evidence to confirm its validity (Imbrie and Imbrie, 1979). Eccentricity has the longest cycle, with a period of 100 ka. This means that the ellipse that is the Earth's orbit around the Sun changes from having a more elongated profile to having a more circular shape every 100,000 years (Fig. 1.5). It is easy to understand how this relates to our climate, if we consider that this variation has an influence on the Earth–Sun distance, which in turn directly affects the intensity of solar energy that reaches the Earth's surface and thus controls the maxima and minima of solar energy every 100 ka. The rest of the cycles are linked to Earth's rotation. The longest cycle, with a 41-ka period, belongs to axial tilt (also called obliquity), the oscillation of Earth's rotational axis. Earth's obliquity is currently 23.5 degrees, but this value oscillates between 22.2 and 24.5 degrees every 41 ka. This oscillation affects the quantity and distribution of incident solar energy and, as a consequence, the climate. Finally, Earth moves similarly to a spinning top, but much

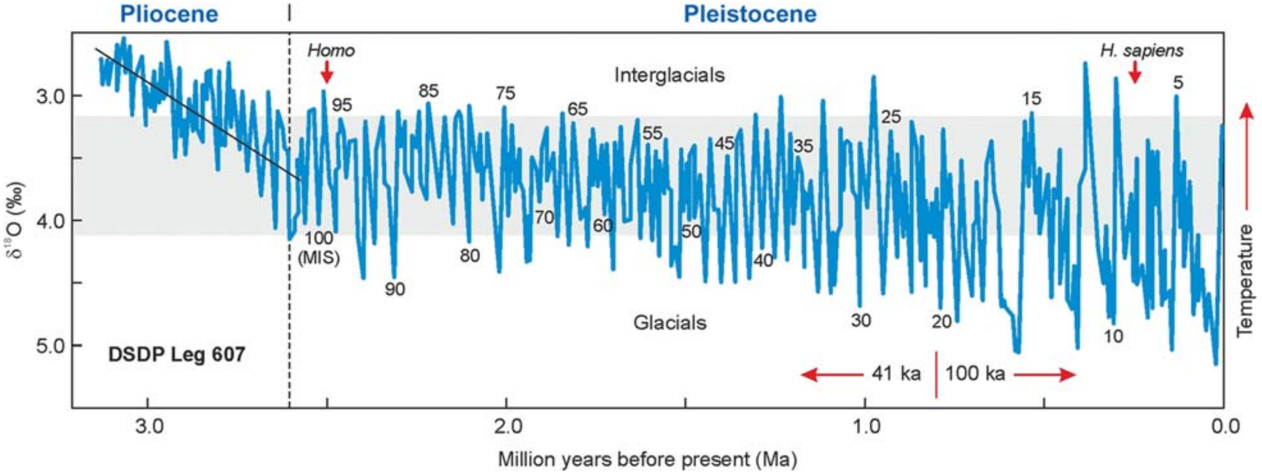

Figure 1.4 Variations in continental ice volume over the last three million years estimated from changes in oxygen isotope composition ($\delta^{18}O$) along a core taken from the Atlantic Ocean floor close to the Azores (DSDP Leg 607) (Raymo, 1994). Numbers from 1 to 100 indicate MISs (Cohen and Gibbard, 2011). MISs attaining values beyond the gray band are considered to be true glaciations/interglacials. The moment of transition in climate cycle periodicity from 41,000 years (41 ka) to 100,000 years (100 ka) and the approximate date of the appearance of the genus *Homo* and the species *Homo sapiens* are marked (see Chapter 5).

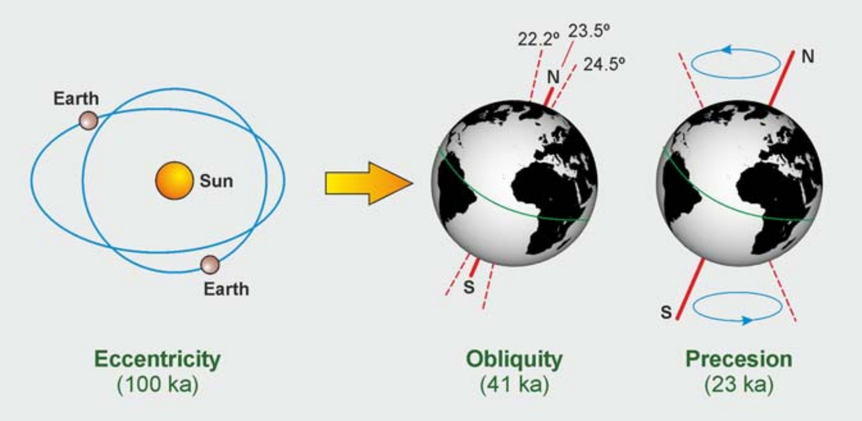

Figure 1.5 Main components of the Milankovitch cycles and their respective periodicities in kiloyears (ka) or thousands of years. The arrow shows the angle of incidence of solar energy for different values of obliquity and precession.

more slowly, as it requires 23,000 years to complete a single turn. This phenomenon is known as precession, and it also influences, in a periodical manner, the solar energy we receive. If we relate these periods with the rhythm of glacial–interglacial cycles, we discover that from the beginning of the Pleistocene glaciations until 800,000 BP, the Earth's obliquity cycle (41 ka) was the main cause of climatic cycles. Since that time, however, during the last eight glaciations, the eccentricity cycle (100 ka) has been in control. We will analyze the last four glaciations in more detail to gain a better understanding of how the glacial–interglacial cycles work.

1.2.2 The last four glaciations

At a million-year resolution, the alternation between glaciations and interglacial phases might seem homogeneous and symmetric (Fig. 1.4), but this is not the case at all, as we discover when increasing the resolution (Fig. 1.6). First of all, glaciations have been considerably longer than interglacial phases. Glacial cycles of the last 800 ka took place every 100 ka, and we find that, of these 100 ka, approximately 80 ka corresponded to glaciations, and only an average of 20 ka, to interglacial phases (Fig. 1.6). In other words, glaciations represent the more usual state, while interglacials are short phases of warmer climate that interrupt such normality (Willis and Whittaker, 2000; Bush et al., 2001). Furthermore, if we analyze the warming and cooling tendencies, we find that they are clearly asymmetric. In fact, glacial cooling phases have a long and gradual tendency interrupted by minor warming

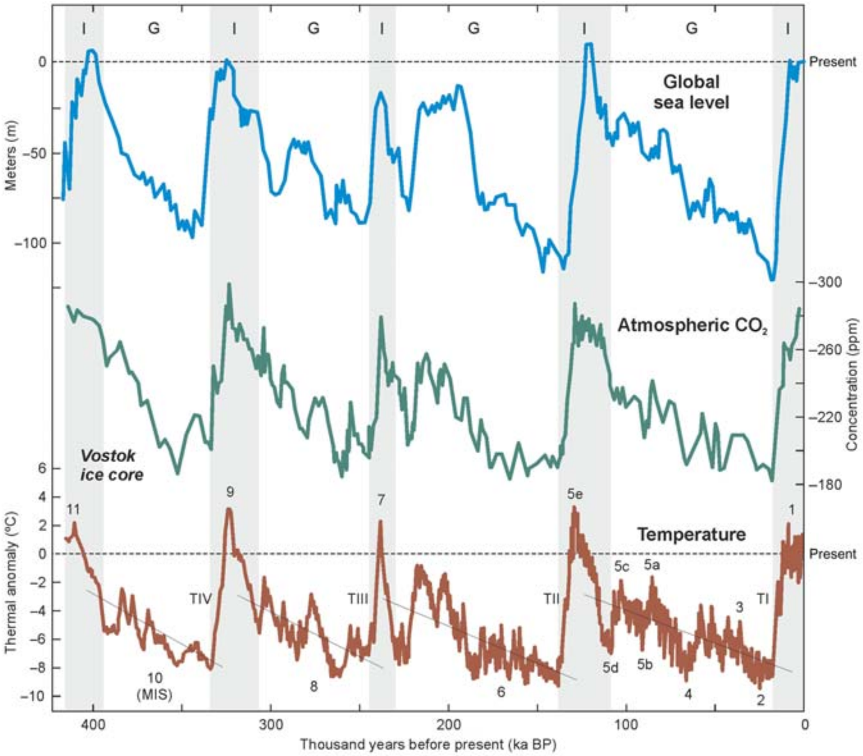

Figure 1.6 Variations in temperature, atmospheric carbon dioxide (CO_2), and global sea level during the last four glaciations. Temperature and global sea-level values are plotted as difference-from-present-day values (anomalies), while CO_2 concentrations are given in parts per million (ppm). Temperature and CO_2 concentration values were obtained from ice cores drilled at the Vostok research station in Antarctica (Petit et al., 1999). Global sea-level values were obtained from seafloor cores from different parts of the world (Hansen et al., 2013). Numbers on the temperature curve indicate MISs, and acronyms TIV to TI are Terminations (T) that mark the end of each glaciation and the beginning of each interglacial. G—glaciation (white), I—interglacial (gray).

events. In contrast, interglacial temperature increases—also known as terminations (T)—are abrupt and display only one peak, after which the temperature quickly starts to decrease again. Interglacial phases appear to have been abnormal situations that called for a rapid recovery to continue with the more "natural" glacial conditions (Rull and Vegas-Vilarrúbia, 2019). This perspective leads to two highly intriguing consequences regarding our species. First, given that the evolutionary origin of *Homo sapiens* dates to approximately 200 ka BP (Section 5.1.4), ours is fundamentally a glacial species. Therefore it seems to be in our nature to accommodate winter cold better than summer heat, which might not be a very popular idea in certain geographical areas. Second, the present interglacial climate may be viewed as an anomaly that should soon be over so that we can return to the glacial normality. Based on the calculations of Milankovitch, the next glaciation should start in one or a few thousand years. However, as will be discussed in Chapter 6, some scholars believe that human influence on the climate is so significant that the present interglacial phase could go on indefinitely due to ongoing Global Warming (GW) (Section 6.1).

Global changes that triggered glacial cycles affected the complete Earth System, not only the climate. For example, sea levels oscillated between values similar to those of today during interglacial phases and levels that were at least 100 m lower during glaciations (Fig. 1.6). Once more, we realize that glacial conditions—that is, lower sea levels—have been dominant over short interglacial events of higher sea-level peaks. The main reason for glacial sea-level fall was the water deficit in the global water cycle due to the growing continental ice mass, which resulted in a decrease in the volume of ocean water. The glacial sea-level fall had profound consequences not only for ocean dynamics but also for the continents, which were left with completely exposed shelves. Similar to what we said about temperature, the current sea level is relatively high within the Pleistocene variability, and the continental shelves are completely covered with water (Fig. 1.7).

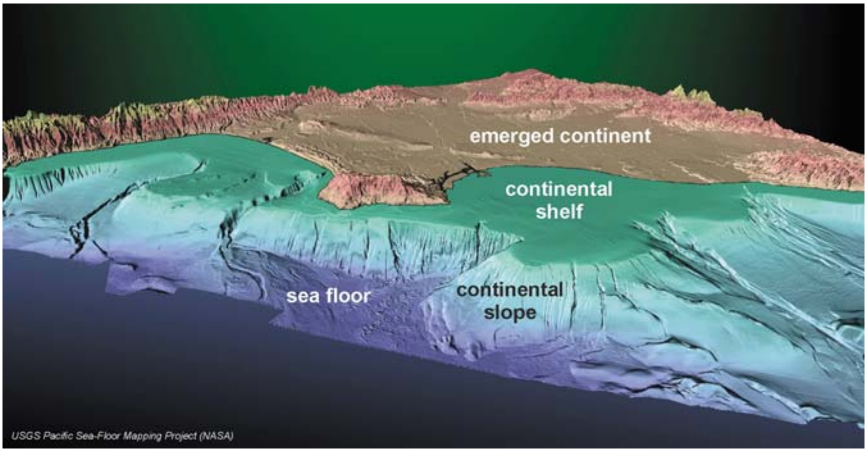

Figure 1.7 Topography and bathymetry of the continental margin off the coast of Los Angeles (CA, United States) as an example of a continental shelf (green). *Base image from the USGS Pacific Seafloor Mapping Project (NASA), publicly available at Visible Earth (visibleearth.nasa.gov).*

During past glaciations, these shelves were exposed, which significantly changed the continental configuration and the way that continents were connected to each other and to surrounding islands. This phenomenon was fundamental in biogeographical, ecological, and evolutionary relations (Chapter 2) and in human migrations (Chapter 5). Discussing the Last Glacial Maximum (LGM) in Section 1.2.4, we will see some interesting examples of the geographical consequences of sea-level fall.

The biogeochemical cycles that formed the basis of the biosphere regarded as a global functional unit were also affected. The composition of the atmosphere is a good indicator—we could even say a diagnostic indicator—of the metabolism of the biosphere, just as the composition of our blood is a diagnostic indicator of our metabolism. Since blood circulates through all of our organs and tissues and is the main agent of chemical exchange among them, it contains a series of components and metabolites that describe our general state of health. It is similar to a chemical synopsis. This is why a blood test is almost always the first thing a doctor asks for when encountering a new patient. If cholesterol values are high, the main concern is the heart; high uric acid points to the kidneys; and transaminase levels tell about the liver. Something similar goes on with the atmosphere. Here, compositional changes follow major reorganizations of gas sources and sinks that can be found in the diverse components of the Earth System and of gas emission or capture processes that take place in them. Some examples of processes that take part in the regulation of atmospheric gas composition are the primary production of vegetation and aquatic biota (as part of the biosphere), rock weathering and volcanic activity (as part of the lithosphere), gas emission and absorption in marshes and oceans (as part of the hydrosphere), and the oxidative capacity of the atmosphere itself.

Similar to oxygen isotopes (Section 1.1), the past atmospheric composition is also measured in air microbubbles trapped in polar ice that was formed at a given time. The most common indicators for these types of reconstructions are carbon dioxide (CO_2) and methane (CH_4), both of which are greenhouse gases. Fig. 1.6 shows how CO_2 underwent variations that were almost parallel to temperature variations of the same time; the case of methane is similar. This suggests that the amount of these gases is related not only to orbital cycles but also to temperature oscillations. The most widely accepted theory today is that astronomical (Milankovitch) cycles set the rhythm of the Pleistocene climate cycles but are not able to provoke sufficient variation in incident solar energy to trigger glaciations on their own. They need signal amplification mechanisms, such as changes in greenhouse gas quantities or in atmospheric and ocean currents, that are responsible for the distribution of solar energy received by the planet. We will talk more about this in Section 1.2.3. This amplification effect is known as a nonlinear response, in which the resulting climate shift (i.e., the glacial—interglacial recurrence) is not proportionate to the intensity of the regulating mechanism (i.e., astronomical cycles), as would be the case of a linear response, but rather is intensified by the action of other processes (i.e., atmospheric and oceanic changes). Another very important factor producing nonlinear responses is albedo, or the solar energy that is reflected by the Earth. When glaciers grow, the albedo increases and reduces the energy available to heat the planet. This enhances ice accumulation and creates a positive feedback that magnifies the glacial expansion that would be expected from insolation reduction due to astronomical causes only (Ellis and Palmer, 2016).

1.2.3 The last glaciation

Further examining Fig. 1.6, we note that while interglacials are distinct, well-defined events, glaciations are not homogeneous and are subject to fluctuations. Let us analyze in more detail the characteristics of glaciation events, taking the last one as an example. In addition to MISs, there are also minor oscillations every couple of thousands of years, which are also enumerated (Fig. 1.8). These minor oscillations are either events of colder climate (stadials) or events of warmer climate (interstadials). We distinguish the so-called Heinrich (H) events within the first group, named in honor of the German geologist Hartmut Heinrich, who discovered them. During Heinrich events, large numbers of icebergs break off from the ice mass covering a substantial part of North America and travel across the Atlantic (Hodell et al., 2008). Interstadials are also known as Dansgaard—Oeschger (D—O) events, honoring two paleoclimatologists, Willi Dansgaard from Denmark and Hans Oeschger from Switzerland, who were pioneers in the study of polar ice as a paleoclimatic archive. According to some authors, D—O events take place with a periodicity of approximately 1500 years or multiples of this quantity, but others disagree and believe that the recurrence of these cycles is random (Schultz, 2002; Ditlevsen et al., 2007). In paleoclimatology, these kinds of events are considered abrupt events compared to climate shifts of major duration and magnitude, such as glaciation.

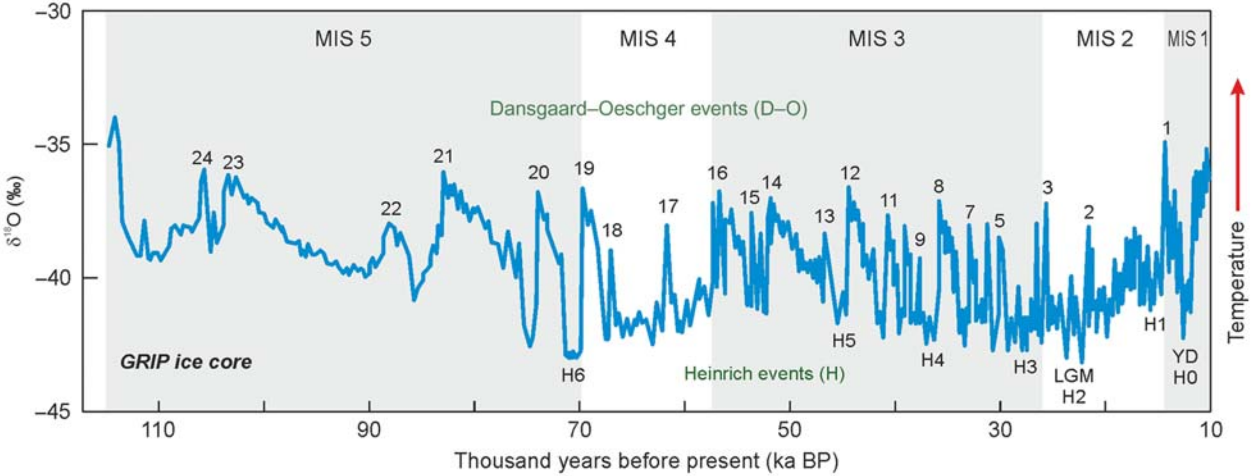

Figure 1.8 Variations in continental ice volume during the last glaciation between 110,000 and 20,000 years before present (BP) recorded in an ice core from Greenland (GRIP) (Dansgaard et al., 1993; Johnsen et al., 1997). Numbers from 1 to 24 indicate D–O events. Acronyms from H0 to H6 indicate Heinrich (H) events. *D–O*, Dansgaard–Oeschger; *LGM*, Last Glacial Maximum; *YD*, Younger Dryas.

The most generally accepted cause behind these abrupt events is related to variations in the so-called thermohaline circulation—or ocean conveyor belt—that transports and redistributes thermal energy from the tropical zones to the poles. It takes this circulation approximately 1000 years to complete one cycle (Fig. 1.9). As the name implies, thermohaline circulation is driven by both temperature and salinity differences that affect seawater density, although in an inverse manner: density decreases with increasing temperature and increases with increasing salinity. In essence, wind creates a surface current of warm ocean water, the well-known Gulf Stream, which gradually cools down on its journey from the tropical Atlantic Ocean toward the North Pole. The temperature decrease and salinity increase due to evaporation increase the density of the water mass, which ends up sinking downwards, by the time it reaches Northern Europe. Thus a cold current is formed that circulates at the bottom of various ocean basins and surfaces again in the Indian and Pacific Oceans due to a decrease in density. There, it becomes a warm surface current once again and returns to the Atlantic. The heat loss of the surface current of the thermohaline circulation has a decisive effect on the climate of the continents. For example, northern and northeastern parts of Europe

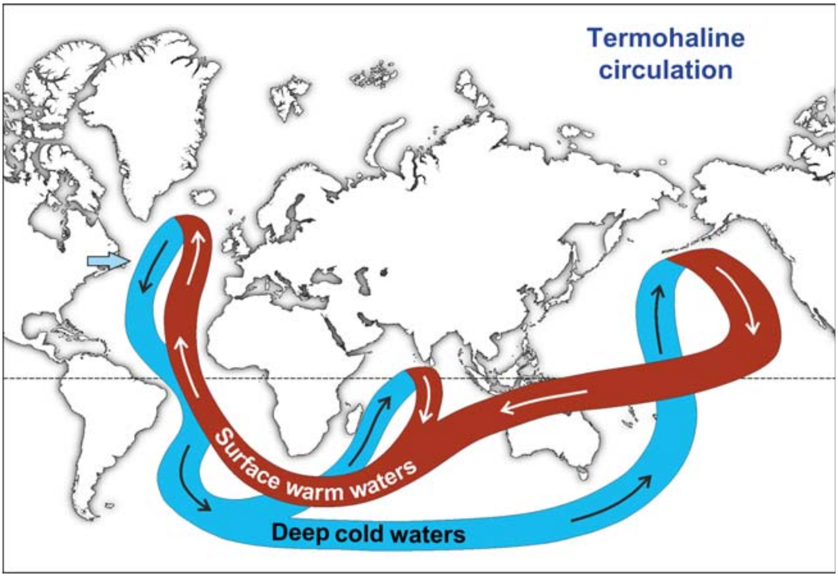

Figure 1.9 General patterns of the thermohaline circulation. The blue arrow shows the iceberg discharge pathway during the last glaciation from the North American ice sheet (Laurentide Ice Sheet) toward the Atlantic Ocean.

would be almost uninhabitable without the Gulf Stream and the heat it provides, as shown by many extremely cold (even uninhabited) North American regions situated at the same latitude as Northern Europe but not benefitting from the heating effect of the Gulf Stream current.

Despite certain controversy regarding this question, it is generally accepted that cold events or stadials—of which the Heinrich events are extreme examples—are linked to large quantities of icebergs escaping from North American glaciers into the Atlantic Ocean (the reason for which is still unknown) (Fig. 1.9). The melting of these icebergs would provide significant amounts of freshwater: enough to decrease water density. This would hinder the descent of the surface current slowing down the thermohaline circulation and, as a consequence, the distribution of equatorial heat toward the poles. Once the glacial discharge is over, the thermohaline circulation returns to its normal state, which results in warmer climates that characterize D–O events. Similar to the glacial–interglacial asymmetry (Fig. 1.6), stadial cooling is more gradual in nature than interstadial warming, with the latter reaching maximum temperatures in only a few decades (Fig. 1.8). Once again, we get the impression that the climate system "suffers" more during warming events and, once the cause for warming disappears, the system gradually relaxes toward a more stable state, waiting for the next warm event to come. From a thermodynamic point of view, warming events appear as perturbations, external energy supplies that bring the system to a more ordered but tense state (interglacial/interstadial), while when this force disappears, entropy starts to increase gradually until reaching a thermodynamically more stable maximum that does not need external energy to persist (Rull and Vegas-Vilarrúbia, 2019).

1.2.4 The Last Glacial Maximum

We will use the last glaciation as an example to obtain a better idea of how Earth appeared during glaciations. We will choose one of the coldest and most well-known stadial phases, called the LGM. The LGM corresponds to a Heinrich event (H2) within MIS 2 (Fig. 1.8). This phase took place between approximately 26 and 21 ka BP, depending on the region considered (Hughes and Gibbard, 2014). It was characterized by the maximum extension of polar ice caps and a global sea-level fall of approximately 120 m. In the Northern Hemisphere, ice covered a large portion of Europe and North America. In Europe a huge ice sheet with a thickness of several kilometers, called the Eurasian Ice Cap, covered Scandinavia and most of the British Islands, reaching today's Germany and Poland (Fig. 1.10). In North America the ice mass, known as the Laurentide Ice Sheet, completely covered Canada down to its border with the United States and was connected to the ice cap blanketing Greenland. In the most important mountain ranges, all over the world, mountain glaciers covered the highest areas and descended 1000 m or more below their current positions. In the Southern Hemisphere, ice was limited to Antarctica due to the lack of significant continental masses near the pole, but it was considerably thicker than today (Fig. 1.10). The situation in the mountains was similar to that in the Northern Hemisphere.

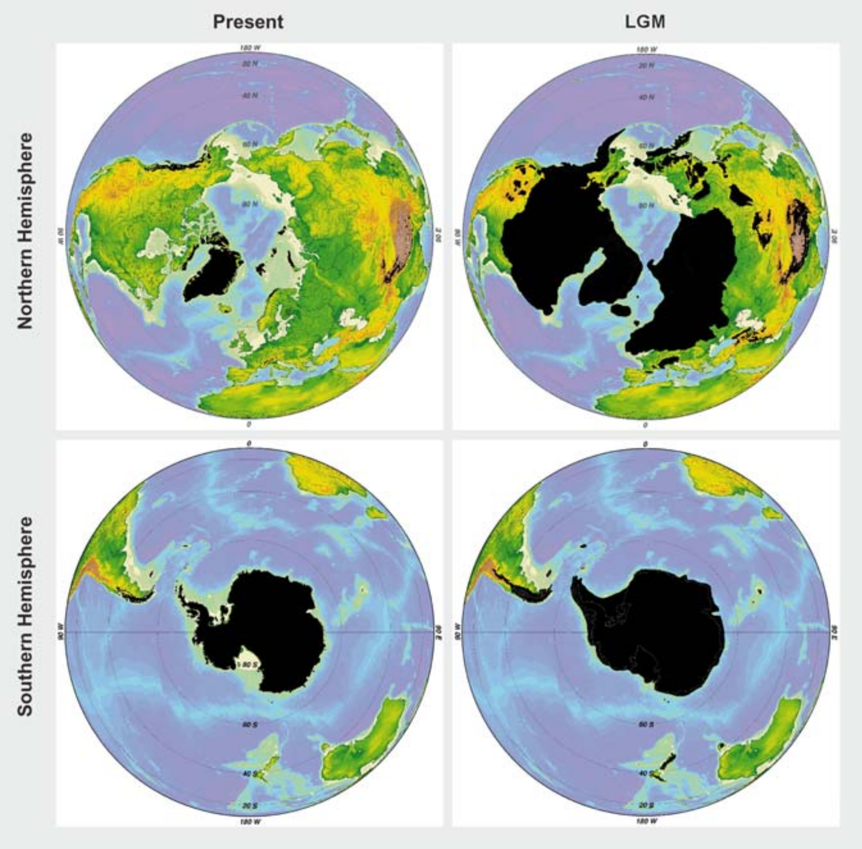

Figure 1.10 Comparison between present-day and LGM continental ice sheet dimensions (black). *LGM*, Last Glacial Maximum. *Modified and redrawn from Ehlers and Gibbard (2007).*

As mentioned earlier (Section 1.2.2), the sea-level fall left the continental shelves uncovered, causing important paleogeographical modifications. For example, several islands positioned close enough to a mainland became connected to it. This was the case for Indonesia: the Indonesian islands were connected to each other and to Asia, forming a new land called Sundaland (Fig. 1.11) that provided fresh pathways for biotic interchange and influenced both the geographical distribution and evolution of several lineages (Chapters 2 and Chapter 3). In other cases, the sea level decrease established the union of large continental masses, such as Eurasia and America. These two continents were connected through the Bering Strait, creating a land known as Beringia, a fundamental migration route that made the human settlement of the Americas possible, as will be discussed in Section 5.1.4. Something similar happened in Northern Europe, where a new land, Doggerland, bridged the British Isles and Scandinavia, playing a decisive role in human cultural evolution.

Not even the areas that were not covered by ice during the LGM could escape the consequences of climate change. In general, the climate zones and large biomes of Earth shifted toward the equator (Section 2.2.4). The general temperature drop was followed by a general decrease in precipitation, resulting in a water deficit in the hydrological cycle and a

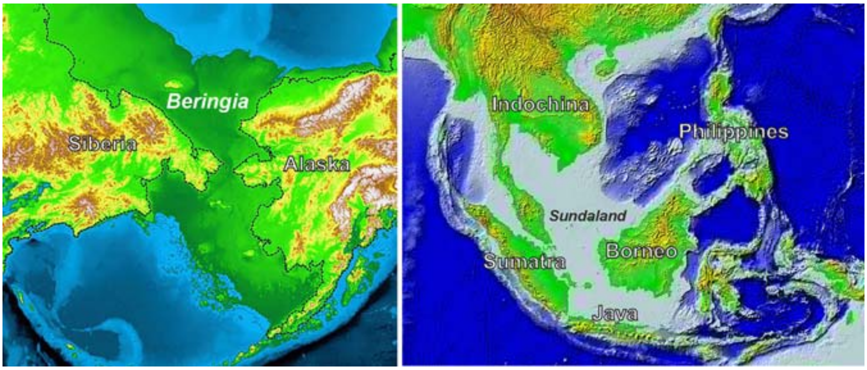

Figure 1.11 Examples of continental and island connections caused by sea-level fall and continental shelf exposure during the LGM. For Beringia (left), which was formed by a physical connection between Eurasia and America, the continental shelf is marked in green, and the present-day continental coastline is marked by a black dotted line. Sundaland (right) was created by the connection between the Indonesian islands (Borneo, Sumatra, and Java) and the Asian continent through the Indochinese Peninsula. The continental shelf is marked in gray. *(Left) Base image from W. Manley, INSTAAR, the University of Colorado (publicly available at smitsonianmag.com). (Right) Base image publicly available at fr.wikipedia.org.*

redistribution of the precipitation patterns, which eventually led to a general expansion of deserts. In tropical areas, mountains suffered the same fate as at higher latitudes: their glaciers expanded and descended. In tropical lowlands, temperatures decreased, although not to the point allowing the accumulation of ice. On the other hand, drought was intensive enough to bring forward significant changes in the distribution of biomes at low latitudes. We will discuss this in more detail in the following chapters; our sole objective here is to point out that glacial conditions had a profound effect on living conditions in every corner of the planet, not only in the glaciated areas and their surroundings.

1.2.5 The Late Glacial and the Holocene

The LGM was followed by a melting phase that led to the present state, which as already mentioned, is an interglacial phase. However, this melting process was far from monotonous or continuous; it also exhibited variations. First of all, melting did not start at the same time everywhere on the globe. For example, in the Northern Hemisphere, deglaciation (Termination I) (Fig. 1.6) started approximately 19–20 ka BP, while in Antarctica, it did not happen until 14–15 ka BP. At different points on the planet, glacial decay started at different moments but almost always within the same range (i.e., between 19–20 and 14–15 ka BP). Regardless, the first important warming pulse (interstadial) of the Late Glacial occurred slightly before 14 ka BP. This was not the definitive interstadial, however, because, after some fluctuations, a very cold climate returned (albeit not as cold as the LGM climate). This cold event, known as the Younger Dryas (YD) interstadial (Carlson, 2013), took place between approximately 13 and 11.7 ka BP (Fig. 1.12). After the YD, the final melting started to announce the end of the Pleistocene and the beginning of the Holocene 11.7 ka BP. The highest temperatures were reached during the so-called Holocene Thermal Maximum (HTM), between 9 and 6 ka BP (Kaufman et al., 2004), after which a slight decrease brought us to the current situation. The HTM was not homogeneous either, given that there was a brief cooling event approximately 8.2 ka BP. In contrast to temperature, sea-level values were more uniform, with a practically continuously increasing tendency until the HTM, when they finally stabilized at their current levels (Fig. 1.12). Some authors have proposed the occurrence of events with a similar timing as but lower intensity than the D-O glacial cycles (Section 1.2.3) during the Holocene, which have

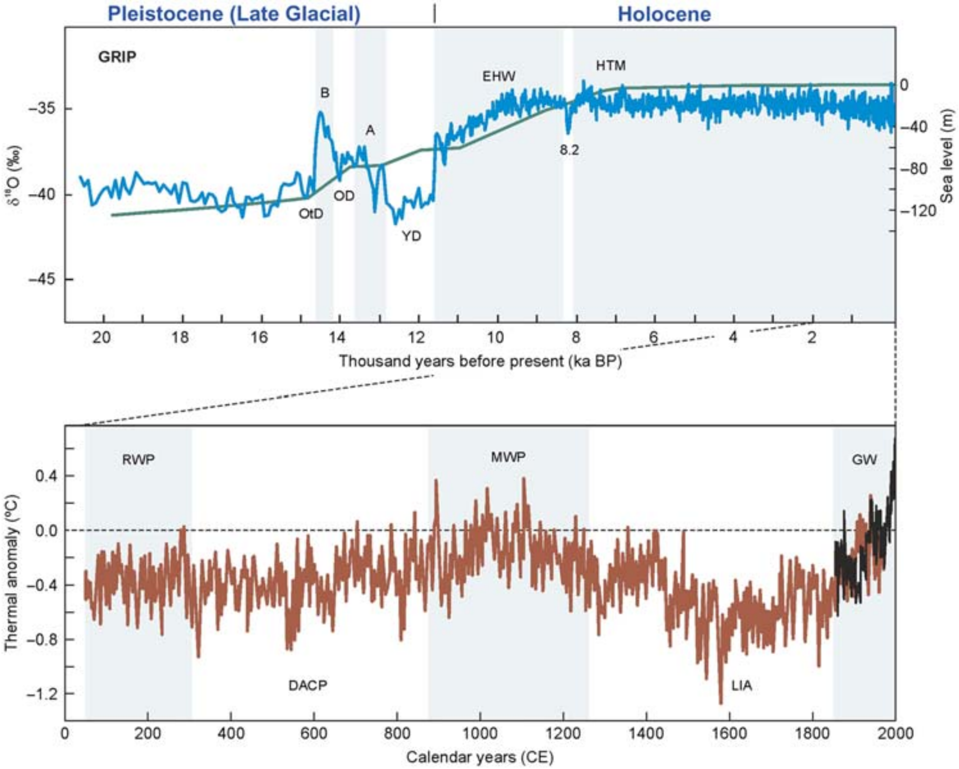

Figure 1.12 Top: variations in continental ice volume (*blue*, left scale) and sea level (*green*, right scale) from the LGM until today. The oxygen isotope curve ($\delta^{18}O$) is based on the same ice core referred to in Fig. 1.8 but with higher resolution (Grootes et al., 1993). The sea-level curve is based on Lambeck et al. (2009). Interstadials and other warm phases are highlighted by gray bands. Bottom: temperature oscillations during the last two millennia, based on tree ring data (Moberg et al., 2005). The black part of the curve covering the last centuries is based on instrumental temperature measurements. Warmer phases in gray. *A*, Allerød; *B*, Bølling; *DACP*, Dark Ages Cold Period; *EHW*, Early Holocene Warming; *GW*, Global Warming; *HTM*, Holocene Thermal Maximum; *LGM*, Last Glacial Maximum; *LIA*, Little Ice Age; *MWP*, Medieval Warm Period; *OD*, Older Dryas; *OtD*, Oldest Dryas; *RWP*, Roman Warm Period; *YD*, Younger Dryas.

been referred to as Bond cycles, named after the American paleoclimatologist Gerard Bond. These cycles would have been caused by the influence of solar cycles (Section 1.2.6) or the changes in ocean circulation (Section 1.2.3). However, both the occurrence and the assumed periodicity of the Holocene Bond cycles have been questioned (Obrochta et al., 2012).

The deglaciation process that took place from the LGM until the HTM was of fundamental importance both for the distribution of life over the planet and for the geographical expression of human culture (Chapter 5). This is quite obvious in the areas that were completely covered by ice, where glacial erosion reached the bedrock and eliminated all traces of life except for so-called nunataks, the highest parts of some mountains, which were free from ice (Section 2.2). The affected areas had to be recolonized as the ice mass was withdrawing; we could say that life had to restart from the beginning in these territories. However, the situation was not very different in the surrounding areas either, where although not covered by ice, the soil and upper sediments were either permanently frozen or undergoing intensive, seasonal freeze–thaw cycles. Such soil and upper sediments are known as permafrost (Vandenberghe et al., 2014). These conditions characterized Central Europe and a large part of the United States. Therefore today's river basins, soils, ecosystems, and human societies (including cities, communication networks, and managed lands) are completely new in these areas, having taken shape as the glaciers retreated. Even if the conditions were not equally as hostile in other regions of the planet, they were still difficult. Therefore it is safe to say that our modern world and our civilization are genuinely newly formed postglacial features, from both biological and cultural points of view.

1.2.6 The last millennia

At the advent of historical times, written documents become available that allow us to follow important events, but—at least until two centuries ago—we must still rely on paleoclimatic proxies to be able to reconstruct the climate. For paleoclimatic reconstructions of recent times, tree rings provide the most appropriate proxies as their thickness and other physicochemical properties—calibrated with the aid of modern analogs—are excellent temperature and precipitation proxies. This method makes it possible to identify different climate phases over the last two millennia, among which the Medieval Warm Period (MWP)—also known as the

Medieval Climate Anomaly (MCA)—and the Little Ice Age (LIA) must be mentioned (Mann et al., 2009) (Fig. 1.12). Both of these events had a profound effect on human societies. Another prominent feature is the GW of the last few centuries that can be recorded and studied via instrumental methods (Stocker et al., 2013). After examining the climatic variability of our planet's history, as we have done in this chapter, the GW can now be placed in a proper perspective, in terms of both duration and magnitude. Chapter 6 analyzes this phenomenon in more detail.

The causes that provoked the MWP and the LIA are still under study, but there are two processes that seem to have been primarily responsible for them: solar activity and volcanic activity (Crowley, 2000). In addition to the orbital variations discussed early as the main causes of glaciations, there exist other mechanisms that are related to the Sun and affect our climate. One of them is the solar magnetic activity cycle, or simply the solar cycle, which has an 11-year period. The most obvious evidence of this cycle is so-called sunspots that are dark areas surrounded by a bright rim (Fig. 1.13). The number of sunspots varies according to solar activity: more spots are observed in phases of more intensive activity. Sunspots have been observed and documented for more than a millennium, and generally systematic records have been compiled since the beginning of the 17th century thanks to the work of Galileo Galilei and scientists of his time (Vaquero, 2007). This is how the Maunder Minimum, a minimum in the number of sunspots named after the British astronomers Annie and Edward Maunder, was discovered. This sunspot minimum also indicates a minimum in solar activity (and therefore, in the radiation that reaches Earth) between 1645 and 1715 (Fig. 1.13), which coincides with the cold phase of the LIA (Figs. 1.12 and 1.13). On the other hand, variations in atmospheric ^{14}C concentrations, used as proxies for solar activity, revealed a maximum in this parameter, the so-called Medieval Solar Maximum, which occurred at the same time as the MWP (Jirikowic and Damon, 1994).

Volcanic eruptions release large quantities of ash and sulfuric acid into the atmosphere, which quickly become dispersed (Fig. 1.14) and attenuate incident solar energy, thereby inducing a temperature decrease in the affected areas (Sigurdsson, 1990). A single volcanic eruption may have consequences of different magnitudes for the regional climate during a short period of time (usually a few years), but a general, ongoing phase of intensive volcanic activity might affect the global climate, bringing about lower temperatures for decades or centuries. Intensified general volcanic activity was documented between the 13th century and the beginning of

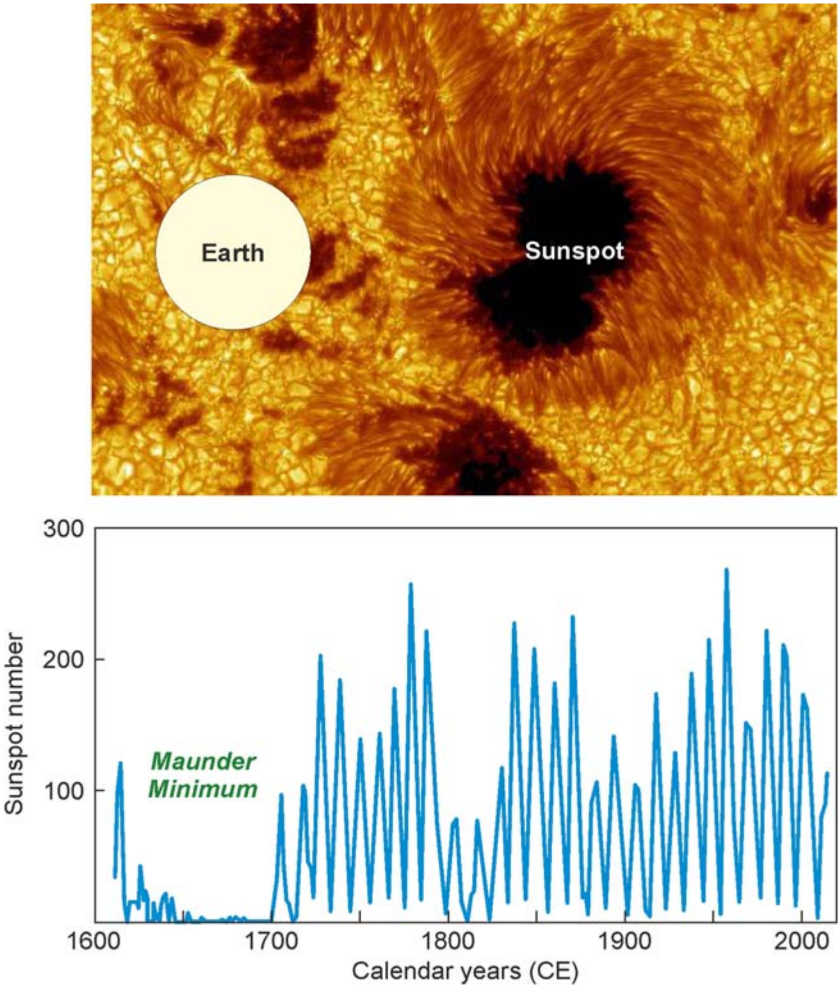

Figure 1.13 An example of a sunspot and its relative size compared to Earth (top). Variations in sunspot number are based on direct observations recorded since the beginning of the 17th century (bottom). The historical minimum level, the so-called Maunder Minimum, which took place during the maximum of the Little Ice Age, is highlighted. *Base images publicly available at solarscience.msfic.nasa.gov.*

the 19th century, which might have been related to the LIA (Miller et al., 2012). By contrast, the MWP coincided with an interval of significantly lower volcanic activity. As usual for other climatic events and trends, more than one factor might have played a role in the climate change of the last millennia, and both the solar cycles and the variations in volcanic activity might be to blame. Another contributing factor, namely, temporary changes

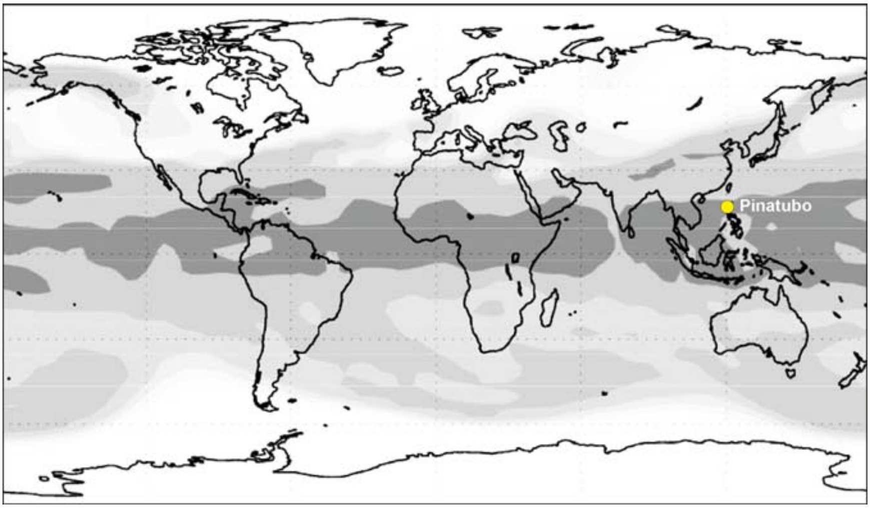

Figure 1.14 Volcanic ash dispersal from the Mount Pinatubo volcano (*yellow dot*), Philippines, after its eruption in June 1991. The map shows how the ashes spread all around the planet (at an altitude of 24 km) by October of the same year, only 4 months after the eruption. *Modified from Textor et al. (2005).*

in thermohaline circulation, has also been suggested by some to have played a role by amplifying the effect of the Sun and volcanoes.

1.2.7 Interannual moisture variations

Until this point, temperature has been the key focus of our discussion, as it is a climatic parameter whose variations are global in nature. Virtually all the variations that we have discussed—with a few exceptions—occurred over the whole planet, even if with variable intensity. Another climatic parameter that exhibits intensive variations is the water balance (also called the hydrological balance or moisture balance), or precipitation−evaporation (P/E) ratio. This parameter makes it possible to classify climates into a wide range of types from perhumid, with the maximum P/E ratio, to hyperarid, where precipitation is minimal and the potential evaporation (which can occur only if there is sufficient water available) is maximal. Climatic extremes can be found in some areas of the Himalayas, which can receive an average of 12,000 mm (12,000 L/m^2) of rainfall per year, and in the Atacama Desert, in Chile, with an average of 10−40 mm per year but where it is quite possible for decades or even centuries to go by without a single drop of water. Hence, the water balance is a rather regional phenomenon that depends on particular climatic mechanisms of the area under study. The total amount of water in the hydrologic cycle, which as discussed previously, is lower in glacial than in interglacial phases, is a quite different issue from how this water is distributed over the planet. The latter depends on atmospheric and oceanic circulation patterns that can be very heterogeneous regionally. This, however, does not decrease the fundamental importance of this parameter for life on the planet, as will be discussed in later chapters.

Paleoclimatic archives provide evidence that a number of regional climate systems affected the climate in the past. One of the most popular among these is the so-called El Niño/Southern Oscillation (ENSO), which controls the rainfall regime of the equatorial Pacific (Trenberth, 2019). It is an interannual cyclical phenomenon that oscillates between two extremes: "El Niño" and "La Niña," with a 2- to 7-year (on average, 4-year) frequency. Under normal conditions the trade winds that blow from the east toward the west in the zone of the equator create a surface sea current that provides sufficient humidity to maintain the high rainfall level in the convection zone (characterized by low pressure and the formation of cumulus clouds saturated with water vapor) situated over Indonesia and neighboring areas (Australia, New Guinea, and Southeast Asia). At the same time the coasts of South America, eastwards, have a much drier climate. The El Niño state evolves when a rise in the Sea Surface Temperature (SST) and the deceleration of the trade winds invert the direction of the equatorial current so that the convection area (which is the area of highest rainfall) is shifted to the central—oriental Pacific, while the western sector becomes drier (Fig. 1.15). Under these conditions the climate of the Pacific coast of South America is warmer and more humid, with frequent heavy rains. In La Niña state the trade winds are intensified, and the SST falls below average values. This increases the east—west precipitation gradient to above average, causing heavy rains in the western sector and intensive drought and a cooler climate in South America. Despite being a regional phenomenon, the ENSO has an indirect effect on the climate of several other parts of the globe, including Africa and North America, although its influence is not as evident over the Eurosiberian region. Therefore its influence is considered quasiglobal. ENSO cycles can be expressed by calculating index numbers. For example, the Oceanic Niño Index (ONI) is based on SST changes in the central region of the equatorial Pacific. Above-average values indicate El Niño conditions, while negative values signal La Niña conditions (Fig. 1.15).

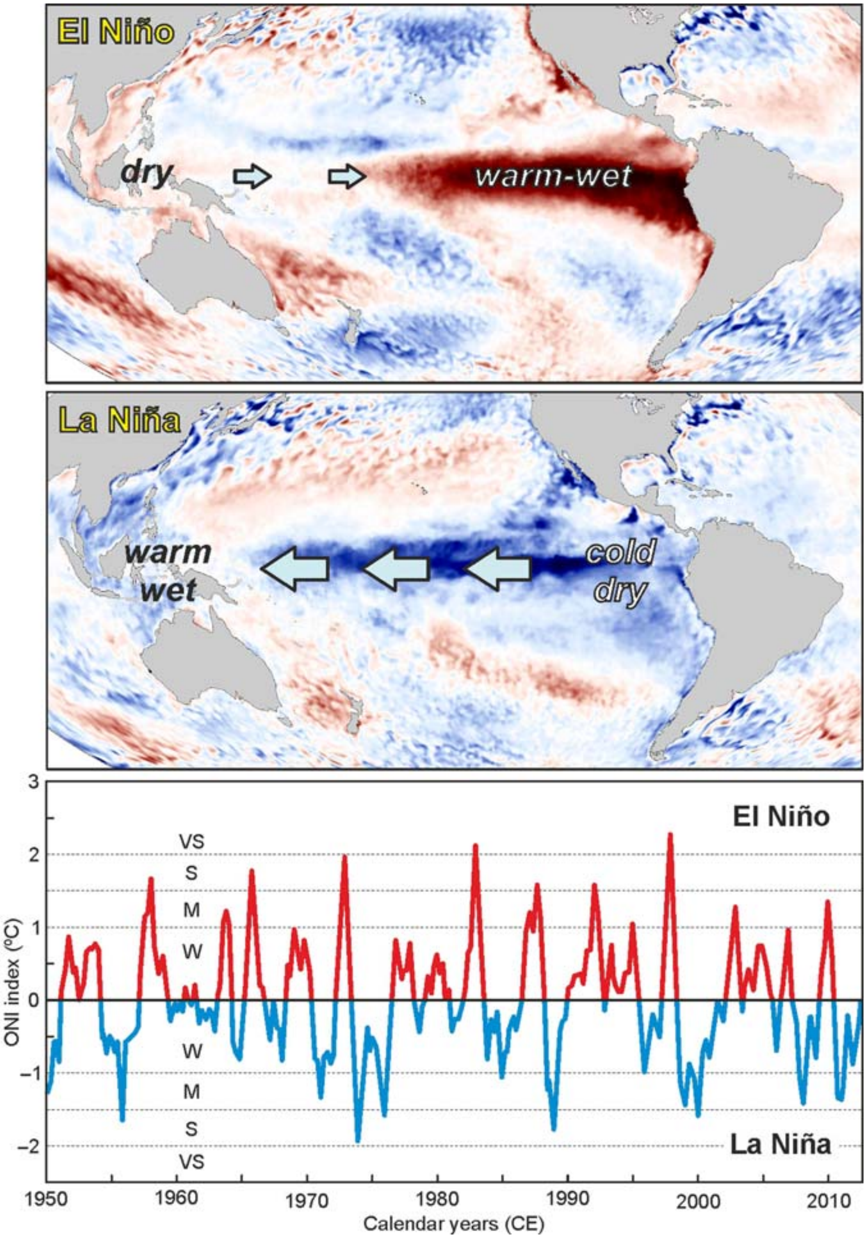

Figure 1.15 Map of the Pacific Ocean showing El Niño (top) and La Niña (middle) conditions. Above-average surface water temperatures are marked in red, and below-average values are marked in blue. Arrows indicate the direction and intensity of trade winds and of the equatorial surface ocean current. The graph in the lower (*Continued*)

ENSO cycles have been operating throughout the Quaternary, and although it is the opinion of some that the pre-Pleistocene warmer climates ensured permanent El Niño conditions, evidence can be found that climate variability compatible with the ENSO cyclicity has existed since the Eocene (Huber and Caballero, 2003). ENSO cycles can be discovered in an indirect manner in paleoclimatic archives based on the existence of 2- to 7-year periodicity in proxies of temperature and precipitation or indexes such as the ONI. The detection of these extremely short cycles requires very high-resolution studies—yearly or seasonal resolution in optimal cases. Such studies can be conducted with paleoclimatic archives, such as growth rings of trees or corals, or a very special archive, called varves, which are annual layers in lake sediments. There are also other interannual climate cycles, such as the North Atlantic Oscillation (NAO) that oscillates between Iceland and the Azores, controlling the rainfall distribution in the North Atlantic from the East Coast of North America to Europe, including the Mediterranean. In contrast to the ENSO, which combines atmospheric and ocean currents, the NAO is a purely atmospheric phenomenon and has a varying, few-year-long periodicity (Hurrel et al., 2003). Similar climate systems include the Arctic Oscillation, the Antarctic Oscillation, and the Pacific Decadal Oscillation, all of which have characteristic periods that make their detection in paleoclimatic records possible.

1.3 Synthesis: unpredictable complexity

The goal of this first chapter was to highlight the large quantity and variety of climatic changes that took place during the Quaternary, including their spatial and temporal dimensions and their originating and controlling mechanisms. This will help us place the history of Quaternary life in the appropriate environmental context, in turn allowing us to better understand the ecological, evolutionary, and cultural upheavals contemplated throughout

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◀ part of the figure illustrates the ONI values as temperature anomalies (i.e., deviations from the mean water temperature in the central Pacific) from 1950 to 2012. Acronyms express the intensity of El Niño and La Niña conditions. *M*, medium; *ONI*, Oceanic Niño Index; *S*, strong; *VS*, very strong; *W*, weak. *Base images from NOAA Climate.gov and Trenberth* (2009).

this book. There is one thing, however, worth noting: none of the mentioned climatic shifts happened in an isolated manner—their cycles overlapped in time. Stadial and interstadial oscillations, for example, occurred not only in the last glaciation but also in all of them. Terminations were always characterized by fluctuations, even if not always with the same trends as in the Late Glacial. The climatic changes of the last millennia were not exclusive phenomena of the Holocene but took place in all of the interglacial phases, although with different temporal and spatial patterns. Even the interannual oscillators played their part throughout the Quaternary. In other words, we need to consider a complex network of changes of various magnitudes and periods that operated simultaneously—sometimes in a coupled and sometimes in an independent manner—to gain a complete understanding of climate variation in the Quaternary. These changes together shaped a continuously adjusting and highly random—that is, a hardly unpredictable—environmental scenario.

From the perspective of life, the central topic of this book, it may seem that this environmental complexity supplied a permanent source of stress demanding adaption and making surviving the Quaternary a real ordeal. In fact, the Quaternary is often considered an extinction phase rather than a diversification phase, especially because of the allegedly catastrophic consequences of glaciations, which are sometimes seen as climatic anomalies. This view is well established in popular culture, likely because we live in an interglacial, which is perceived as the normal situation. However, we can adopt a different point of view. First of all, we have seen that glaciations account for approximately 80% of the duration of the Quaternary, while interglacial phases—such as the Holocene, in which we live—appear as warm stages of short duration that can be regarded as the real anomalies in an almost permanently glaciated world. Furthermore, our living world, from the simplest of organisms to the most complex ecosystems, is the result of a series of ecological and evolutionary processes that were and are conditioned by a continuously changing environment. Other types of variations would have given rise to a different type of biosphere. In the words of Stephen J. Gould, if we could go back in time and rerun Earth's evolution under different conditions, it would give a totally different result, and our species probably would never have existed. This also applies to the Quaternary time frame. Therefore the present facet of life on Earth could be regarded as the most logical outcome given the circumstances, instead of the result of a continuous battle against ephemeral climatic conditions. We are going to adopt this approach in the following pages, with the hope to convey to the reader our knowledge of how organisms changed their ranges and evolved during the Quaternary and how ecosystems assembled and disassembled repeatedly in response to the changing environmental conditions.

In summary, if we are happy—or at least comfortable—with the biosphere we have to live in, we must thank the complex environmental variability of the Quaternary for it. Without such variability, everything would be completely different. The popular catastrophic view of this geological period, with glaciations as the main disrupting agents, is hardly realistic, as we will see in Chapter 3. With this book, we hope to contribute to changing this perspective and accepting the idea that today's organisms, including ourselves, and ecosystems are what they are not despite climatic changes but thanks to them.

References

Amstrong, H.A., Brasier, M.D., 2005. Microfossils. Blackwell, Malden.

Anderson, D.E., Goudie, A.S., Parker, A.G., 2007. Global Environments Through the Quaternary. Oxford University Press, Oxford.

Birks, H.J.B., Lotter, A.F., Juggins, S., Smol, J.P. (Eds.), 2012. Tracking Environmental Change Using Lake Sediments. Vol. 5: Data Handling and Numerical Techniques. Kluwer, Dordrecht.

Boyle, J.F., 2001. Inorganic geochemical methods in palaeolimnology. In: Last, W.M., Smol, J.P. (Eds.), Tracking Environmental Change Using Lake Sediments, vol. 2. Physical and Geochemical Methods, Kluwer, Dordrecht, pp. 83−141.

Bradley, R.S., 2015. Paleoclimatology. Reconstructing Climates of the Quaternary. Elsevier-Academic Press, Oxford.

Bush, M.B., Stute, M., Ledru, M.-P., Behling, H., Colinvaux, P.A., De Oliveira, P.E., et al., 2001. Palaeotemperature estimates for the lowland Americas between 30°S and 30°N at the Last Glacial Maximum. In: Markgraf, V. (Ed.), Interhemispheric Climate Linkages. Academic Press, San Diego, CA, pp. 293−306.

Carlson, A.E., 2013. The Younger Dryas climate event. Encycl. Quat. Sci 3, 126−134.

Castañeda, I.S., Schouten, S., 2011. A review of molecular organic proxies for examining modern and ancient lacustrine environments. Quat. Sci. Rev. 30, 2851−2891.

Cohen, K.M., Gibbard, P.L., 2011. Global Correlation Stratigraphic Table for the Last 2.7 Million Years. International Commission on Stratigraphy, Cambridge.

Cronin, T.H., 2009. Paleoclimates. Understanding Climate Change Past and Present. Columbia University Press, New York.

Crowley, T., 2000. Causes of climate change over the past 1000 years. Science 289, 270−277.

Dansgaard, W., Johnsen, S.J., Clausen, H.B., Dahl-Jensen, D., Gundestrup, N.S., Hammer, C.U., et al., 1993. Evidence for general instability of climate from a 250-kyr ice-core record. Nature 364, 218−220.

Ditlevsen, P.D., Andersen, K.K., Svensson, A., 2007. The DO-climate events are probably noise induced: statistical investigation of the claimed 1470 years cycle. Clim. Past 3, 129−134.

Ehlers, J., Gibbard, P.L., 2007. The extent and chronology of Cenozoic global glaciaion. Quat. Int. 164−165, 6−20.

Ellis, R., Palmer, M., 2016. Modulation of ice ages via precession and dust-albedo feedbacks. Geosci. Front. 7, 891–909.

Flint, R.F., 1971. Glacial and Quaternary Geology. Wiley, New York.

Grootes, P.M., Stuiver, M., White, J.W.C., Johnsen, S., Jouzel, J., 1993. Comparison of oxygen isotope records from the GISP2 and GRIP ice cores. Nature 336, 552–554.

Hansen, J., Sato, M., Russell, G., Kharecha, P., 2013. Climate sensitivity, sea level and atmospheric carbon dioxide. Philos. Trans. R. Soc. A 371, 20120264.

Hodell, D.A., Channell, J.E.T., Curtis, J.H., Romero, O.E., Röhl, U., 2008. Onset of "Hudson Strait" Heinrich events in the eastern North Atlantic at the end of the middle Pleistocene transitions (~640 ka)? Paleoceanography 23, PA4218.

Huber, M., Caballero, R., 2003. Eocene El Niño: evidence for robust tropical dynamics in the "hothouse". Science 299, 877–881.

Hughes, P.D., Gibbard, P.L., 2014. A stratigraphical basis for the Last Glacial Maximum (LGM). Quat. Int. 383, 174–185.

Hurrel, J.W., Kushnir, Y., Ottersen, G., Visbeck, M. (Eds.), 2003. The North Atlantic Oscillation: Climatic Significance and Environmental Impact. American Geophysical Union, Washington, DC.

Imbrie, J., Imbrie, K., 1979. Ice Ages: Solving the Mystery. Macmillan, London.

Ito, E., 2001. Application of stable isotope techniques to inorganic and biogenic carbonates. In: Last, W.M., Smol, J.P. (Eds.), Tracking Environmental Change Using Lake Sediments. Vol. 2: Physical and Geochemical Methods. Kluwer, Dordrecht, pp. 351–371.

Jirikowic, J.L., Damon, P.E., 1994. The Medieval solar activity maximum. Clim. Change 26, 309–316.

Johnsen, S.J., Clausen, H.B., Dansgaard, W., Gundestrup, N.S., Hammer, C.U., Andersen, U., et al., 1997. The δ^{18}O record along the Greenland Ice Core Project deep ice core and the problem of possible Eemian climatic instability. J. Geophys. Res. 102, 26397–26410.

Jouzel, J., Koster, R.D., Suozzo, R.J., Russell, G.L., 1994. Stable water isotope behavior during the last glacial maximum: a general circulation model analysis. J. Geophys. Res. 99, 25791–25801.

Kaufman, D.S., Ager, T.A., Anderson, N.J., Anderson, P.M., Andrews, J.T., Bartlein, P.J., et al., 2004. Holocene thermal maximum in the western Arctic (0–180°W). Quat. Sci. Rev. 23, 529–560.

Lambeck, K., Rouby, H., Purcell, A., Sun, Y., Sambridge, M., 2009. Sea level and global ice volumes from the Last Glacial Maximum to the Holocene. Proc. Natl. Acad. Sci. U.S.A. 111, 15296–15303.

Last, W.M., Smol, J.P. (Eds.), 2001a. Tracking Environmental Change Using Lake Sediments. Vol. 1: Basin Analysis, Coring, and Chronological Techniques. Kluwer, Dordrecht.

Last, W.M., Smol, J.P. (Eds.), 2001b. Tracking Environmental Change Using Lake Sediments. Vol. 2: Physical and Geochemical Methods. Kluwer, Dordrecht.

Mann, M.E., Zhang, Z., Rutherford, S., Bradley, R.S., Hughes, M.K., Shindell, D., et al., 2009. Global signatures and dynamic origins of the Little Ice Age and Medieval Climate Anomaly. Science 326, 1256–1260.

Miller, G.H., Geirsdóttir, A., Zhong, Y., Larsen, D.J., Otto-Bliesner, B.L., Hollamd, M. M., et al., 2012. Abrupt onset of the Little Ice Age triggered by volcanism and sustained by sea-ice/ocean feedbacks. Geophys. Res. Lett. 39, L02708.

Moberg, A., Sonechkin, D.M., Holmgren, K., Datsenko, N.M., Karlén, W., 2005. Highly variable Northern Hemisphere temperatures reconstructed from low- and high-resolution proxy data. Nature 433, 613–617.

Obrochta, S.P., Miyahara, H., Yokohama, Y., Crowley, T.J., 2012. A re-examination of evidence for the North Atlantic "1500-year cycle" at site 609. Quat. Sci. Rev. 55, 23–33.

Petit, J.R., Jouzel, J., Raynaud, D., Barkov, N.I., Barnola, J.-M., Basile, I., et al., 1999. Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. Nature 399, 429–436.

Prothero, D.R., Ivany, L.C., Nesbitt, E., 2003. From Greenhouse to Icehouse. The Marine Eocene-Oligocene Transition. Columbia University Press, New York.

Raymo, M.E., 1994. The initiation of Northern Hemisphere Glaciation. Annu. Rev. Earth Planet. Sci. 22, 353–383.

Rull, V., Vegas-Vilarrúbia, T., 2019. Pantepui as a dynamic biogeographical concept. In: Rull, V., Vegas-Vilarrúbia, T., Huber, O., Señaris, C. (Eds.), Biodiversity of Pantepui, the Pristine 'Lost World' of the Neotropical Guiana Highlands. Elsevier-Academic Press, London, pp. 55–67.

Schultz, M., 2002. On the 1470-year pacing of Dansgaard-Oeschger warm events. Paleoceanography 17, 1014.

Sigurdsson, H., 1990. Assessment of atmospheric impact of volcanic eruptions. In: Sharpton, W.L., Ward, P.D. (Eds.), Global Catastrophes in Earth History; an Interdisciplinary Conference on Impacts, Volcanism and Mass Mortality, 247. Geological Society of America Special Publication, pp. 99–110.

Smol, J.P., Birks, H.J.B., Last, W.M. (Eds.), 2001a. Tracking Environmental Change Using Lake Sediments. Vol. 3: Terrestrial, Algal, and Siliceous Indicators. Kluwer, Dordrecht.

Smol, J.P., Birks, H.J.B., Last, W.M. (Eds.), 2001b. Tracking Environmental Change Using Lake Sediments. Vol. 4: Zoological Indicators. Kluwer, Dordrecht, Last, W.M., Smol, J.P. (Eds.), 2001.

Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., et al., 2013. Climate Change 2013: The Physical Science Basis. Cambridge University Press, Cambridge.

Talbot, M.R., 2001. Nitrogen isotopes in palaeolimnology. In: Last, W.M., Smol, J.P. (Eds.), Tracking Environmental Change Using Lake Sediments. Vol. 2: Physical and Geochemical Methods. Kluwer, Dordrecht, pp. 401–439.

Textor, C., Graf, H., Longo, A., Neri, A., Ongaro, T.E., Papale, P., et al., 2005. Numerical simulation of explosive volcanic eruptions from the conduit flow to global atmospheric scales. Ann. Geophys. 48, 818–842.

Trenberth, K.E., 2019. El Niño Southern Oscillation (ENSO). Encycl. Ocean. Sci. 6, 420–432.

Vandenberghe, J., French, H.M., Gorbunov, A., Marchenko, S., Velichko, A.A., Jin, H., et al., 2014. The Last Permafrost Maximum (LPM) map of the Northern Hemisphere: Permafrost extent and mean annual air temperatures, 25-17 ka BP. Boreas 43, 652–666.

Vaquero, J.M., 2007. Historical sunspot observations. Adv. Space Res. 40, 929–941.

Walker, I.R., 2001. Midges: chironomids and related diptera. In: Smol, J.P., Birks, H.J.B., Last, W.M. (Eds.), Tracking Environmental Change Using Lake Sediments. Vol. 4: Zoological Indicators. Kluwer, Dordrecht, pp. 43–66.

Walker, M., 2005. Quaternary Dating Methods. Wiley, Chichester.

Willis, K.J., Whittaker, R., 2000. The refugial debate. Science 287, 1406–1407.

Wolfe, B.B., Edwards, T.W.D., Elgood, R.J., Beuning, K.R.M., 2001. Carbon and oxygen isotope analysis of lake sediment cellulose: methods and applications. In: Last, W. M., Smol, J.P. (Eds.), Tracking Environmental Change Using Lake Sediments. Vol. 2: Physical and Geochemical Methods. Kluwer, Dordrecht, pp. 373–400.

CHAPTER TWO

Organisms: adaption, extinction, and biogeographical reorganizations

Contents

One of the first things we learn in ecology is that living beings are not able to live in all places; each species has its own particular environmental preferences and requirements. The study of species and their populations in this sense is called autecology (or population ecology) and differs from synecology (or community ecology), which is the study of whole communities consisting of a mixture of populations of different species (Walter and Hengeveld, 2000). In this chapter, we focus on autecology; synecology will be the topic of Chapter 4. If environmental conditions were to never change, ecology would be much simpler than it actually is. Organisms would always live in the same place, and their evolution over time would be of a much smaller scale than they actually are. However, as discussed in the last chapter, environmental changes have been constant throughout the Quaternary and have occurred at a wide range of temporal and spatial scales. They induced alterations in the evolution and spatial distribution of species on the Earth, as well as in the structure and dynamics of ecosystems. All these changes provoked by the constantly changing environment are called biotic responses to environmental shifts.

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2.1 How do species respond to climatic changes?

2.1.1 The ecological niche

Whether any given species is able to live, develop, and reproduce in a given time and space depends on its ecological requirements, including the presence of an appropriate substratum (soil, water, tree trunks, etc.) and that each environmental factor (geology, climate, physicochemical properties of water, etc.) is within the appropriate range for the organism under consideration. The habitat of each species is characterized by these factors and could be defined as the physical context that makes the life of that given species possible. As examples, we could name the polar sea and ice for polar bears, mountain rivers and lakes for trout, and rainforests for many tropical orchids. Some species construct their own habitat. This is the case for beavers and ants, which change their environment to suit their needs, and for bees, birds, and spiders, which build their respective homes (hives, nests, and webs) anew. In addition to habitat the niche also includes the relations that organisms and the population maintain with the rest of the components of the ecosystem (feeding, competition, predation, pollination, etc.). The concept of the niche not only refers to a physical place but also encompasses the functional relationships of the species within the ecosystem (Chase and Leibold, 2003). For example, fish consumption, competition with carp, and the existence of pollinators are parts of the niche of polar bears, trout, and orchids, respectively. The prominent Spanish ecologist Ramón Margalef defined the habitat as the living place and the niche as the "job" of a species within the ecosystem (Margalef, 1974). By building their habitat, beavers, ants, bees, birds, and spiders also create their niche because the new habitat has an influence on various processes, such as reproduction and resource management.

The influential British ecologist G. Evelyn Hutchinson, regarded by many as the father of modern ecology, defined the ecological niche as a multidimensional space or hypervolume where each dimension is an environmental factor that conditions life for a given species and the range of that variable marks the limits of the species (Hutchinson, 1957). Characteristics of the niche differentiate each species from others in ecological terms. This is why we say that species are idiosyncratic (Hol et al., 2011), as if they all had their own way of seeing the world and understanding life. This idiosyncrasy reduces the intensity of competition and other possibly excluding interactions between species and makes their coexistence possible within a given ecosystem. Coexistence would not be viable if all species shared the same ecological niche (which is exactly what is going on with humans). This differentiation is called niche segregation or partitioning (Chase and Leibold, 2003). Ecological dynamics—and mainly biotic relationships—modify the niche of each species. Therefore we must distinguish between the hypervolume in which the species could possibly live (potential niche) and another, smaller part of this hypervolume where it effectively lives (effective niche). The effective niche is conditioned by various factors, such as competition with other species and the availability of food or pollinators, among many others.

Other important concepts within this topic are the so-called niche breadth and niche overlap. Niche breadth determines whether a species is a specialist, a generalist, or anything in between. We illustrate this through the example of a single variable, temperature. Each species has a suitable temperature range defined by a maximum and a minimum value. The thermal optimum of that species, where its populations reach maximum development, is somewhere within this range (Fig. 2.1). Species able to develop under a wide range of temperatures are called eurythermal, while others that tolerate only a narrow temperature range are called stenothermal. Marine species can be euryhaline or stenohaline, regarding

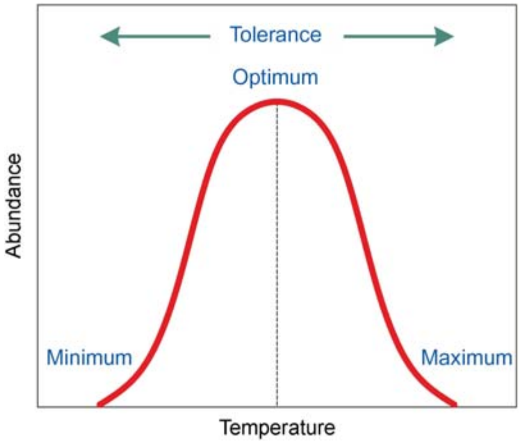


Figure 2.1 Schematic diagram showing the abundance of a hypothetical species as a function of temperature. Tolerance range is defined as the interval between the maximum and minimum temperatures that the species is able to tolerate. Thermal optimum is the temperature at which the populations of the species reach their maximum development.

their tolerance to water salinity. In terms of light tolerance, we can define euryphotic and stenophotic species, and so on. In general terms, without one given parameter in mind, the most generalist species (with the widest niche breadth) are called eurytopic, and the most specialized species are named stenotopic. As is quite obvious, stenothermic species are more sensitive to temperature changes than are eurythermic ones, and this characteristic is what mostly determines their response to climatic changes. Niche overlap defines the part of the niche that is shared by two or more species, which is the preferred arena for interspecific competition.

2.1.2 Types of biotic responses

Not all species respond in the same way to environmental changes, not only because of their different tolerances but also because of other equally idiosyncratic particularities that determine whether their responses are faster or slower. The shorter the life cycle of an organism is, the faster its response to climatic changes is (Lenoir et al., 2008). For example, the yellow fever mosquito, *Aedes aegypti*, has a life cycle from the egg to adult stage that oscillates between approximately 10 days at 36°C and 40 days at 16°C (Marinho et al., 2016). Therefore this mosquito is able to respond to climatic oscillations of very short duration by regulating the duration of its life cycle, which may result in reproductive rates four times higher at 36°C than at 16°C. This is an example of a very fast reaction regarding temperature changes where the response lag (the time it takes for the response to take place) to a given temperature change is from weeks to months. At the other extreme of the scale, we find organisms with very long life cycles, such as centennial trees, where the response lag can last for centuries or millennia (Hofgaard et al., 1991). The intensity and duration of the climatic change and the life cycle phase in which the species encounters the change are also of outstanding importance. For example, populations of the mentioned mosquito are able to react both to minor transitory changes and to the most intensive and persistent ones, while a spruce tree, for example, would respond only to the latter. A short climatic change could affect spruce if it happened at the time of flowering and fruiting or during seed germination, since, in these cases, it could alter the size of future populations (entailing, at the same time, a significant delay). The same climatic change, however, would go unnoticed, at the population level, if it happened at another time. In conclusion, a climatic change would affect a species with a long life cycle only if it was sufficiently intense, long-lasting, and timely, but it will always follow a response lag that is proportionate to the life cycle of the species.

A response may happen in several ways independently of the response lag: the question is whether or not the effect of the climatic shift is within the tolerance of the species. A eurythermic species has a wide tolerance range and thus might be able to adopt a different state within its range of possibilities (Fig. 2.2). We call this phenomenon acclimation (also acclimatation or acclimatization), and it is based on the phenotypic plasticity of the species, which means its ability to persist under suitable or acceptable conditions by only the alteration of its phenotype—that is, its physical, behavioral, or physiological traits—without genetic modifications. These phenotypic variations usually consist of morphological or metabolic variations that are more suitable for a given environment. For example, plants have the ability to vary their rate of photosynthesis, since the operation of enzymes that control this process is a function of temperature (Gunderson et al., 2010). A eurythermic species can regulate its photosynthesis to live in a satisfactory manner at suboptimal temperatures without changing its genome or genotype. In other words, this species has high phenotypic plasticity that allows it to acclimate to thermal conditions that are not optimal. In contrast the phenotypic plasticity and, thus, the acclimation capacity of stenothermic species are low. Nevertheless, although eurythermic species are able to tolerate more intense thermal variations than stenothermic ones, they still have a limit. If the climatic oscillations exceed the tolerance range of these species, they have three possible alternatives: adaption, emigration, or extinction.

Adaption (or adaptation) and acclimation—which could even be used as synonyms in everyday use—mean very different things in this context. Adaption implies genetic modifications. This means that the given species may evolve to be able to continue living in the same place despite the climatic shift. In other words, it may modify its genome to be able to carry out its vital functions even beyond its possibilities of acclimation. To continue with the example of photosynthesis, the genes that encode the formation of enzymatic proteins may be modified so that they produce a somewhat different enzyme able to operate in an optimum fashion under the new climatic conditions. This is possible only if genetic variability is sufficient for natural selection to produce the desired outcome. If the species is unable to produce the required type of photosynthetic enzyme, the probability of adaption is nil. A higher probability of creating different enzymes for the same function means a higher evolutionary capacity in

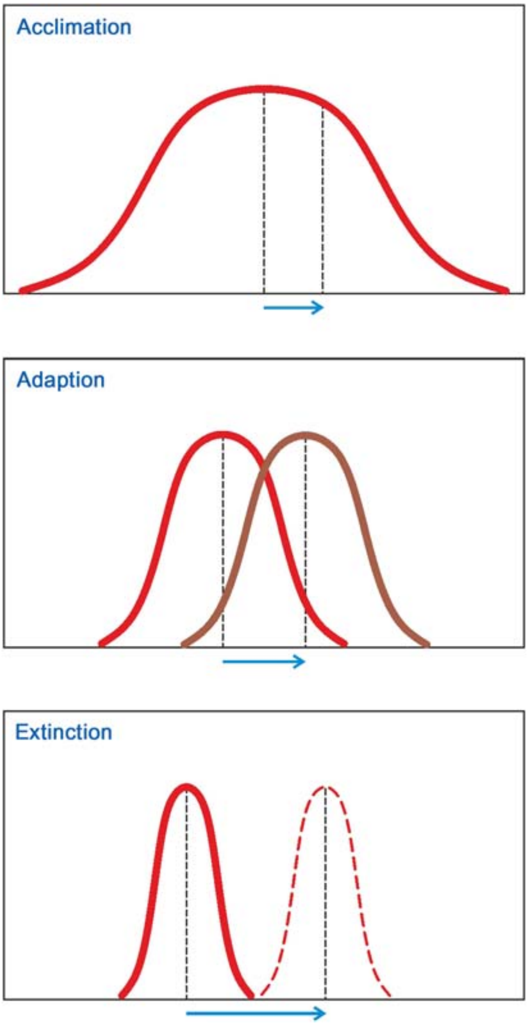


Figure 2.2 Hypothetical examples of acclimation, adaption, and extinction represented as abundance/temperature diagrams (Fig. 2.1). In the case of acclimation (top), a eurythermic species makes the use of its phenotypic plasticity to continue living under suboptimal conditions in spite of a temperature increase (*blue arrow*). During adaption (middle) the temperature is close to the upper limit tolerated by this species, but the species is able to modify its genotype, which, in turn, shifts its tolerance range toward values more similar to the new environmental conditions. In the case of extinction (bottom), the temperature increase is outside the tolerance range of this stenotherm species, and it happens at rates that render survival strategies impossible and result in extinction.

response to an environmental change (Becklin et al., 2016). In contrast to acclimation, which is an almost automatic and relatively fast process, adaptation, similar to all evolutionary changes, requires more time, and there is always a risk of extinction before the species is able to adapt to the new conditions (Merilä, 2012).

Another alternative is to migrate to areas where the climate is the same as or similar to that required by the species or is at least within its tolerance range, making acclimation possible. According to the eminent Canadian ecologist Evelyn E. Pielou, species are able to modify their distribution area in three main ways: by diffusion, secular migration, or jump dispersal (also long-distance dispersal) (Pielou, 1979). Diffusion is the gradual motion of populations through areas where conditions are favorable for life over generations. Secular migration also happens through favorable habitats, but it is of a much longer duration, which gives evolutionary changes time to take place. Jump dispersal, on the other hand, happens over short time intervals (usually within the lifetime of individuals) but between faraway regions that are separated by habitats that would not make life for the migrating species possible. In biogeography, these inhospitable habitats are called barriers, as they hinder or completely block diffusion and secular migration. Hereafter, we are going to use this classification in a simplified manner by merging the first two options under the term "migration" and calling the third one simply "dispersal." Migration entails the existence of a colonization front (or migration front) where the moving population progressively occupies the neighboring areas in a given direction (Fig. 2.3). This motion does not require any additional means of transport. A good example of migration is the progressive shift toward the poles or high-mountain areas that several species are experiencing as a consequence of contemporary Global Warming (GW) (e.g., Parmesan and Yohe, 2003; Scheffers et al., 2016) (Fig. 2.4). Dispersal, on the other hand, requires a means of transport other than the motion of the species that is capable of transporting it over large distances (Fig. 2.3). Seed transport by wind or by migratory birds crossing oceans and deserts is a good example of dispersal. Another difference between migration and dispersal is that dispersal alone does not guarantee success, given that transported species must be able to establish and develop populations at the destination. This does not depend solely only on the capacities of the dispersed species but also on the eventual difficulties posed by autochthonous species in terms of competition and other ecological interactions. Successful establishment after dispersal may be possible only after several attempts (Van der Pijl, 1969).

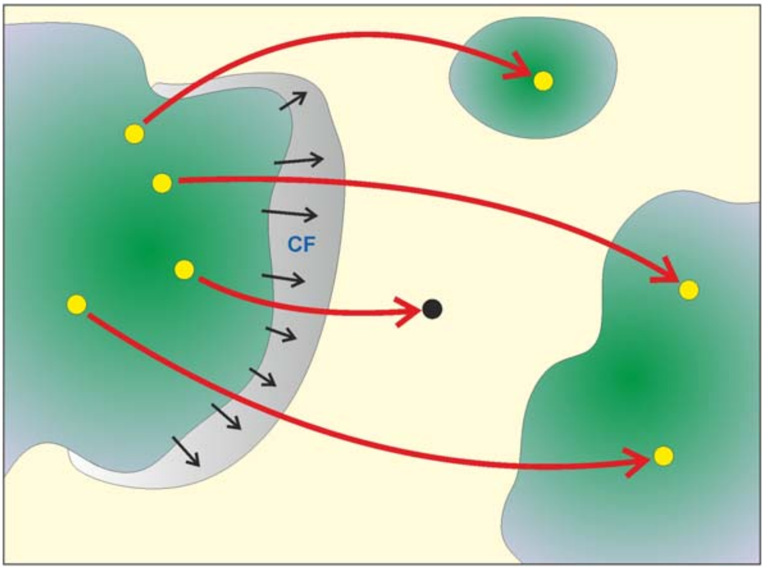


Figure 2.3 Graph showing the difference between migration (*black arrows*) and dispersal (*red arrows*) of a hypothetical species. The favorable habitat is marked in green. Individuals reaching favorable areas can develop (*yellow circles*), while those arriving to an unfavorable area (yellow) will not live (*black circle*). *CF*, Colonization front.

Other ways to modify the distribution area of a species due to climatic changes do not necessarily involve changing the position or location of the distribution area but its size and shape. These are called in situ alterations. Following a favorable environmental change, a species can expand its territory by invading areas belonging to other species that are less competitive under the new conditions (Fig. 2.5). For example, a temperature decrease combined with an increase in precipitation of sufficient duration would make it possible for a beech forest to expand at the expense of surrounding holm oak groves, which are better adapted to warmer and drier climates. In the case of an unfavorable environmental change, the distribution area of a species can diminish in two different ways: by shrinking either into one small area or into several smaller patches. The latter is called fragmentation. In our earlier example the reestablishment of warmer and drier conditions could result in expansion of the holm oak grove and a reduction in the beech forest to one or several smaller patches of favorable climate, which could be the shadier slopes of a mountain range, where temperature and evaporation are lower and moisture is

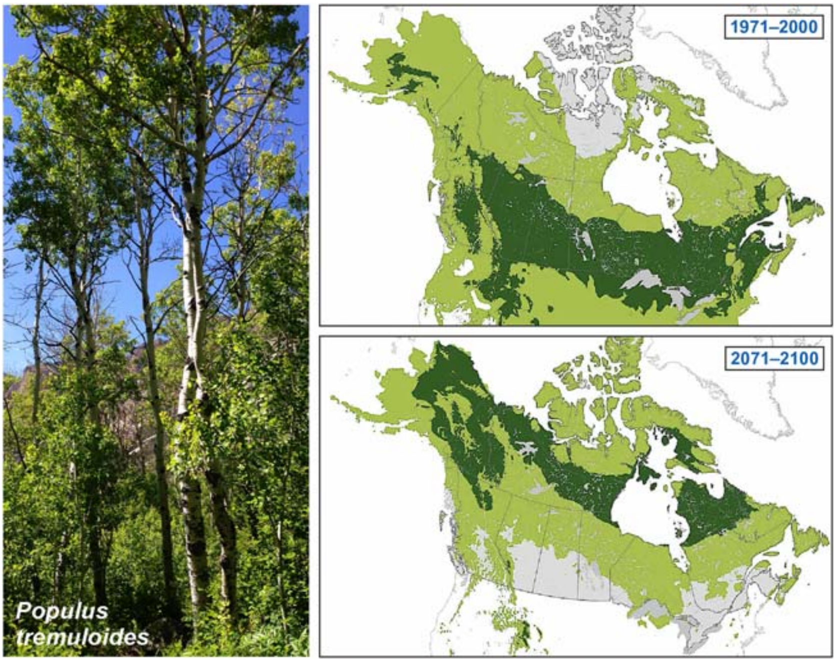


Figure 2.4 Boreal forest species are experiencing progressive migration toward the North Pole due to Global Warming. This figure compares the present-day (1971–2000) distribution of the American aspen (*Populus tremuloides*) with its future distribution (2071–2100), supposing that the present forecast of a 2°C–4°C temperature increase holds true (Stocker et al., 2013). Light green marks the distribution of the species within the complete temperature range, while dark green shows the distribution under optimal conditions (Fig. 2.1). *Based on maps from the Canadian Forest Service (publicly available at www.nrcan.gc.ca/forests) and Famartín's photograph under the Creative Commons license.*

better preserved. These patches are generally called refugia and can be of different types (Section 2.2.2). Therefore species can survive an unfavorable climatic change in certain places not only by means of acclimation or adaption, as discussed previously, but also by means of suitable refugia, where local environmental conditions are still favorable despite the generally unfavorable climate (Ashcroft, 2010).

Extinction can also be regarded as a response to climatic changes. It occurs when a species is unable to acclimate, adapt, or migrate. Area reduction processes (with or without fragmentation) are often involved in extinction when the reduction causes the population size to fall below the size of the so-called minimum viable population (Traill et al., 2007). Extinction can be local, when populations of the species persist in other

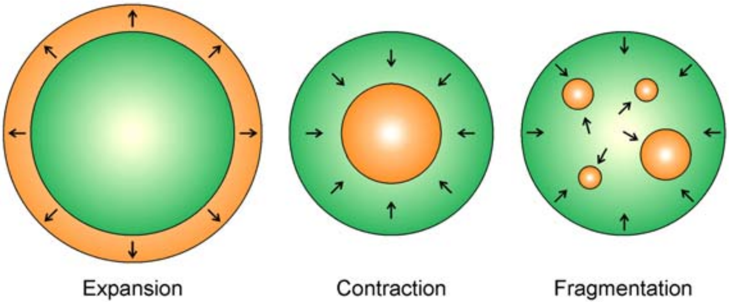


Figure 2.5 Hypothetical examples of expansion, contraction, and fragmentation of a species' distribution area. The original distribution is marked in green, and the new distribution is marked in orange.

areas, or global, when the species disappears completely from the face of the Earth. The first case can also be called extirpation (Ladle and Whittaker, 2011). It seems quite obvious that stenothermic species are more susceptible to extinction than are eurythermic species, but eurythermic species are also at risk from intensive and persistent environmental variations. In these cases, variables other than the temperature tolerance range also play an important role. One of the key parameters is the rate of environmental change. A gradual climatic change gives species enough time to acclimate, evolve, or migrate, but intense, abrupt shifts may outweigh species' capacities to adopt such survival strategies and thus bring about their extinction independently of their environmental tolerance ranges (Nilsson-Örtman and Johansson, 2017).

Extinction can be caused by the disappearance of the typical habitat of certain species. We call this extinction by habitat loss. For example, if a forest is removed, all the habitats related to its structure disappear, causing the extirpation of many species. One example could be birds nesting in trees. This is usually a local extinction, but at present deforestation rates, regional or global extinctions could take place in the not-too-distant future. Contemporary GW is occurring at a rather high speed (Stocker et al., 2013). Within the context of Quaternary climatic changes, it falls within the abrupt category (Section 1.2.3). This warming is causing the migration of numerous species toward the peaks of the mountains where they live, and if this tendency continues, several species adapted to the cold climate of high-mountain areas are expected to go extinct, as this habitat is beginning to disappear (Dirnböck et al., 2011). Loss of habitat might also be caused by the replacement of natural ecosystems by crops, cities, communication routes, or

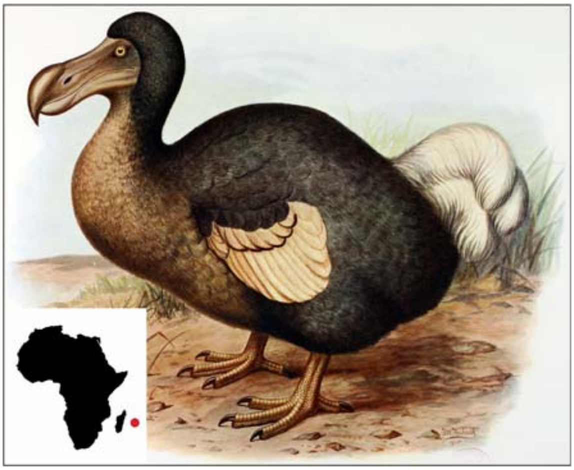


Figure 2.6 One of the best known historical extinctions is that of the dodo (*Raphus cucullatus*), a flightless bird in the family of pigeons and doves (*Columbidae*) that lived on the island of Mauritius until the 17th century, when it went extinct due to human activity [hunting, introduction of new competitors (mainly pigs and macaques), and destruction of its habitat]. The location of the island of Mauritius (*red dot*), eastward of the island of Madagascar, is marked on the map of Africa. *Based on Frederik W. Frohawk's (1861–1946) restoration of the dodo, under the Creative Commons license (en.wikipedia.org).*

other types of anthropogenic infrastructure that are in constant development. All of these changes related to human activity, together with the direct annihilation of certain species by overhunting or overfishing, are reducing the Earth's biodiversity to such an extent that some people already call it the sixth mass extinction (Barnosky et al., 2010) (Fig. 2.6). The fifth mass extinction happened at the end of the Cretaceous period, approximately 66 million years ago, when the dinosaurs and many other land and aquatic organisms disappeared.

2.2 Biotic responses to the climatic changes of the Quaternary

2.2.1 Survival in situ

When discussing the ecological niche, we mentioned that some species build their own habitats—either completely or partly, and we listed some well-known examples (beavers, birds, ants, and spiders). A case less widely known but very interesting due to its paleoecological significance is that of certain rodents that build their homes, known as middens, out of all kinds of materials that they cement with their urine and excrements. The result is a very resistant material able to persist for tens of thousands of years. A basic component of the building materials they use is different types of plant debris that they collect randomly from their surroundings. Therefore a detailed analysis of the plants that form these constructions gives us a quite thorough idea of the local flora. If we have a series of fossil middens of different ages at our disposal, we can form a rather comprehensive picture of how the vegetation of a given place or region developed over time in terms of the presence or absence of species.

Jackson et al. (2005) studied pollen and macroscopic plant residues in a series of middens in the Dutch John Mountains (Utah, United States) that encompassed a period from the end of the last glaciation until today. They were able to verify that despite changes in the composition of vegetation provoked by climatic changes of the last 20,000 years, certain species have been present in the region permanently. Some of these species were the Rocky Mountain juniper (*Juniperus scopulorum*), the winterfat (*Krascheninnikovia lanata*), and the snakeweed (*Gutierrezia sarothrae*). This means that these species, in contrast to all the rest, were able to withstand every temperature and moisture variation since the end of the last glaciation, in the same place. Their area of distribution might have suffered alterations, but they were always present. Having a closer look at the autecology of these three species, we discover that they are euryhydric, meaning that they tolerate a wide range of hydrologic conditions and are able to live under conditions with an ample water supply as well as in arid climates. This surely helped them survive the characteristic arid phases of the Late Glacial. The authors of the same study wondered whether the persistence of these xerophilic species (i.e., species that are able to live in xeric habitats with a low availability of water) is due to their high phenotypic plasticity, which would allow acclimation, or their genetic variability, which would facilitate adaption. Another possible hypothesis of the discussed study was the continuous existence of xeric habitats in the region, perhaps in the form of refugia during the LGM, alternating with periods when these habitats were more extensive, such as today.

The persistence of several vascular plants in the mountain forests of the tropical Andes throughout the Quaternary is even more astonishing. Pollen and spores preserved in the sediments of a large, now nonexistent

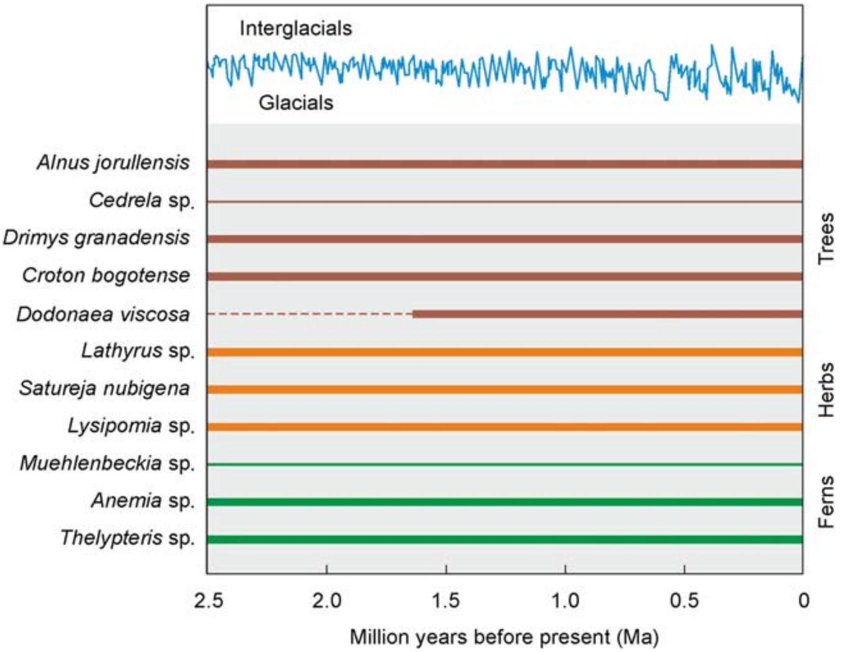


Figure 2.7 Persistence of several tree, grass, and fern species in the montane forests of the northern tropical Andes (Colombia) during the Quaternary. Continuous presence is marked by wide bars; almost continuous presence, by narrow bars; and discontinuous presence, by dashed lines. In the upper part the curve of Figure 1.4 is shown to highlight glacial and interglacial periods. *Modified from Hooghiemstra (1984) and Bennett (1997).*

lake in Funza, close to Bogotá (Colombia), revealed the presence of several species of vascular plants from the beginning of the Pleistocene until today (Hooghiemstra, 1984; Bennett, 1997) (Fig. 2.7). This lake was situated at an altitude of approximately 2500 m above sea level, where the Andean rainforest currently reaches its full development. During glaciations, glaciers descended 1000–2000 m below their current position and did not cover the area under study, but the average temperature difference between the glacial and interglacial phases was approximately 7°C–8°C, which is a very high value in terms of the tolerance of rainforest species. We must remember that in contrast to the plant fragments in the earlier example that are always from local vegetation, pollen and spores can be transported by wind. Therefore we cannot be sure if the pollen found in lake sediments belongs to local species. However, this study demonstrates that the Andean forests did not disappear at the elevation of the Funza lake, despite the extreme thermal oscillations of the glacial–interglacial periods. Once again, the possibilities of acclimation, adaption, and survival in refugia remain open.

The role of refugia during glaciations is more obvious in some parts of southern Europe, where several tree species of present-day Central Europe survived the last glaciations. A classic example is the north of Greece, precisely the city of Tenaghi-Philippon, where lake sediments reflecting the last approximately 1.4 million years, including the last four glacial cycles, were studied (Tzedakis, 1993; Tzedakis et al., 2006). Pollen analysis of these sediments revealed the continuous presence of pine (*Pinus*), oak (*Quercus*), fir (*Abies*), beech (*Fagus*), elm (*Ulmus*), and hazel (*Corylus*) trees that disappeared from most of the European continent due to the harshness of the climate during glaciations, which resulted in cold and dry steppes instead of today's deciduous and mixed forests. Thus these species survived the last four glaciations in refugia, such as the one in Greece, thanks to the locally warmer and more humid climate and expanded northward again during interglacial periods (Fig. 2.8). More examples of refugia can be found in France, Italy, the Iberian Peninsula, and the southern United States, but this topic will be further discussed in Section (2.2.2) because the formation and subsequent expansion of glacial refugia imply both changes in distribution area and migration as survival strategies.

2.2.2 Traveling with climate

As discussed in Chapter 1, glacial–interglacial alternations provoked latitudinal and altitudinal shifts in the climatic zones of the Earth. The survival of many species was due to their capacity to move similarly, in search of optimal living conditions, that is, their ecological niche. A classic example of this phenomenon took place in North America after the LGM. Margaret B. Davis, the great American palynologist and paleoecologist, was the first to discover this phenomenon, through her studies of tree species covering the continent today. In her work, which is among the classics in the field, she mapped all the points from palynological studies that covered the interval from the LGM until today and manually drew curves called isopolls (pollen isolines)—similar to isolines of depth in a lake (isobaths) or of temperature in meteorology (isotherms)—that showed the time at which each species reached a given latitude during its postglacial migration from the southern glacial refugia (Davis, 1984). This kind of study is still performed in the same manner and, despite the more

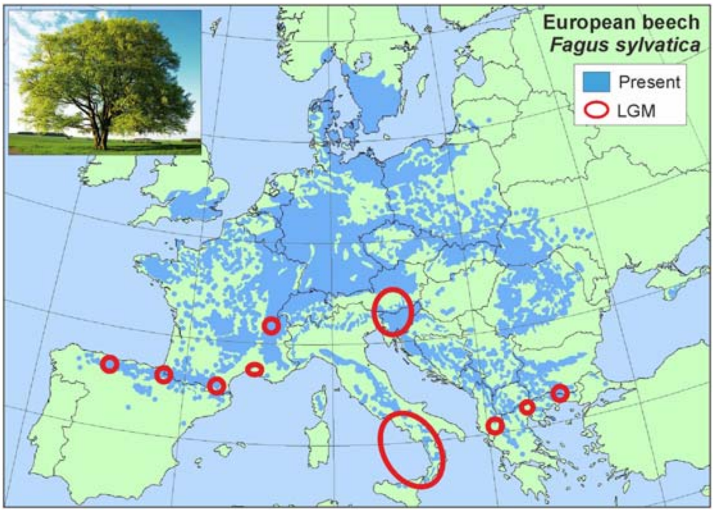


Figure 2.8 Present-day distribution of the European beech (*Fagus sylvatica*) (in blue) and approximate location of its refugia during the LGM (*red outlines*). *LGM*, Last Glacial Maximum. *Base map: EUFORGEN (publicly available at www.euforgen.org); refuge areas based on Magri et al. (2006).*

sophisticated geographical representation tools, follows the same logic. Davis conducted her studies using species of boreal, mixed, and deciduous forests of the eastern part of North America and discovered several interesting facts (Fig. 2.9).

First of all, not all species migrated following the climatic isotherms that shifted northward in a relatively orderly manner regarding latitude. For example, boreal forest species and *Quercus* exhibited a migration trend similar to the northward shift of the isotherms, but this was not the case for most mixed and deciduous forest species. Second, different species had different glacial refugia, even within the same forest type. The migration velocity also varied not only between species but also within the same species among different time intervals. For example, oak (*Quercus* spp.) and maple (*Acer* spp.) migration was relatively fast, but the migration of Jack pine (*Pinus banksiana*) and balsam Fir (*Abies balsamea*) was slower, especially after 10 ka BP. Considering that the rate and magnitude of climate change were the same for all species, Davis concluded that the response of each species was idiosyncratic both in time and in space and that these species never reached a stable equilibrium with the climate they tried to keep pace with, in a clearly stressful situation. We will come back to this concept in Section 4.4.4. In Europe the British paleoecologists Brian Huntley and

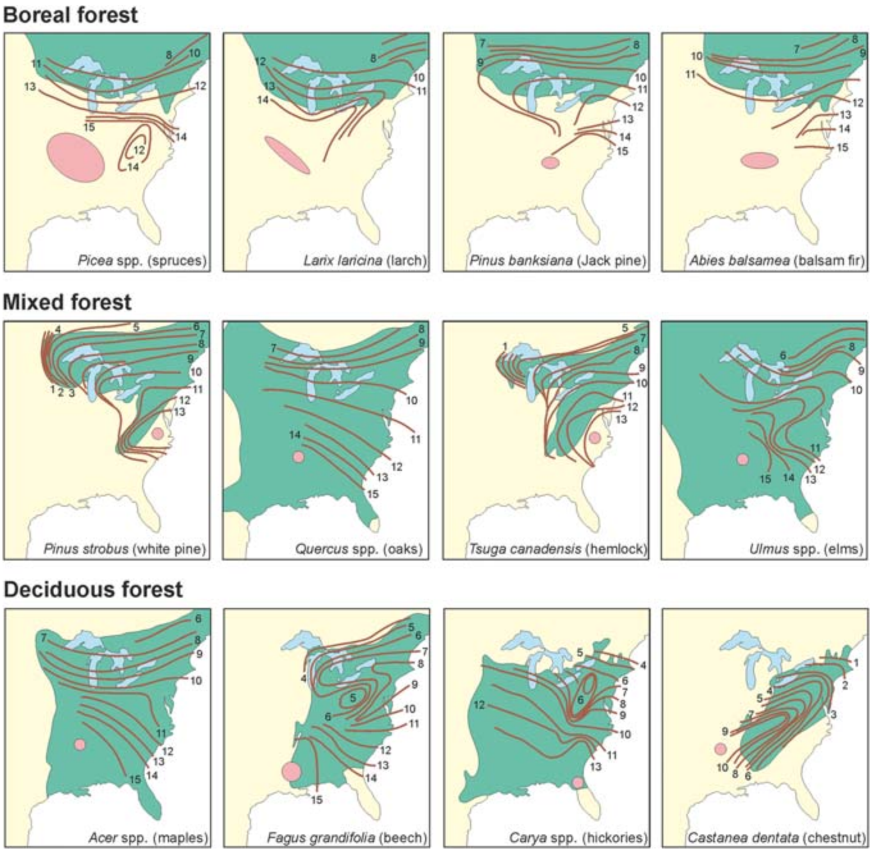


Figure 2.9 Late Glacial and Holocene colonization of the eastern part of North America (yellow) by several tree species of boreal, mixed, and deciduous forests. Green areas show the present distribution of each species, and brown lines (isopolls) mark colonization fronts in each time interval represented in thousands of years before present (ka BP). Greater distances between isopolls indicate higher migration rates. The most probable location of the glacial refugia of each species is shown in pink. The blue area shows the Great Lakes on the United States–Canadian border. *Redrawn from* Davis (1984).

John Birks conducted similar studies and reached similar conclusions (Huntley and Birks, 1983). Subsequent studies using the most state-of-the-art digital geographical technologies on both continents were able only to confirm the pioneering observations published in the 1980s. One of the differences between the continents is that the location of glacial refugia for both plant and animal species is much more homogeneous in Europe. Even so, migration routes and velocities are highly variable (Fig. 2.10),

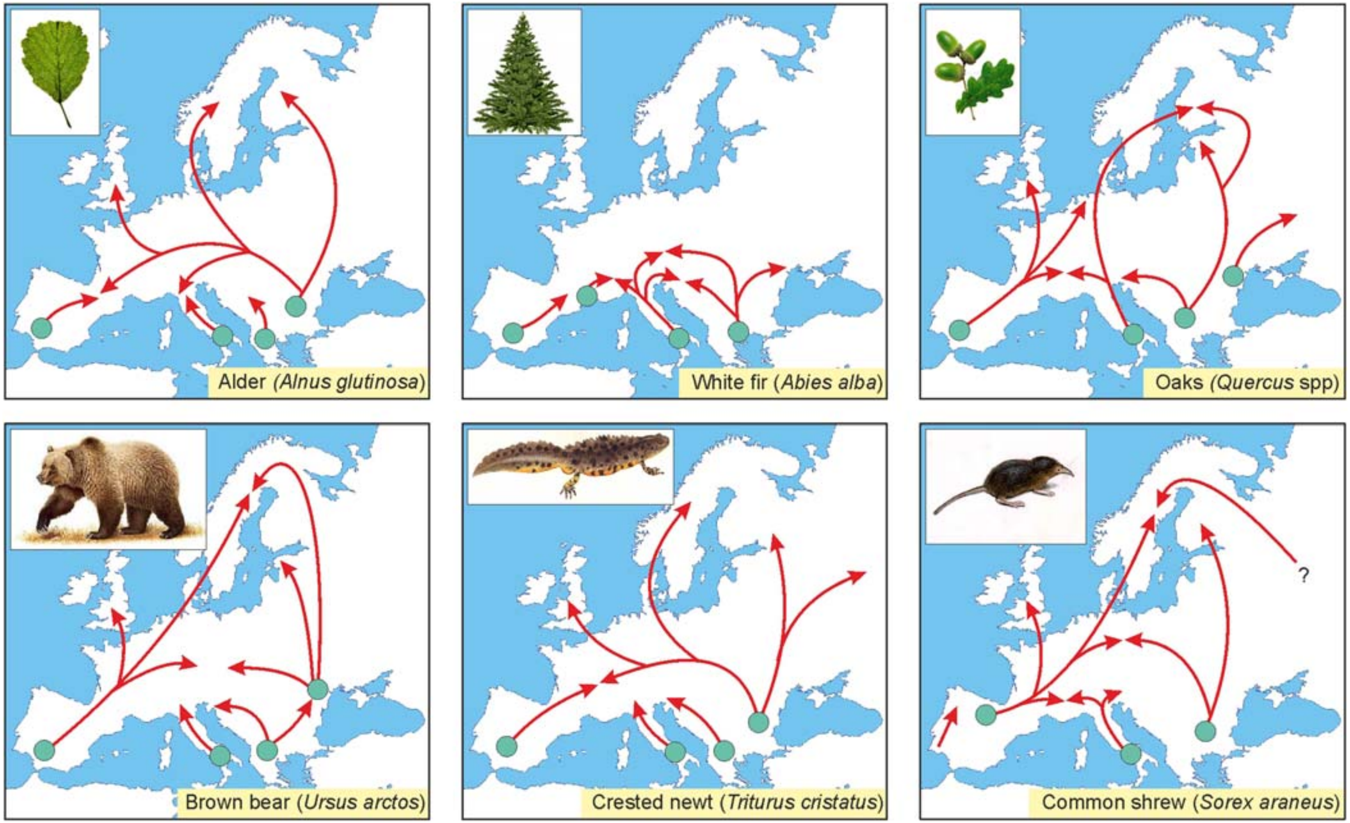


Figure 2.10 Glacial refugia (*green circles*) of some European animal and plant species and migration routes during the Late Glacial–Holocene expansion (*red arrows*) that led to their current distributions. In Section 3.5, we will discuss in detail how these maps were drawn. Redrawn and modified from Hewitt (1999).

which demonstrates, once again, the individual response each species has to climatic changes according to its biological characteristics. This has important consequences for communities and ecosystems, as will be discussed in Chapter 4.

A corollary of these studies is that northward postglacial colonization should have proceeded at incredible rates. Estimates vary between 200 and 400 m per year, in the case of American species, and reach up to 1000 m per year, in Europe. At the daily scale, these values are 0.5–2.7 m, meaning that we should be able to see the forest move and that we could not build a house at the edge of the woods because a month later, there would be trees in our kitchen. This does not occur, but the estimates are based on empirical evidence, a conundrum that has been called Reid's paradox (Clark et al., 1998). The estimated colonization rates could be explained by dispersal, which facilitates the colonization of faraway areas much faster than does migration. In Europe, for example, the main transportation agent might have been rivers, which dominantly flow north, in the direction of postglacial expansion. However, in North America, where most rivers flow to the south, this is not a plausible explanation. An alternative hypothesis is built on the possible existence of glacial microrefugia situated farther away from the southern refugia, scattered throughout the continent, that could have acted as secondary dispersal centers and thus accelerated the colonization of former glacial or periglacial territories. Microrefugia have been defined as relatively small areas of favorable conditions within a large area of regionally unfavorable climates, where a few populations of a given species can survive outside its main distribution area, which is called a macrorefugium or simply a refugium (Rull, 2009).

From a theoretical point of view, three main types of microrefugia have been defined relative to the macrorefugium (Fig. 2.11). In Europe, for example, refugia situated in the south, in the circum-Mediterranean area, are considered macrorefugia (Figs. 2.8 and 2.10), while microrefugia may have been dispersed over the rest of the continent, including areas covered by glaciers, where they could have been situated on so-called nunataks, elevated areas without an ice cover where life was possible (Fig. 2.12). Until now, it has been difficult to find clear examples of glacial microrefugia using paleoecological methods, since their small size reduces the likelihood of finding sedimentary records that fall precisely within that area. Examples of contemporary microrefugia are well known, however, especially in places with a microclimate that differs from the general environment. Such examples are oases in deserts, high-mountain

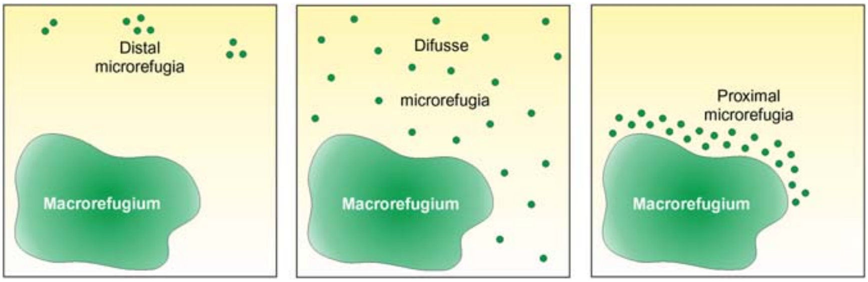


Figure 2.11 Schematic representation of three main types of microrefugia based on their position relative to the macrorefugium. Distal microrefugia are sometimes referred to as remote, widespread as diffuse, and proximal as ecotonal. The regionally inhospitable climates are in yellow. *Redrawn and modified from Rull (1999).*

screes, some small valleys, and the mentioned nunataks. But why do we have to talk about refugia or microrefugia in an interglacial period, such as the Holocene? Because some species—especially those well adapted to cold climates—might need shelter from the interglacial heat instead of the glacial cold. In contrast to the examples that we have seen so far, cold-preferring species were more widely dispersed during glaciations and restricted to smaller areas during interglacial phases. This is particularly noticeable for high-mountain species that are taking refuge in the mountains during the warm climate of the Holocene. A rather extreme case is that of the Alpine grasshopper, *Stenobothrus cotticus*, which lives in two high-mountain areas situated quite far from each other: one in the French Alps and one in the Rila Mountains in Bulgaria (Berger et al., 2010). The straight-line distance between these two refugia is more than 1300 km. Only a few populations of this species live in the two places, and the species is considered to be in danger of extinction by the International Union for Conservation of Nature (IUCN). This grasshopper does not seem to be happy about the interglacial period at all and surely longs for glacial climates, in which colder temperatures would make it possible for high-mountain habitats to move downhill and the distribution areas of cold-climate species to expand and be joined together. The huge gap in the present-day distribution area of the grasshopper has been considered evidence that, during the last glaciation, it roamed freely throughout the Southern European lowlands.

Another possible approach to the study of refugia is niche modeling. This method is based on the quantification of the main environmental variables that condition the life of a given species (i.e., the niche of this

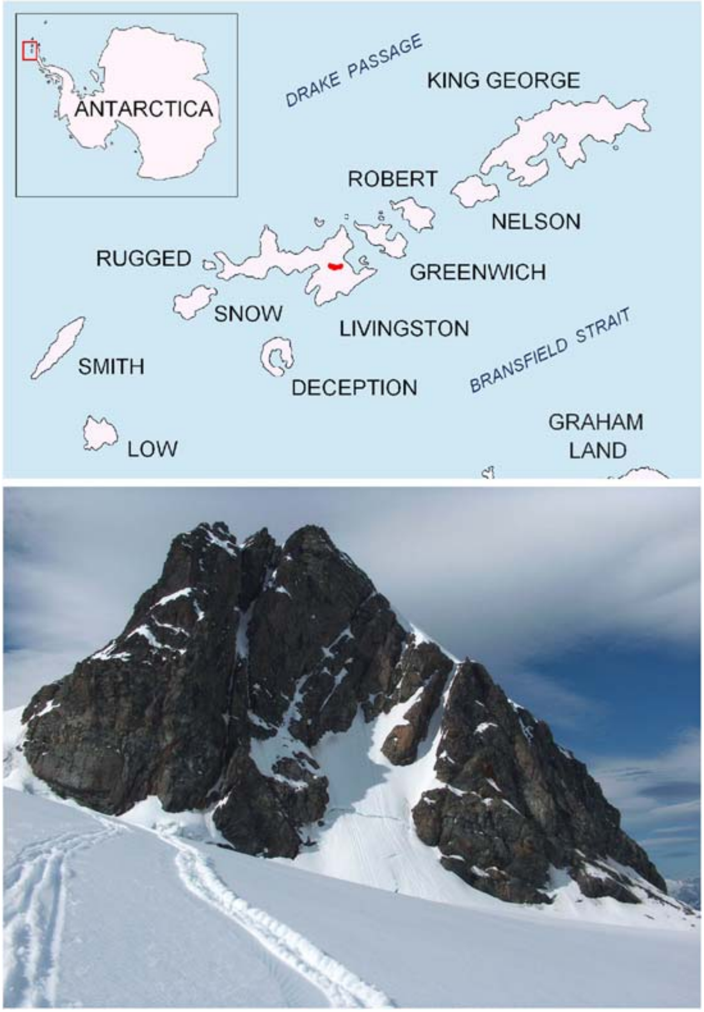


Figure 2.12 Example of a present-day nunatak. The Atanasoff Nunatak (below), on Livingston Island, Antarctica (above). The location is marked by a red spot on the map. *Photo by Lyubomir Ivanov, used under the Creative Commons license (es.wikipedia.org).*

species), in order to extrapolate this information to the past and to obtain the potential distribution of the species during each time period with known environmental conditions. To illustrate this approach, we use the example of the Asia Minor ground squirrel (*Spermophilus xanthoprymnus*), another cold-loving species with well-known temperature and precipitation preferences. During the last interglacial maximum (approximately

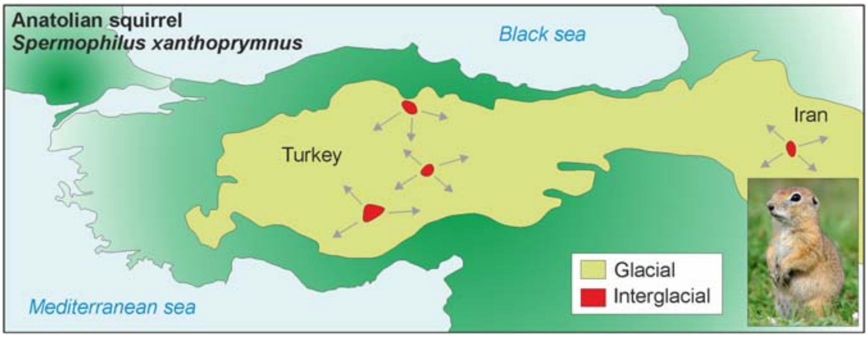


Figure 2.13 Map of the Anatolian Peninsula showing the distribution of the potential niche of the Asia Minor ground squirrel (*Spermophilus xanthoprymnus*) during the last interglacial maximum (approximately 120 ka BP) in red and the LGM (approximately 21 ka BP) in yellow. *LGM*, Last Glacial Maximum. *Modified and redrawn from Gür (2013)*.

120 ka BP; Fig. 1.6), the potential niche of this species was limited to some small patches in the center of Turkey and in northern Iran (Fig. 2.13). However, during the LGM (approximately 21 ka BP), favorable conditions prevailed over a much larger area of the Anatolian Peninsula, permitting the geographical expansion of the species (Gür, 2013). In the current Holocene interglacial, it is in recession again, although not as endangered as the abovementioned alpine grasshopper.

A third way to identify refugia and microrefugia is related to the genetic variability of populations of a given species. It is assumed that genetic variability increases with the time during which a population or populations of the species remain permanently in a given place (refugium). Contrarily, populations that only recently colonized an area represent only a sample of the genetic possibilities of the species, so their genetic variability is lower (Hewitt, 2000). This is a manifestation of the founder effect, which will be explained in Section 3.1.1. Therefore the study of the genome in current populations of the species can provide us with information on its refugia during periods with unfavorable environmental conditions, either glacial or interglacial phases. This idea is at the heart of phylogeography, which we will examine in detail in the next chapter. For now, one example in relation to interglacial refugia will suffice. The mountain bumblebee, *Bombus monticola*, is a species adapted to cold climates that currently takes refuge from the interglacial heat of the Holocene in mountain areas of northern and southern Europe (Scandinavia, British Isles and the Iberian, Italian, and Balkan Peninsulas). Although it is able to live at different elevations (even at sea level in Northern Europe due to the colder climate), the highest genetic variability of this species is reported in high-mountain areas, where some entomologists have described three different species, one of them with several subspecies, that are limited to the highest parts of mountain ranges. This phenomenon has been interpreted as evidence for a decrease in the distribution area of this bumblebee caused by migration toward high-mountain areas due to the temperature increase that has taken place since the LGM (Martinet et al., 2018). This study could be combined with niche modeling to simulate the extension of the distribution area of the species during the LGM, as already done for several species of the same genus, which demonstrate potentially widespread distributions during glaciations and significant postglacial reductions.

The existence of refugia, however, does not seem so evident in other parts of the planet. A good example can be found in the Neotropics, specifically in the mighty Amazon basin, where the huge extensions of rainforests require a rainy climate to develop. The first paleoclimatic studies indicated that most of this region was significantly drier during the LGM and that the landscape mainly included deserts and savannas instead of forests (Damuth and Fairbridge, 1970). This led to the following question: where did today's rainforests come from? Initial theories claimed that they were fragmented in refugia with a favorable climate, which triggered a massive search for such refugia (Prance, 1982). The first attempts aimed to identify areas with higher biodiversity and endemism, based on the assumption that the alleged climatic stability would have favored the survival of a larger number of species than that in dry or desert areas. Another hypothesis was that regions with more rainfall today could have served as glacial refugia for forests since a basin-wide, homogeneous decrease in precipitation would have had a diminished effect in more humid areas. By combining these two patterns, a series of patches was identified as potential glacial refugia of the Amazonian rainforests (Whitmore and Prance, 1987) (Fig. 2.14). The Neotropical rainforests are, then, supposed to have expanded from these patches during the Late Glacial and the Holocene until they reached their current configuration. Problems started to arise when some paleoecological records, particularly pollen, revealed the presence of rainforests during the LGM (Colinvaux et al., 1996). These findings opened up a new wave of ideas suggesting that the Amazonian rainforests were not fragmented during the LGM but formed a continuous cover. Supporters of this idea claim that the climate was not dry but cold (although not as cold as in extratropical areas), which

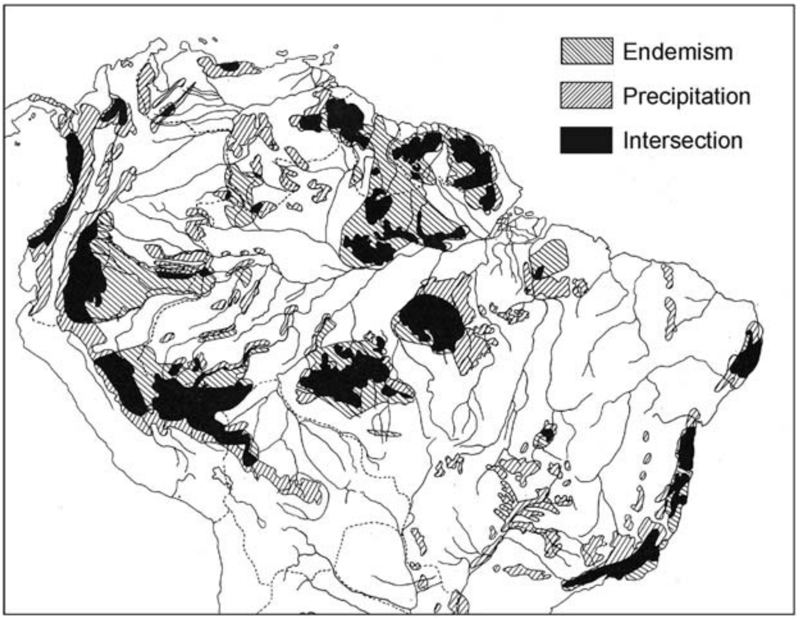


Figure 2.14 Map of tropical South America showing the areas with the highest plant, butterfly, and bird endemism, areas with the most rainfall, and the intersections of these areas. This approach was used to define possible glacial refugia of rainforests during the LGM. *LGM*, Last Glacial Maximum. *Modified from Whitmore and Prance (1987).*

resulted in the descent of species from the surrounding mountains and the interweaving of lowland and mountain species (Colinvaux et al., 2000). The debate is still ongoing, and studies defending one or the other of the two views are frequently published. In Section 3.2, we will further analyze this case by reason of its evolutionary consequences, especially as far as the origin of today's tropical biodiversity is concerned.

Altitudinal migrations occurred repeatedly during the climatic cycles of the Pleistocene, especially due to temperature changes. They took place in both temperate and intertropical regions, the latter referring to the zone situated between the Tropic of Cancer and the Tropic of Capricorn. There was no escape from the effects of glacial—interglacial oscillations. A good example, also related to the previous Amazonian case, can be found in the northern Andes. The recognized Dutch palynologist Thomas Van der Hammen (1974) demonstrated that not only species but also entire altitudinal ecological belts suffered from vertical shifts of up to 1000 m or more (Fig. 2.15) as a result of global temperature changes, which in this region could have

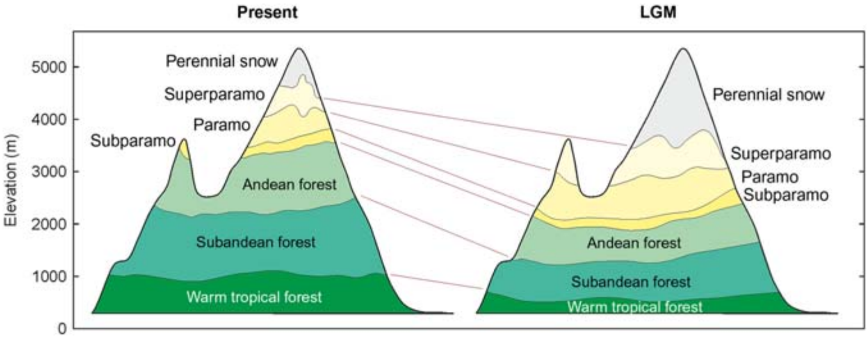


Figure 2.15 Comparison between current and LGM positions of altitudinal belts of the tropical Andes of Colombia. *LGM*, Last Glacial Maximum. *Modified and redrawn from Van der Hammen (1974).*

included declines of 8°C with respect to present temperatures, on average. This temperature decrease was beyond the tolerance range of several Andean species that migrated in search of their niche that shifted downhill. We can imagine that in response to more than 40 glacial—interglacial episodes that occurred during the Pleistocene (Section 1.2.1), mountain species had to continuously move up and down, which also had evolutionary consequences (see next chapter). A large amount of evidence shows that this example can be generalized to every mountain range on the planet, and it also supports the previous observations of mountain bumblebees, which are currently restricted to higher elevations but were more widespread during glacial times (Martinet et al., 2018).

When temperature changes do not reach the magnitude of those during a glaciation, only the more sensitive species respond, while the others remain apparently unaffected. The tropical Andes of Venezuela provide us with an example of this situation. In Section 1.2.5, we saw that deglaciation after the LGM did not occur as a monotonous temperature increase but included several oscillations of colder (stadial) and warmer (interstadial) phases. The most intensive stadial phase, the YD, took place between approximately 13 and 11.7 ka BP, that is, right before the Holocene (Fig. 1.12). In the northern Andes, YD temperatures dropped approximately 2°C—3°C below current values, which made some species migrate downward, while others remained unaffected (Rull et al., 2010). One of the most sensitive species turned out to be *Polylepis sericea*, which is locally called coloradito. Its upper distribution limit shifted approximately 400 m below its actual distribution, while other eurythermic trees, such as the alder (*Alnus* ssp.), carried on practically unaltered. The alder is precisely one of the Andean trees that seemed to be least affected by glaciations during the Pleistocene (Fig. 2.7). At the end of the cold YD, when the temperature began to increase to Holocene values, the coloradito ascended the slopes again until it reached its earlier position and went even farther until it reached its present-day position (Fig. 2.16). This example corroborates once more the idiosyncratic responses of species to climatic changes, and it also illustrates what we call a past analog. This term refers to a phenomenon that took place in the past and provides solid empirical evidence to forecast the future. In this case the warming that occurred after the temperature minimum of the YD was very similar—in terms of both rate and magnitude—to the GW that has been predicted for the 21st century (Cole, 2009). This is why we consider the YD−Holocene transition as a proper past analog of the current GW. Based on this analog, we can expect the Andean populations of coloradito to ascend approximately 400 m during this century, if temperature

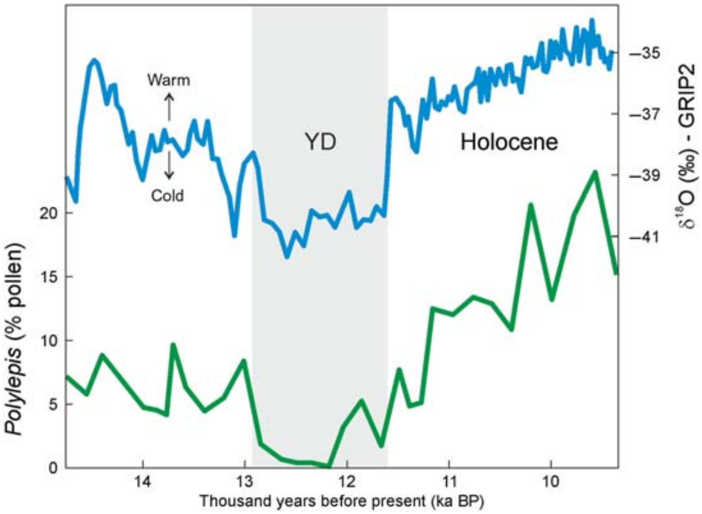


Figure 2.16 Temperature changes and the response of *Polylepis sericea* in the tropical Andes of Venezuela. Temperature changes are expressed in terms of the oxygen isotope curve (blue) of the GRIP2 ice core of Greenland (Fig. 1.8). *Polylepis* abundance (green) is expressed in terms of pollen percentage in a high-mountain lake core. The YD stadial is highlighted by a gray color. The decrease in *Polylepis* pollen percentage indicates a downward shift of its populations until it disappears from the sampling area, while an increase indicates its return to that place. *Polylepis* pollen is not easily transported by wind, and it tends to deposit in situ. Therefore its quantity is proportional to its abundance in the surroundings of the sampling point. *YD*, Younger Dryas. *Modified and redrawn from Rull et al. (2010, 2015).*

prognoses prove correct. The alder, on the other hand, is unlikely to exhibit important changes (Rull et al., 2015).

There is still another migratory process that we have not examined in detail, one that is due to sea level fall during glacial phases, which may result in the complete exposure of continental shelves (Section 1.2.4), in turn, connecting islands and continents and thus creating new migration pathways for terrestrial species. We use the example of Sundaland, which as mentioned in the first chapter, connected the southeastern Asian continent, particularly the Indochinese Peninsula, to the Indonesian islands Sumatra, Java, and Borneo (Fig. 2.17). Evidence based on paleofauna (i.e., animal fossils) suggests that fauna of the Indonesian islands was autochthonous from the beginning of the Pleistocene (approximately 2.6 Ma) until at least 1.5 Ma (Van den Berg et al., 2001). Interestingly, this fauna was lacking in mammals. Although there had been several glaciations before

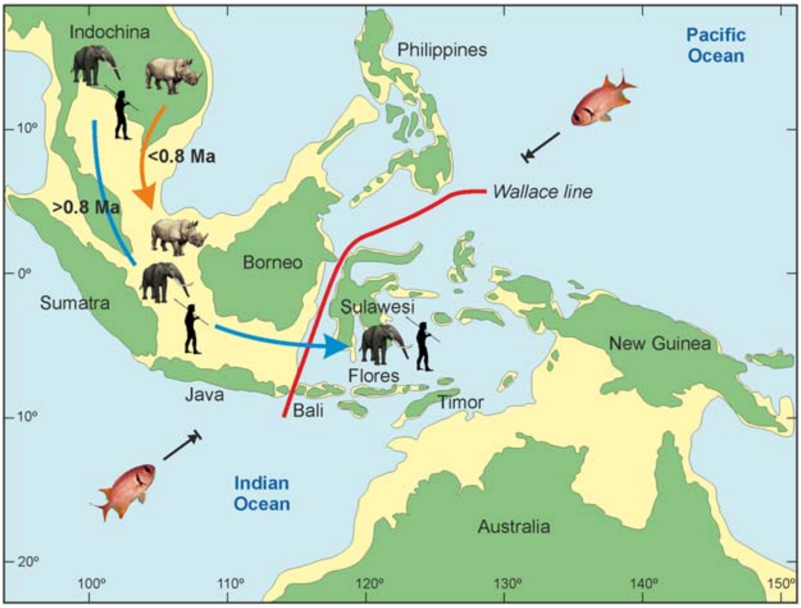


Figure 2.17 Map of Indonesia and part of Australasia, with the current coastline shown in green and the continental shelf that was exposed during the LGM shown in yellow. The blue arrow marks the first faunal migrations (Elephantidae and hominids) that took place when the sea level fall was insufficient to completely connect the continent to the islands (> 0.8 Ma). Subsequent migrations (<0.8 Ma; represented by a rhinoceros) are marked by an orange arrow. *Myripristis* (soldierfish) is also represented because Indonesia acted as a migration barrier for this species during the LGM. *Based on original data from Van den Berg et a. (2001) and Craig et al. (2007).*

1.5 Ma, the corresponding sea level fall had been insufficient to connect the islands to the continent. The first emigrants from the Asian continent were mammals: some species of the Elephantidae family, hippopotamuses, and deer that arrived by the end of the Early Pleistocene, between 1.5 and 0.8 Ma. At this time the islands were not completely connected to the continent, but the presence of this continental fauna proves that migration was possible.

The complete connection started to develop at the end of the Early Pleistocene, approximately 800 ka BP, when the periodicity of glacial—interglacial cycles changed from 41 to 100 ka (Fig. 1.4), glaciations became more intense, and the sea level dropped 120 m or more below current levels (Van den Berg et al., 2001). Since that point, fauna have been able to colonize Indonesia during each of the eight ensuing glaciations. This is how pangolins (*Manis*), otters (*Lutrogale*), elephants (*Elephas*), rhinoceroses (*Rhinoceros*), hippopotamuses (*Hexaprotodon*), deer (*Rusa*), pigs (*Sus*), bears (*Ursus*), bovids (*Capricornis*, *Bibos*), macaques (*Macaca*), orangutans (*Pongo*), porcupines (*Hystrix*), slow lorises (*Nycticebus*), surilis (*Presbytis*), and many others, including *Homo erectus* (Chapter 5), landed there. *H. erectus* possibly arrived by 900 ka ago, while our species, *Homo sapiens*, walked the same path during the last glaciation, between 125 and 60 ka BP. Paleontological studies of islands that could not possibly be connected via shelves, such as Sulawesi, Bali, and Flores (Fig. 2.16), showed that the Asian continental fauna crossed even the so-called Wallace Line, a classic biogeographical boundary line that separates the typical Asian biota from the biota of Australasian origin (i.e., that of Australia and New Guinea). A possible explanation for this fact is that, during low-sea-level periods, even if the shelves could not be connected because of a deep oceanic trench, the distance between the coastlines was sufficiently short for some species to cross by swimming. For example, today's elephants have proved to be able to swim distances up to 50 km (Johnson, 1978), which is approximately the distance that existed between the coasts of Borneo and Sulawesi during a glaciation phase with very low sea levels. It is still unclear, though, what motivated the Pleistocene elephants to venture to cross the Wallace Line (unknowingly, of course), but they certainly did. The long droughts during glaciations might have been among the possible catalysts of emigration. *H. erectus* (Section 5.1.2) also crossed the Wallace Line, as proven by findings of artifacts made by hominids on the island of Flores, where a new endemic species (*Homo floresiensis*) emerged (Section 5.1.2). These tools were probably used for hunting, since they were found together with fossils of elephants of the *Stegodon* genus (Van den Berg et al., 2001).

The situation for marine species was quite the opposite, since lands that emerged during glaciations represented a migration barrier that disappeared only during interglacial periods, when sea levels rose. The blotcheye soldierfish (*Myripristis berndti*), for instance, is widely distributed today in the tropical zones of the Indian and Pacific Oceans, including near the Indonesian archipelago and the Australasian islands (Fig. 2.17). It lives at depths between 10 and 50 m around coral reefs. A study on the genetic variability of this fish revealed that, during the LGM, sea level fall converted the region of Indonesia and Australia into the main barrier that separated *Myripristis* populations of the Pacific from those of the Indian Ocean (Craig et al., 2007). The latter, furthermore, were significantly reduced in size because of the lack of a continental shelf and the consequent shortfall of coral reefs. It is possible that the glacial refugia of these fish were situated in the corals that lived on the upper part of the continental slope, which is currently more than 120 m deep. The species would have expanded from these refugia during the Late Glacial and the Holocene until reaching its present-day distribution.

2.2.3 Extinction

Compared with other geologic periods, there were not quite as much extinctions in the Quaternary. The impression that many people have about the disappearance of a large number of species during the Quaternary is largely influenced by one relatively recent and rather spectacular extinction event. We are referring to the extinction of late Quaternary megafauna at the end of the Pleistocene, between 50 and 10 ka BP, or in other words, between the end of the last glaciation and the transition to the Holocene (Koch and Barnosky, 2006). In this event, more than half of the genera of megamammals, defined as mammalian genera whose species weighed over 45 kg in their adult stage, disappeared across continents in a heterogeneous fashion (Table 2.1). Indeed, the extinction did not happen synchronously all over the planet but occurred at different times on different continents. Megafaunal extinctions had a great influence on the composition and functioning of terrestrial ecosystems, in which these animals acted as keystone species (Section 4.1.1) due to their strong influences on vegetation, trophic interactions, ecosystem function, and global biogeochemical cycles, the last

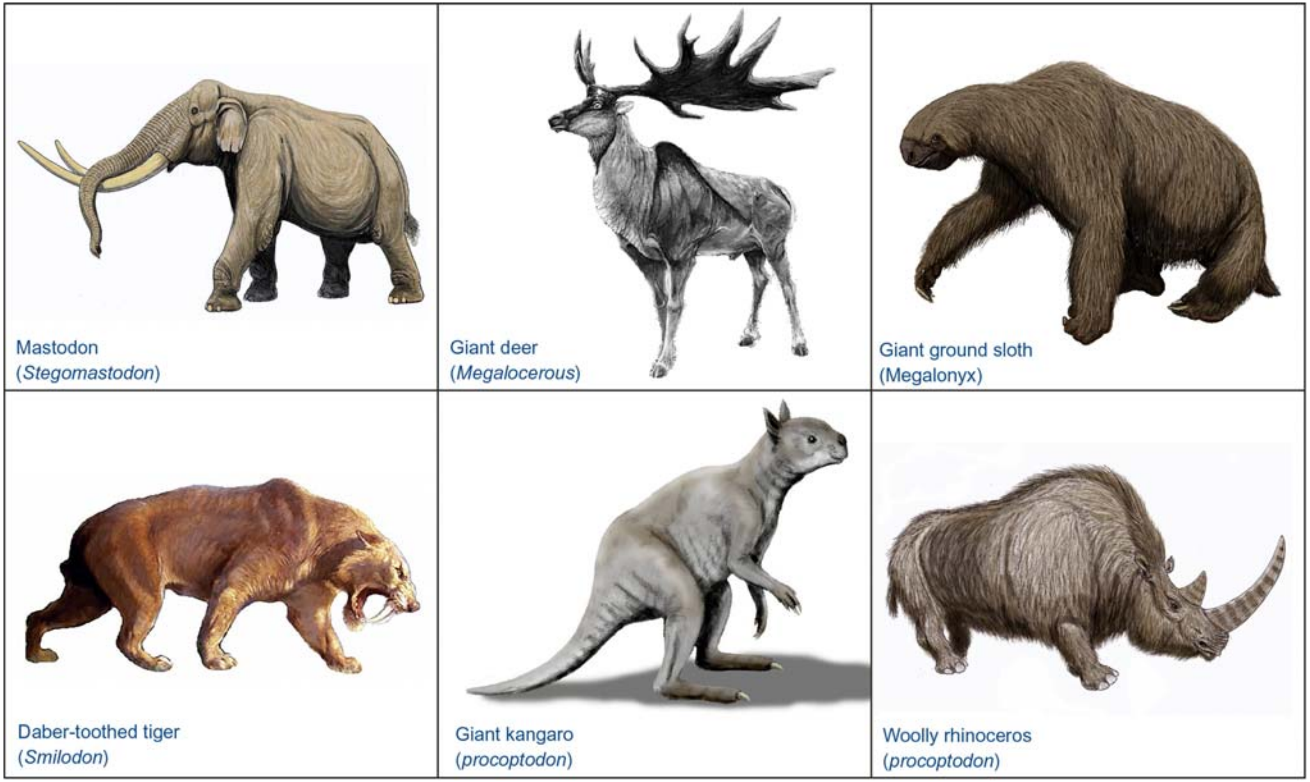
Table 2.1 Megamammal extinction and survival, at the genus level, during the late Quaternary.

Continent	Total	Extinct	Survivors	% Extinction	% Survival
Africa	48	10	38	20.8	79.2
Australia	16	14	2	87.5	12.5
Eurasia	26	9	17	34.6	65.4
North America	47	34	13	72.3	27.7
South America	60	50	10	83.3	16.7
Total	197	117	80	59.4	40.6

Source: Based on data Koch et al. (2006).

of which was driven by a significant reduction in methane emissions (Smith et al., 2016). It has been proposed that the niche left behind by these animals was occupied by the humans of those times who, logically, modified it and adapted it to their needs.

The continents that most suffered from the megafaunal extinction were Australia and South America, where more than 80% of large mammals went extinct, followed by North America, with approximately 70% (Table 2.1). In Eurasia the number amounted to approximately 35%, and Africa had the lowest extinction rate (approximately 21%), as large mammals are still abundant in the extensive African savannas in terms of both diversity and population density. Emblematic examples of this extinction event are the mammoth (*Mammuthus*), mastodon (*Stegomastodon*), woolly rhinoceros (*Coelodonta*), giant deer (*Megaloceros*), giant kangaroo (*Procoptodon*), giant ground sloth (*Megatherium*), and saber-toothed tiger (*Smilodon*), among others (Fig. 2.18). The cause of these extinctions is still under debate, and no general agreement has been reached. Two of the suggested hypotheses should be mentioned here because they are at the center of the controversy. The first one posits that a climatic change that the large fauna could not tolerate was the cause of the extinction, while the second one points to mass hunting by humans as the culprit. According to the climate shift hypothesis, it was—interestingly—not the cold but the warm temperatures that wiped out this fauna. For example, according to a very recent study conducted in Eurasia and North America, there is a good correlation between extinction phases and Dansgaard−Oeschger events (Cooper et al., 2015), which are warmer intervals (interstadials) that last for a few millennia (Section 1.2.3; Fig. 1.8). This, together with the absence of extinctions during the LGM (the coldest period before the deglaciation) and the return of extinction events after it, during the initial Holocene warming,



Mastodon
(*Stegomastodon*)

Giant deer
(*Megalocerous*)

Giant ground sloth
(Megalonyx)

Daber-toothed tiger
(*Smilodon*)

Giant kangaro
(*procoptodon*)

Woolly rhinoceros
(*procoptodon*)

Figure 2.18 Reproductions of megamammals that went extinct at the end of the Pleistocene. *All images are used under the Wikimedia Commons license, from several Wikipedia sites.*

supports the hypothesis that warm weather was decisive in the extinction of the Pleistocene megafauna. Climatic changes might have exerted a direct influence on the living conditions of animals and their populations, or the effect might have occurred indirectly through the alteration of vegetation.

The defenders of the anthropogenic hypothesis argue that the Pleistocene fauna endured at least eight similar glacial–interglacial transitions without similar extinction events. They also stress that the main differences between the last deglaciation and the earlier ones were the presence of *H. sapiens* on all continents and the remarkable development of its populations and hunting technology. Not surprisingly, this hypothesis is also called the overkill hypothesis, which was first proposed by the well-known American geoscientist Paul Martin (1973) and has been supported by the chronological coincidence of megafaunal extinction and the arrival of humans (Surovell et al., 2016). In addition to overhunting, *H. sapiens* might have interfered with the megafauna's niche by destroying their habitats, mostly due to the use of fire—humans of this period were nomadic hunter-gatherers and did not yet use agriculture (Section 5.2)—and by the introduction of exotic, competing species, as has occurred, for example, on ocean islands during the last 1000–2000 years. A challenge to the anthropogenic hypothesis is the survival of more mammal species in Eurasia and Africa (Table 2.1) despite their prolonged coexistence with humans. This is especially relevant for the African continent, which was the cradle of humans (Chapter 5) but on which megafaunal extinctions were minimal (21%). A crucial piece of empirical evidence commonly used to support the anthropogenic hypothesis is provided by so-called kill sites. These are fossil deposits of remains of megamammals and other vertebrates together with human-made spearheads. Nevertheless, according to the proponents of the climatic hypothesis, the abundance and spatial distribution of the sites discovered to date seem not to be sufficient to justify a global extinction phenomenon. As usual, there is a good chance that the joint effects of climate and humans together were mostly responsible for the megafaunal extinction. A thorough review of global megafaunal extinctions and their possible causes can be found in Koch and Barnosky (2006).

Regarding plants, only one global extinction has been documented during the Quaternary. It is *Picea critchfieldii*, a spruce that was rather widespread in eastern North America during the LGM and went extinct after the deglaciation (Jackson and Weng, 1999). Once again, a warm climate is the prime suspect. Other extinctions occurred at a regional or continental scale. A classic example of this can be found in Europe, where several tree genera disappeared during the Pleistocene that are still present on other continents (Magri et al., 2017). We have discussed how certain European tree genera survived glacial–interglacial upheavals in refugia of the southern peninsulas (Iberia, Italy, and Greece). Others, however, could not endure the Quaternary climatic shifts, not even in refugia. Some examples are the swamp cypress (*Taxodium*), the Japanese umbrella pine (*Sciadopitys*), the gutta-percha tree (*Eucommia*), and the Persian ironwood (*Parrotia*), which still live on other continents, especially Asia and North America (Fig. 2.19). These trees went extinct at different times between the Early Pleistocene (approximately 1.5 Ma) and the end of this epoch. Although it would be hard to attribute all of these extinctions to a single environmental factor, almost all of them are trees of humid climates that today live in mountain forests with high rainfall or in lowland swamps. This fact suggests that the dry climate during glaciations might have been mostly responsible for their disappearance in Europe (Magri et al., 2017).

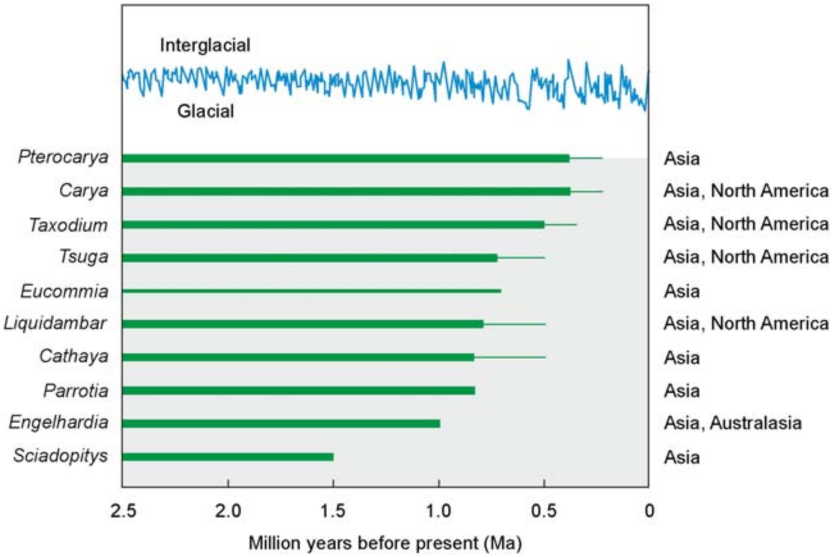


Figure 2.19 Principal genera of trees that went extinct in Europe during the Pleistocene. Green bars show the time period during which these genera lived in European forests. Continents where these species still exist are shown on the right. *Based on original data from Magri et al. (2017).*

We cannot find traces of extinctions, at either a global or a regional scale, in tropical or subtropical areas. The assumption that glaciations caused global extinction of several plants originates from the still existing, unfortunate trend in the natural sciences to extrapolate processes or findings from temperate zones—especially Europe and North America—to the whole planet. The truth is that only one global-scale extinction has been documented to date and that all others were either local, regional, or continental.

2.2.4 The biomes

As biomes are defined on the basis of their climate and their species composition, it is reasonable to infer that the spatial reorganization of climates and species during the Quaternary resulted in significant changes in the biomes themselves. By definition, biomes are biogeographical regions of the planet with similar climates and a characteristically adapted biota (Cain et al., 2014). A biome consists of a group of characteristic communities and ecosystems and, in the case of terrestrial biomes, is defined by the dominant vegetation and fauna. Several criteria can be used to divide Earth into land biomes—with practically the same outcome (Fig. 2.20). These classifications are based on potential vegetation, which is deduced from the climatic and soil characteristics of each region, since a significant part of these biomes is now altered by human activity and infrastructure.

Fig. 2.21 shows some representative reconstructions of the biome configuration during the LGM. We focus on Europe and North America because this is where most information is available, and we include Africa as an example of a continent that only indirectly suffered from the effects of extensive glaciations. As we can see, most of Central Europe, today part of the temperate deciduous forest biome, belonged to the tundra and cold steppe biome, while the south, today a domain of the Mediterranean biome, was covered by dry and cold steppe occasionally interrupted by the already mentioned temperate forest refugia (Section 2.2.1). In North America the situation was similar, but the biomes were more fragmented due to large mountain ranges that run north to south. Today's tundra and other typical forests were reduced and limited to the southern part of the United States, while Mexico and Central America were covered by savannas instead of today's mountain forests and tropical rainforests. The tropical rainforests were narrowed down to the current area of Panamá. In Africa, deserts were even more extensive and drier than they are today,

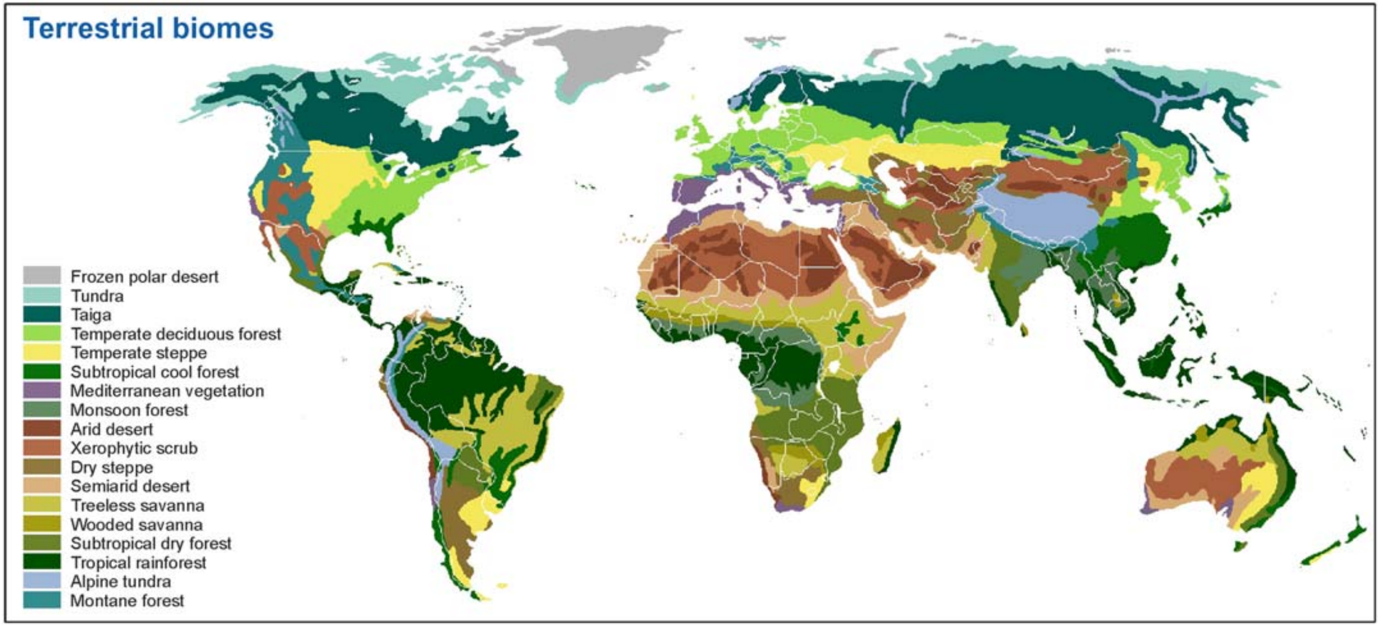


Figure 2.20 Land biomes classified according to vegetation type. *Map from Ville Koistinen, used under the Wikimedia Commons license (en.wikipedia.org).*

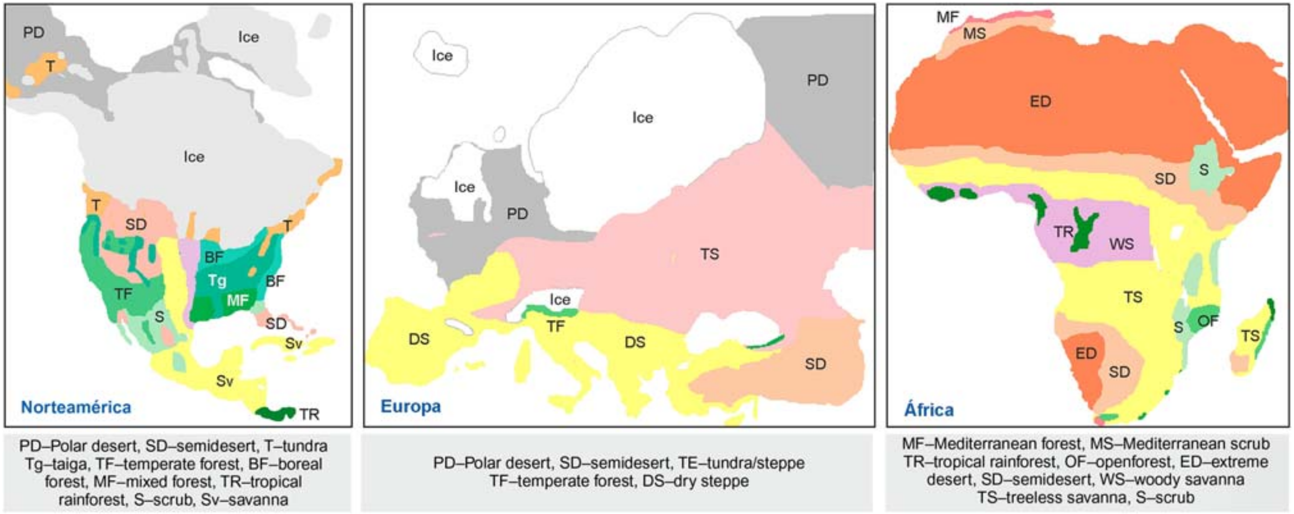


Figure 2.21 Reconstruction of LGM biomes in North America, Europe, and Africa based on paleoecological evidence. The coastline of these continents, and of all the others, was modified by the sea level fall (approximately 120 m) that exposed the continental shelf (Section 1.2.2, Fig. 1.7). *LGM*, Last Glacial Maximum. *Redrawn and modified from maps compiled by Jonathan Adams (publicly available at https://www.esd.ornl.gov/projects/gen/nerc.html#maps).*

and the currently vast tropical rainforests were fragmented in refugia. In the north, there were also refugia of Mediterranean-type vegetation, which colonized Europe at the end of the glaciation.

2.3 Synthesis: more complexity, idiosyncrasy, and geographical shifts

We must touch upon complexity again but, in this case, complexity amplified by the great variety of responses that different species displayed to the already complex system of climatic changes. The idiosyncrasy of species is an important lesson of this chapter; each species responded to climatic changes of the Quaternary in its own way, according to the configuration of its particular niche. In addition to the alteration of habitat, we must also take into account the indirect influence of climatic oscillations on species via the alteration of their ecological relations with competitors, predators, parasites, and pollinators, among others. Another conclusion to draw is that the most common of all possible responses to Quaternary climatic changes was the modification of species' distribution areas by means of expansion, contraction, migration, fragmentation, or a combination of these. There is also evidence of species that remained in the same place by acclimation or adaption or in refugia and microrefugia. Despite the mentioned cases of extinction, biogeographical reorganization was the dominant strategy (Willis and Bhagwat, 2009). Quaternary extinctions are closer to legend than to reality: there were extinctions, and they were spectacular if we think about the great Pleistocene mammals that disappeared, but in terms of biodiversity, they have not been transcendent, at least not to date.

References

Ashcroft, M.B., 2010. Identifying refugia from climate change. J. Biogeogr. 37, 1407–1413.

Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B., et al., 2010. Has the Earth's sixth mass extinction already arrived? Nature 471, 51–57.

Becklin, K.M., Anderson, J.T., Gerhard, L.M., Wadgymar, S.M., Wessinger, C.A., Ward, J.K., 2016. Examining plant physiological responses to climate change through an evolutionary lens. New Phytol. 172, 635–649.

Bennett, K.D., 1997. Evolution and Ecology: The Pace of Life. Cambridge University Press, Cambridge.

Berger, D., Chovanov, D.P., Mayer, F., 2010. Interglacial refugia and range shifts of the alpine grasshopper *Stenobothrus cotticus* (Orthoptera: Acrididae: Gomphocerinae). Org. Diversity Evol. 10, 123–133.

Cain, M., Bowman, W., Hacker, S., 2014. Ecology. Sinauer, Sunderland, MA.

Chase, J.M., Leibold, M.A., 2003. Ecological Niches: Linking Classical and Contemporary Approaches. University of Chicago Press, Chicago, IL.

Clark, J.S., Fastie, C., Hurt, G., Jackson, S.T., Johnson, C., King, C., et al., 1998. Reid's Paradox of rapid plant migration. BioScience 48, 13–24.

Cole, K., 2009. Vegetation response to early Holocene warming as an analog for current and future changes. Conserv. Biol. 24, 29–37.

Colinvaux, P.A., De Oliveira, P.E., Moreno, J.E., Miller, M.C., Bush, M.B., 1996. A long pollen record from lowland Amazonia: forest and cooling in glacial times. Science 274, 85–88.

Colinvaux, P.A., De Oliveira, P.E., Bush, M.B., 2000. Amazon and Neotropical plant communities: the failure of the aridity and refuge hypothesis. Quat. Sci. Rev. 19, 141–169.

Cooper, A., Turney, C., Hughen, K.A., Brook, B.W., McDonald, H.G., Bradshaw, C.J. A., et al., 2015. Abrupt warming events drove Late Pleistocene Holarctic megafaunal turnover. Science 349, 602–606.

Craig, M.T., Eble, J.A., Bowen, B.W., Robertson, D.R., 2007. High genetic connectivity across the Indian and Pacific Oceans in the reef fish *Myripristis berndti* (Holocentridae). Mar. Ecol. Prog. Ser. 334, 245–254.

Damuth, J.E., Fairbridge, R.W., 1970. Equatorial Atlantic deep-sea arkosic sands and ice-age aridity in tropical South America. Geol. Soc. Am. Bull. 81, 189–206.

Davis, M.B., 1984. Climatic instability, time lags, and community disequilibrium. In: Diamond, J., Case, T.J. (Eds.), Community Ecology. Harper and Row, New York, pp. 269–284.

Dirnböck, T., Essl, F., Rabitsh, W., 2011. Disproportional risk for habitat loss of high-altitude endemic species under climate change. Global Change Biol. 17, 990–996.

Gunderson, C.A., O'Hara, K.H., Campton, C.M., Walker, A.V., Edwards, N.T., 2010. Thermal plasticity of photosynthesis: the role of acclimation in forest responses to a warming climate. Global Change Biol. 16, 2271–2286.

Gür, H., 2013. The effects of the Late Quaternary glacial-interglacial cycles on Anatolian ground squirrels: range expansion during the glacial periods? Biol. J. Linn. Soc. 109, 19–32.

Hewitt, G., 1999. Post-glacial recolonization of European biota. Biol. J. Linn. Soc. 68, 87–112.

Hewitt, G., 2000. The genetic legacy of the Quaternary ice ages. Nature 405, 907–913.

Hofgaard, A., Kullman, L., Alexandersson, H., 1991. Response of old-growth montane *Picea abies* (L.) Karst. forest to climatic variability in northern Sweden. New Phytol. 119, 585–594.

Hol, W.H.G., Meyer, K.M., Van der Utten, W.H., 2011. Idiosyncrasy in ecology – what is in a word? Front. Ecol. Environ. 9, 431–433.

Hooghiemstra, H., 1984. Vegetation and climatic history of the high plain of Bogotá, Colombia: a continuous record of the last 3.5 million years. Diss. Bot. 79, 1–368.

Huntley, B., Birks, H.J.B., 1983. An Atlas of Past and Present Pollen Maps for Europe: 0-13,000 Years Ago. Cambridge University Press, Cambridge.

Hutchinson, G.E., 1957. Concluding remarks. Cold Spring Harbor Symp. Quant. Biol. 22, 415–427.

Jackson, S.T., Weng, C., 1999. Late Quaternary extinction of a tree species in eastern North America. Proc. Natl. Acad. Sci. U.S.A. 96, 13847–13852.

Jackson, S.T., Betancourt, J.L., Lyford, M.E., Gray, S.T., Rylander, K.A., 2005. A 40,000-year woodrat-midden record of vegetational and biogeographical dynamics in northeastern USA. J. Biogeogr. 32, 1085−1106.

Johnson, D.L., 1978. The origin of island mammoths and the Quaternary land bridge history of the Northern Channel Islands, California. Quat. Res. 10, 204−225.

Koch, P.L., Barnosky, A.D., 2006. Late Quaternary extinctions: state of the debate. Annu. Rev. Ecol., Evol. Syst. 37, 215−250.

Ladle, R.J., Whittaker, R.J. (Eds.), 2011. Conservation Biogeography. Wiley-Blackwell, Chichester.

Lenoir, J., Gégout, J.C., Marquet, P.A., de Ruffray, P., Brisse, H., 2008. A significant upward shift in plant species optimum elevation during the 20th century. Science 320, 1768−1771.

Magri, D., Vendramin, G.G., Comps, B., Dupanloup, I., Geburek, T., Gömöry, D., et al., 2006. A new scenario for the Quaternary history of European beech populations: palaeobotanical evidence and genetic consequences. New Phytol. 171, 199−221.

Magri, D., Di Rita, F., Aranbarri, J., Fletcher, W., González-Sampériz, P., 2017. Quaternary disappearance of tree taxa from southern Europe: timing and trends. Quat. Sci. Rev. 163, 23−55.

Margalef, R., 1974. Ecología. Omega, Barcelona.

Marinho, R.A., Beserra, B.E., Bezerra-Gusmão, M.A., Porto, V.S., Olinda, R.A., Dos Santos, C.A., 2016. Effects of temperature on the life cycle, expansion, and dispersal of *Aedes aegypti* (Diptera: Culicidae) in three habitats in Paraiba, Brazil. J. Vector Ecol. 41, 1−10.

Martin, P.S., 1973. The discovery of America: the first Americans may have swept the Western Hemisphere and decimated its fauna within 1000 years. Science 179, 969−974.

Martinet, B., Lecocq, T., Brasero, N., Biella, P., Urbanová, K., Valterová, I., et al., 2018. Following the cold: geographical differentiation between interglacial refugia and speciation in the arcto-alpine species complex *Bombus monticola* (Hymenoptera: Apidae). Syst. Entomol. 43, 200−217.

Merilä, J., 2012. Evolution in response to climate change: in pursuit of the missing evidence. BioEssays 34, 811−818.

Nilsson-Örtman, V., Johansson, F., 2017. The rate of seasonal changes in temperature alters acclimation and performance under climate change. Am. Nat. 190, 743−761.

Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421, 37−42.

Pielou, E.C., 1979. Biogeography. John Wiley and Sons, New York.

Prance, G.T. (Ed.), 1982. Biological Diversification in the Tropics. Columbia University Press, New York.

Rull, V., 2009. Microrefugia. J. Biogeogr. 36, 481−484.

Rull, V., Stansell, N.D., Montoya, E., Bezada, M., Abbott, M.B., 2010. Palynological signal of the Younger Dryas in the tropical Venezuelan Andes. Quat. Sci. Rev. 29, 3045−3056.

Rull, V., Vegas-Vilarrúbia, T., Montoya, E., 2015. Neotropical vegetation responses to Younger Dryas climates as analogs for future climatic change scenarios and lessons for conservation. Quat. Sci. Rev. 115, 28−38.

Scheffers, B.R., De Meester, L., Bridge, T.C.L., Hofman, A.A., Pandolfi, J.M., Corlett, R.T., et al., 2016. The broad footprint of climate change from genes to biomes to people. Science 354, aaf7671.

Smith, F.A., Hammond, J.I., Balk, M.A., Elliot, S.M., Lyons, S.K., Pardi, M.I., et al., 2016. Exploring the influence of ancient and historic megaherbivore extirpations on the global methane budget. Proc. Natl. Acad. Sci. U.S.A. 113, 874−879.

Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., et al., 2013. Climate Change 2013: The Physical Science Basis. Cambridge University Press, Cambridge.

Surovell, T.A., Pelton, S.R., Anderson-Sprecher, R., Myers, A.D., 2016. Test of Martin's overkill hypothesis using radiocarbon dates on extinct megafauna. Proc. Natl. Acad. Sci. U.S.A. 113, 886–891.

Traill, L.W., Bradshaw, C.J.A., Brook, B.W., 2007. Minimum viable population size: a meta-analysis of 30 years of published estimates. Biol. Conserv. 139, 159–166.

Tzedakis, P.C., 1993. Long-term tree populations in northwestern Greece through multiple Quaternary climatic cycles. Nature 297, 2044–2047.

Tzedakis, P.C., Hooghiemstra, H., Pälike, H., 2006. The last 1.35 million years at Tenaghi Philippon: revised chronostratigraphy and long-term vegetation trends. Quat. Sci. Rev. 25, 3416–3430.

Van den Berg, G.D., de Vos, J., Sondaar, P.Y., 2001. The late Quaternary palaeogeography of mammal evolution in the Indonesian Archipelago. Palaeogeogr. Palaeoclimatol. Palaeoecol. 171, 385–408.

Van der Hammen, T., 1974. The Pleistocene changes of vegetation and climate in tropical South America. J. Biogeogr. 1, 3–26.

Van der Pijl, L., 1969. Principles of Dispersal in Higher Plants. Springer, Berlin.

Walter, G.H., Hengeveld, R., 2000. The structure of the two ecological paradigms. Acta Biotheor. 48, 15–46.

Whitmore, T.C., Prance, G.T., 1987. Biogeography and Quaternary History in Tropical Latin America. Oxford University Press, New York.

Willis, K.J., Bhagwat, A.A., 2009. Biodiversity and climate change. Science 326, 806–907.

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CHAPTER THREE

Biodiversity: diversification or impoverishment?

Contents

The popular idea that, during the Quaternary, evolution has been insignificant and species have remained practically invariant, in evolutionary terms, is unfounded. The notion that the species that lived at the beginning of this geological period was basically the same as those that live today—disregarding extinctions, of course—is also untenable. A quick look to our own evolution is enough to refute these conceptions. Indeed, *Homo sapiens* is one of the youngest species on Earth, emerging approximately during the penultimate glaciation (Section 5.1.4). As will be discussed in Chapter 5, there existed other species of the genus Homo whose origin dated back to almost the beginning of the Quaternary. If a picture is worth a thousand words, a quick look at Fig. 3.1 is enough to realize that Quaternary evolution is a fact. This phenomenon not only applies to humans but also can be generalized, as will be discussed in this chapter.

The key topic of this chapter is evolution, and the main aim is to give a documented account of the processes that took place during the Quaternary

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Figure 3.1 Reconstruction of a *Homo habilis* female (left) who lived in Africa at the beginning of the Pleistocene, compared to a photo of a contemporary representative of *Homo sapiens* (right), to illustrate evolution during the Quaternary. Images from Wikipedia.org.

and that gave rise to the current biodiversity and its geographical distribution. An underlying question of this subject is whether the Quaternary has been an epoch of diversification or of impoverishment, in other words, whether biodiversity has increased or decreased. As in many other cases of scientific research, both views exist, and we shall discuss the arguments and empirical evidence for both of them. But first, we must provide some terminological and conceptual background together with an introduction to the methodology and types of evidence used in this field, which are quite different from the paleoclimatic and paleoecological evidence seen in earlier chapters. We start with the most important terms and concepts in relation to biodiversity, its evolutionary origins and its geographical distribution around the planet.

3.1 What is biodiversity and how does it originate?

In the broad sense of the term, biodiversity, or biological diversity, can be defined as the variety and variability of life at different levels, from the genetic to the ecological level (Gaston and Spicer, 2004). In a more practical sense, biodiversity is a measure of this variety at a particular moment in time and space. In the context of our study, we can say, for example, that the Mediterranean region is more biodiverse than the Scandinavian region, which means that there are more species of living beings in the Mediterranean than in Scandinavia. The most intuitive—and, indeed, the most commonly used—method of measuring biodiversity is counting the number of species; however, there are also other options that take into account other characteristics (Pielou, 1975). For example, the ecological diversity of a given ecosystem takes into consideration the number of species and their relative abundances, making it an indicator of the ecological complexity and functionality of an ecosystem. Two ecosystems with the same number of species differ in ecological functioning if, in one of them, there are a few (or only one) dominant species, while in the other one, all species are equally represented. A large number of indexes have been developed to define different concepts of biodiversity (Magurran, 1996), but here, we mostly use the number of species, or species richness, which can be applied to Earth in general or to any of its continents, biomes, ecosystems, regions, or particular sites. In biogeography, biodiversity is also considered in the context of space: α-diversity is the diversity within a given habitat or ecosystem, β-diversity refers to the distribution of diversity between habitats/ecosystems or along environmental gradients, and γ-diversity is the diversity of a large region composed of a number of ecological communities, such as a biome or a continent (Whittaker, 1960; Rosenzweig, 1995). For example, the diversity of a given Mediterranean oak community is an example of α-diversity, the diversity trends of Mediterranean ecosystems along elevational gradients are examples of β-diversity, and the diversity of the whole Mediterranean biome is an example of γ-diversity.

Biodiversity is a function of both ecological and evolutionary factors. In general terms, evolution can be said to produce biodiversity, while ecology is in charge of maintaining it (Moritz, 2002). Evolution produces new species in a more or less continuous manner, but species will persist or not depending on the ecological conditions and relationships that define their coexistence with others. For example, several tree species that compete for water can coexist in a given area or ecosystem only if their niches are sufficiently segregated in terms of this resource. Otherwise, some of these species would either disappear or be forced to migrate in order to survive, which would decrease local biodiversity. In general, biodiversity is the balance between species input and output (Fig. 3.2). The main mechanism of species input is speciation (i.e., the evolutionary process by which new species appear), while outputs are mostly caused by

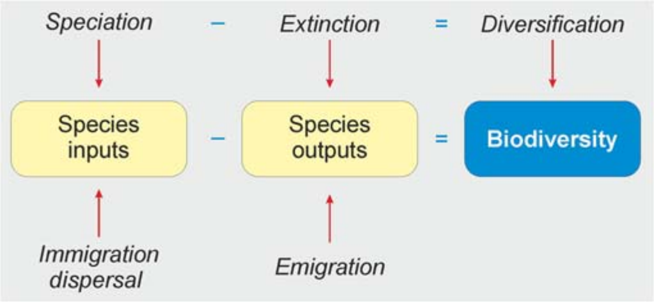

Figure 3.2 Processes that take part in the generation of biodiversity.

extinction. The balance between speciation and extinction is the net increase in the number of species, which is called diversification (Cracraft, 1985). In a given geographical context, new species can also appear by means of immigration or jump dispersal or disappear by emigration. Therefore migration and long-distance dispersal should be added to the biodiversity equation (Fig. 3.2). To gain a better understanding of the process of diversification, we elaborate slightly on the main processes and mechanisms of speciation and extinction.

3.1.1 Speciation

Details of the theory of evolution are beyond the scope of this book; we simply recap that evolution works through natural selection on the genetic variability of species at the population level. In contrast to the popular belief that natural selection acts according to the law of survival of the strongest, in reality, natural selection favors the fittest genotypes, which are the ones that are best adapted to current ecological conditions and are able to transmit this fitness to their offspring. Strictly speaking, we cannot call this theory Darwinism since Charles Darwin (1809—82), who discovered natural selection, did not know that inheritance was transmitted by genes. The existence of genes themselves was only surmised by a contemporary Austrian scientist, Gregor Mendel (1822—84), who called them units of heredity; later, genes received their name from the Danish scientist Wilhelm Johansen, in 1905. Mendel's work was largely ignored by the scientific community at the time; Darwin himself was unaware of Mendel's discoveries. In 1900 the Dutch scientist Hugo de Vries unknowingly repeated Mendel's experiments and obtained the same conclusions regarding hereditary transmission. De Vries discovered Mendel's work after finishing his experiments and gave him the deserved recognition. Today, Mendel is considered the father of modern genetics. Rumor has it that de Vries did not fully understand what he did until reading Mendel's work. The modern evolutionary theory (Mayr, 1996), also called the modern synthesis or neo-Darwinism, which merged Darwin's natural selection with Mendel's genetics, was developed at the beginning of the 20th century. See Kutschera and Niklas (2004) for more details on the origin and developments of the modern evolutionary synthesis.

In this chapter, we focus on the evolutionary origin of species, which as discussed, is the taxonomic unit usually used to define biodiversity. However, we will also consider intraspecific categories with the potential to develop into new species, which are also included within the concept of the Evolutionarily Significant Unit (ESU) (Ryder, 1986; Moritz, 1994). Speciation, or the formation of new species from existing ones, is considered a macroevolutionary phenomenon, whereas evolutionary processes within a given species at the level of subspecies, races, varieties, ecotypes, or populations are usually called microevolutionary processes (Mayr, 1982; Jablonski, 2000). A complete account of what is currently known about speciation processes and mechanisms is provided by Coyne and Orr (2004), from which the following terms and concepts have been derived. Not all speciation processes result in an increase in biological diversity. For example, anagenesis—that is, the gradual evolution of a species into a new one—does not affect diversity since the old species disappears and is replaced by the new one. Speciation by hybridization, which is the formation of fertile hybrids from two different parent species, increases biodiversity only if at least one of the parent species also survives. The type of speciation that most frequently contributes to biodiversity is cladogenesis, when a species splits into two or more new species. Usually, new species emerge from populations of the parent species that, for some reason, become isolated by barriers that impede reproduction (i.e., gene flow) between populations. This eventually leads to the gradual differentiation of these populations into new species until they can no longer reproduce. The mentioned barriers can be physical, such as mountain ranges or oceans; ecological, such as preferences for different habitats or a mismatch in breeding seasons; ethological (i.e., behavioral), such as the lack of mutual attraction; or mechanical, such as the morphological incompatibility of reproductive organs. Even in cases when mating is possible, other mechanisms of reproductive isolation can play a role. This is the case for sterile hybrids, which are able to live a complete life as individuals but are unable to perpetuate their lineage. A well-known example is the mule, which is a sterile hybrid produced by a cross between a mare and a donkey.

There are different types of cladogenetic speciation (Fig. 3.3). In the case of physical or geographical reproductive barriers, allopatric speciation, which has two main types, namely, vicariance and dispersal-mediated speciation, takes place. Vicariance occurs when newly formed reproductive barriers divide the original distribution area of the species into two or more populations, which eventually become as many different species. The Isthmus of Panama provides a classic example of this. Formed at the end of the Pliocene, approximately 3 million years ago (Ma), it connected Central America to South America, creating an insurmountable reproductive barrier for marine species, which have been developing into different species on the two sides of the isthmus ever since (Steeves et al., 2005; Thacker, 2017). In biogeography, species that, due to their recent common origin, are similar both in morphology and in their niche but are separated by physical barriers are called vicariant species (Lomolino et al., 2016). On the

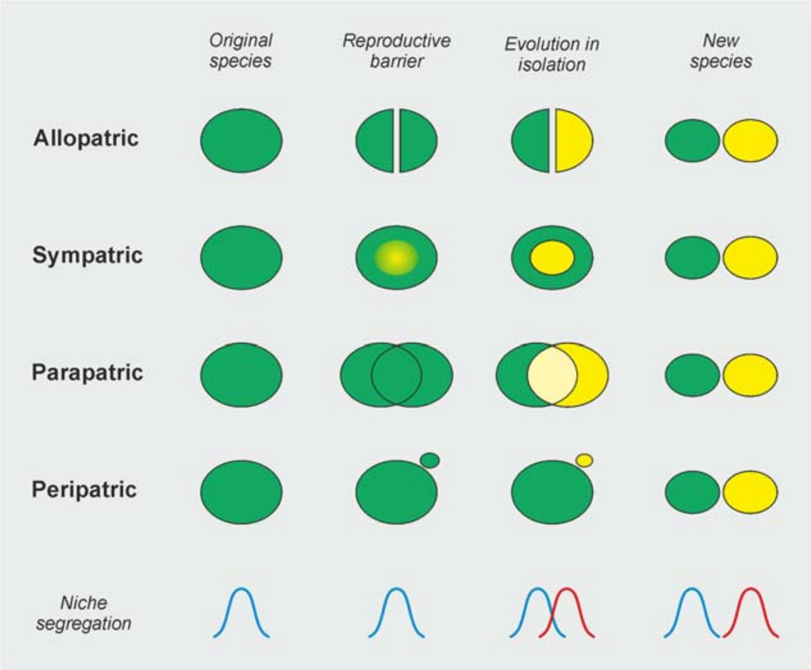

Figure 3.3 Main types of cladogenetic speciation, with the corresponding stages and niche differentiation or segregation (below), based on Fig. 2.1. *Modified from an illustration by Ilmari Karonen, under Creative Commons license (Wikimedia).*

other hand, if the original species is jump-dispersed over an area already fragmented by barriers, the subsequent speciation due to adaption to the new environment is called speciation by dispersal and further allopatry. If the dispersal and subsequent adaption result in different species adapted to a variety of environments, the process is called adaptive radiation, which is a special case of speciation by dispersal. We can find classic examples of adaptive radiation in oceanic archipelagos, where organisms arrive by dispersal and scatter among different islands. There, new species emerge, which are usually endemic, meaning that they exist only in the archipelago or on some of its islands. Finches and turtles of the Galapagos Islands, described by Darwin himself, are popular examples of this case but not the only ones. Tree houseleeks (*Aeonium*) of the stonecrop family (Crassulaceae) of the Canary Islands first arrived at this archipelago during the Miocene, approximately 14–16 Ma. They have been spreading over all the islands of the archipelago ever since (also by dispersal) and have diversified into almost 40 species (33 of which are endemic to one of the islands) by means of allopatric speciation (Fig. 3.4) (Jorgensen and Olessen, 2001; Kim et al., 2008).

Sympatric speciation takes place within the distribution area of the species, with no physical barriers to separate the genetically different populations (Fig. 3.3). Barriers in this situation can be ecological or ethological. The example of freshwater fishes of the cichlid family (Cichlidae) is often cited to illustrate sympatric speciation. These fishes live in lakes of Africa and Central and South America. Several species of the same genus that are very similar but not identical can live in the same lacustrine ecosystem without reproducing with each other. In this case, there are diverse nonphysical reproductive barriers, such as habitat segregation due to very strict territorialism, specialization in the use of resources (especially in food types), or differences in coloration, which is a sign of sexual attractiveness within the same species and thus impedes mating between members of different species (Van Doorn et al., 1998). Parapatric speciation is a third and rather rare type of speciation that occurs when the differentiating populations are not completely separated physically but the gene flow between them is very low or nonexistent. Peripatric speciation is the case of a marginal, usually peripheral population that becomes physically isolated and evolves into a new species. Peripatric and allopatric speciation are very similar; thus the first is often considered a special category of the second.

We must also mention speciation by genetic drift, which is almost an evolutionary sacrilege since it does not involve natural selection, Darwin's

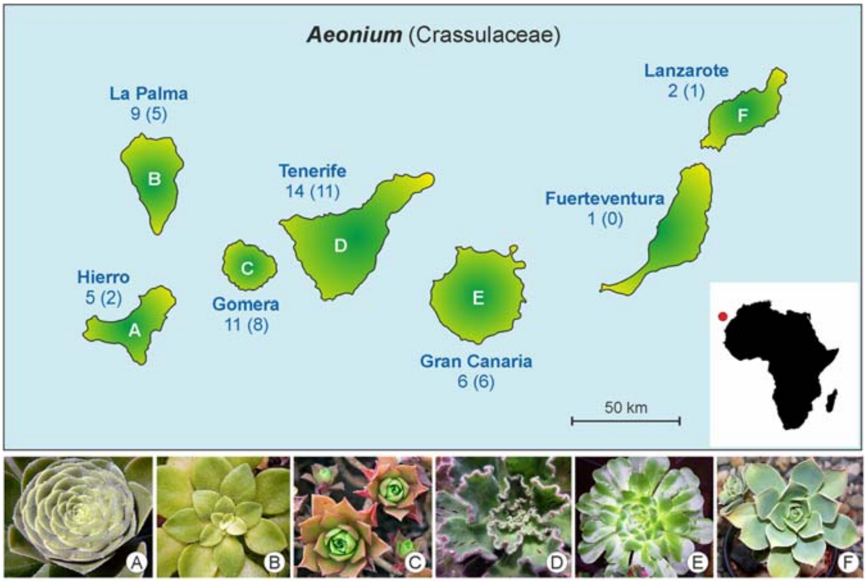

Figure 3.4 Distribution of species of the genus *Aeonium* of the Canary Islands, with examples of representative endemic species. Below each island name the total number of species and (in parentheses) the number of endemic species are shown. Capital letters match species in the photographs. (A) *Aeonium valverdense*, (B) *Aeonium goochiae*, (C) *Aeonium decorum*, (D) *Aeonium smithii*, (E) *Aeonium undulatum*, and (F) *Aeonium lanzarottense*. A red circle shows the position of the archipelago on the map of Africa. *Original data from Jorgensen et al. (2001) and Kim et al. (2008). Images of species are used under the Wikimedia Commons license.*

principal legacy. In theory, if all genotypes are equal in terms of adaption (a situation known as selective neutrality), they are all equally able to reproduce and transmit the given quality to the next generation. In this way the population will exhibit no genetic variation. However, we know that all gametes are not genetically equivalent because the chromosome recombination that takes place during the formation of gametes distributes genes randomly. Therefore the genes that ultimately take part in reproduction are only a small part, a sample, of the whole. This random sampling either increases or decreases the probability of the transmission of certain genes to the next generation and of their remaining in or disappearing from the population—despite the genes being selectively neutral. From this perspective, evolutionary change is a function of purely statistical factors and not of the fitness of given genotypes. Genetic drift is particularly obvious in cases where one or a few members of a population that have a small fraction of the gene pool of the original population manage to disperse and establish in a new environment, where there is a large probability of the formation of a new species. We know this phenomenon as the founder effect (Templeton, 1980).

3.1.2 Extinction

When we think about extinction, we usually picture catastrophic events that completely erase one or several species, even entire biotas. This idea surely comes from the information we have about great mass extinctions that took place throughout the geological history of our planet. In reality, there are at least four types of extinctions, only one of which—so-called phyletic extinction—might be catastrophic (Delord, 2007). This type of extinction wipes out all members of a species, whose gene pool totally disappears forever from the face of Earth. Such extinction does not necessarily result from a catastrophe, such as a meteorite impact or an extreme phase of volcanic activity. It might happen, for example, because the habitats of the species gradually disappear until its populations decrease below the size of the minimum viable population (Section 2.1.2). In all other extinction types the gene pool of the extinct species does not vanish completely. This is why some call them pseudoextinctions. The three types of speciation mentioned above can also be used to describe extinctions. Anagenetic extinction occurs when a species disappears because it transforms into a new species. In the case of cladogenetic extinction the extinct species diverges into two or more new species. Finally, extinction by hybridization occurs when the two parent species that gave rise to a fertile hybrid disappear and the hybrid occupies their niche (Fig. 3.5).

Extinction rates are not easy to measure since they are based on fossil records, which tend to be fragmentary and incomplete. Only organisms with hard body parts can be fossilized, and only if they were deposited in an appropriate environment with low decomposition rates, such as an environment with anoxic, acidic, and/or cold conditions. Recent developments in organic chemistry and molecular genetics have made it possible to include other organisms in fossil studies: organisms that are without fossilized hard structures but that leave specific biomarkers behind, especially DNA (Hofreiter et al., 2012; Orlando and Cooper, 2014; Slatkin and Racimo, 2016; Parducci et al., 2017). By using these biomarkers, we can find proof of the presence of organisms in rocks and

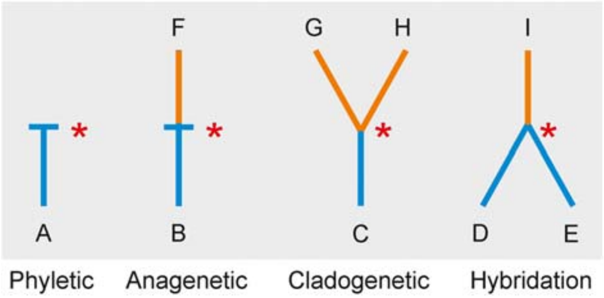

Figure 3.5 Extinction types observed in the fossil record. Disappearing species (A, B, C, D, and E) are shown in blue, and emerging species (F, G, H, and I) are shown in orange. Asterisks mark extinction events. *Modified and redrawn from Delord (2007).*

sediments and can record their eventual extinction. Hopefully, this new technology will help us take a leap forward and develop a more precise and complete vision of the extinction of living beings.

3.2 Latitudinal gradients of biodiversity

The distribution of biodiversity over the planet is neither completely homogeneous nor totally random. One of the most spectacular global biogeographical patterns is the gradient of decreasing biodiversity from the equator, where species richness is at its highest, toward the poles, which are practically uninhabited (Fig. 3.6). This pattern is known as the Latitudinal Diversity Gradient (LDG) and is probably the best known and most global example of β-diversity. The mentioned gradient is particularly evident in plants, mammals, birds, fish, amphibians, and other groups but can be generalized to most organisms, with very few exceptions (Lomolino et al., 2016). Diversity gradients were discovered at the end of the 18th century by the first explorers and naturalists, such as the German researcher Georg Forster (1778), who traveled around the world in company of the famous Captain James Cook, and Alexander von Humboldt (1850), who is regarded as the father of modern geography. From the beginning the immense tropical diversity was at the center of the mystery. We still do not know whether this high diversity is due to higher tropical speciation rates (i.e., the cradle hypothesis), lower extratropical extinction rates (i.e., the museum hypothesis), or both (Stebbins,

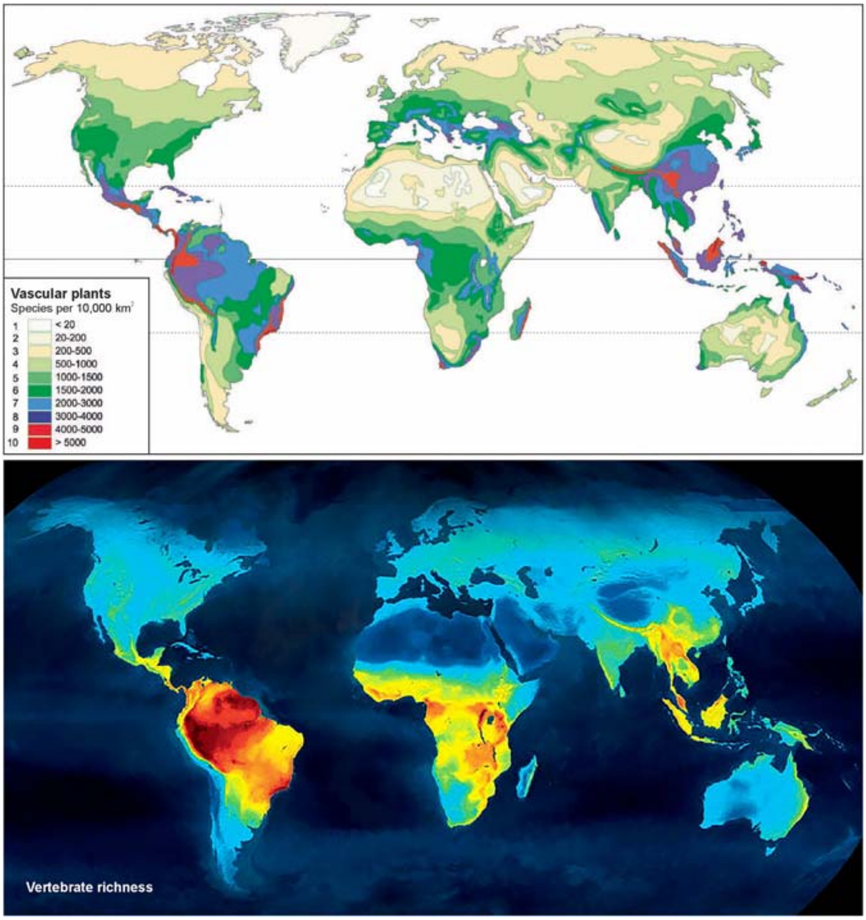

Figure 3.6 Examples of latitudinal gradients of diversity in vascular plants (above) and in vertebrates (below). For vertebrates, red colors indicate maximum diversity and blue colors indicate minimum diversity. In Africa the gradient is interrupted by the Sahara Desert. *Modified from Mutke and Barthlott (2005) and Mannion et al. (2014).*

1974). In addition, even if we knew the answer, it would not be enough; we would still need an explanation, in ecological and evolutionary terms, for the LDG.

A large number of hypotheses exist that have been reviewed in Mittelbach et al. (2007), Brown (2014) and Rull (2019), among others, where extensive literature lists are provided. Some assign the high tropical diversity to a single factor. For example, the energy-gradient hypothesis claims that, in tropical regions, the incident solar radiation is higher than that in extratropical regions and thus provides more energy for life, which eventually leads to higher species richness. Climate stability in the intertropical zone has also been suggested to favor niche diversification, while climatic changes might have advanced extinction in extratropical areas. This is the climate-stability hypothesis. The time-area hypothesis holds that the tropical continental area is larger than the extratropical area and has remained in its present position for longer, both of which could have had a positive effect on species accumulation. The niche conservatism hypothesis contends that tropical species are older and have preserved their niche and, thus, their diversity for a longer time. According to yet another hypothesis, the dispersal hypothesis, the great majority of species emerged in the tropics and colonized extratropical areas by dispersal but did not disappear from their original tropical area, which is therefore more diverse. As already discussed, ecological factors need to be combined with these evolutionary alternatives to explain coexistence. A series of mechanisms has been suggested to justify tropical coexistence (i.e., how to avoid extinction or migration). These mechanisms are related to the heterogeneity of habitat, competition, predation, the capacity for colonization, differential growth and mating habits, among other factors.

Once again, we can observe how the whole approach is biased toward temperate zones. High tropical biodiversity is considered an anomaly compared to the patterns and degree of biodiversity in temperate zones, which are taken as standard. Despite recent developments, the tropics are still much less known from the ecological and evolutionary points of view. In addition, we should not forget that the scientific study of the tropics has clear colonial roots and that this mentality has largely directed tropical research (Raby, 2017). If it were the other way around, and these sciences were based on tropical zones, the low extratropical biodiversity would need to be explained (McGlone, 1996). Under such circumstances, it is possible that the progress in biodiversity-related sciences would have been very different. However, as we said in the introduction, science is a contingent enterprise, and we must follow the course of past events and findings. Nevertheless, it would be interesting to try to adopt a different approach and see what results an alternative view would yield. This is not a proposal for a tropics-focused approach (which would be equally biased) but for a more global and general biogeographical—evolutionary—ecological approach to explain LDGs (e.g., Pontarp et al., 2019).

3.3 The molecular revolution

Until a few decades ago, the only evidence available for testing evolutionary hypotheses of diversification was provided by the geographical distribution of living organisms and fossil evidence combined with paleoecological reconstruction and modeling. Most evolutionary hypotheses and models are based on biogeography and paleontology, both of which have rather limited verification potential (Bennett, 2004; Willis and Niklas, 2004). Biogeography is able to provide only present-day evidence (while it is past occurrences that we are interested in), and paleontology is fragmentary and unable to produce complete and continuous information about the life of past organisms (this is the so-called museum syndrome mentioned in the introduction). Nevertheless, we cannot complain. Even with these limitations, these studies have led to amazing discoveries. In fact, almost all that we know about evolution was gained from biogeography, paleontology, and paleoecology and the theoretical models derived from these sciences. The rest is a question of verifying other hypotheses already provided by the same sciences, which form the bases of present and future studies. However, the last few decades have seen a methodological revolution that has provided us with a fundamental tool for the study of speciation and the understanding of the origin and maintenance of biodiversity. We are referring to the spectacular development of genomics, which is the study of genomes at the molecular level. Two branches of genomics are of special interest in evolutionary studies: molecular phylogenetics and phylogeography.

Phylogenetics is the discipline that studies the evolutionary relationships within a given group of organisms with common ancestry. The final outcome of these studies is a phylogenetic or evolutionary tree representing the lineages of the taxa that forms the group and that constitutes a model of the evolutionary history of this group. The phylogenetic tree par excellence is the so-called tree of life, which represents the progressive division of lineages, from the first living organism—known as the Last Universal Common Ancestor (LUCA)—to present-day species. Phylogenetic trees, as all models, are built by statistical methods on the basis of similitudes between organisms established from observable and measurable parameters. Classic phylogenetics was principally based on phenotypic characteristics (mostly morphological and chemical parameters), which although genotypic expressions, could be influenced by the environment. Due to the molecular revolution, we can currently use the true units of evolution, that is, genes, to construct phylogenetic trees, thereby obtaining more realistic (or natural) evolutionary relationships. The change the new technology produced has been dramatic. In addition to modifications to evolutionary relationships and the classification of many taxonomic groups, even the most basic classification of living beings had to be reorganized. Indeed, instead of the original five kingdoms (Monera, Protista, Fungi, Plantae, and Animalia), there are now three domains: two in Monera (Archaea and Bacteria) and one of eukaryotes (Eukarya) that contains the other four kingdoms of the former classification (Fig. 3.7) (Woese et al., 1990). There are many books on the theory and methods of phylogenetics, including Nei and Kumar (2000), Hall (2011) and Wiley and Lieberman (2011).

Usually, phylogenetic studies are conducted on present-day organisms, thus evolutionary information is extracted from the genome of living beings, which can be considered a summary of the evolutionary history of each particular group. These studies are based on molecular changes (mutations) that happen in certain genes due to alterations in the nucleotide sequence of DNA. Each mutation causes the formation of a different amino acid, which modifies the composition of proteins, the vehicles of gene expression. Three different types of molecular mutations may be highlighted: substitutions, insertions, and deletions (Fig. 3.8). The quantification of these types of differences in a given gene in the group of species under study provides the basis of the phylogenetic tree. As a general rule, a smaller number of differences means a closer phylogenetic relationship between two taxa, and vice versa. The likeness or difference between two taxa regarding this parameter is called genetic distance. It is still not a straightforward task to draw a phylogenetic tree based on genetic distances; often, sophisticated mathematical and statistical algorithms are needed. The remarkable development of informatics has made it possible to use methods that require limitless iterations and comparisons, something that was impossible in the recent past. Recent developments of databases and their accessibility have also provided an enormous advantage since, today, studied molecular sequences are stored digitally, which makes work much easier and helps avoid useless repetitions.

Different types of phylogenetic trees exist, but they are all usually composed of nodes and branches (Fig. 3.9). Monophyletic groups, where all members descend from the same common ancestor, are also called clades. Groups that do not meet this criterion are called paraphyletic groups. In the first instance, branches represent genetic distance, but within the context of

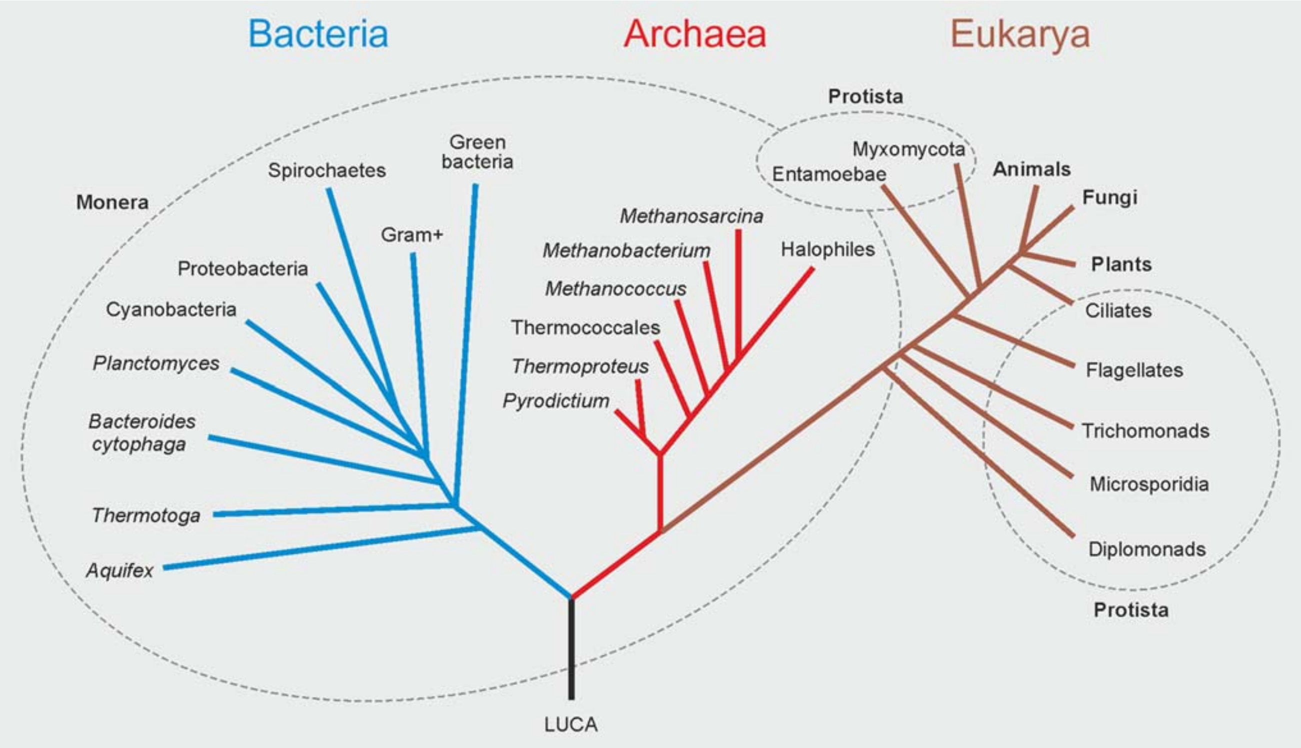

Figure 3.7 Phylogenetic tree of life based on molecular genomic studies. Formerly used kingdoms (Monera, Protista, Fungi, Plantae, and Animalia) are marked with bold font. *LUCA*, Last Universal Common Ancestor. *Redrawn and adapted from Woese et al. (1990).*

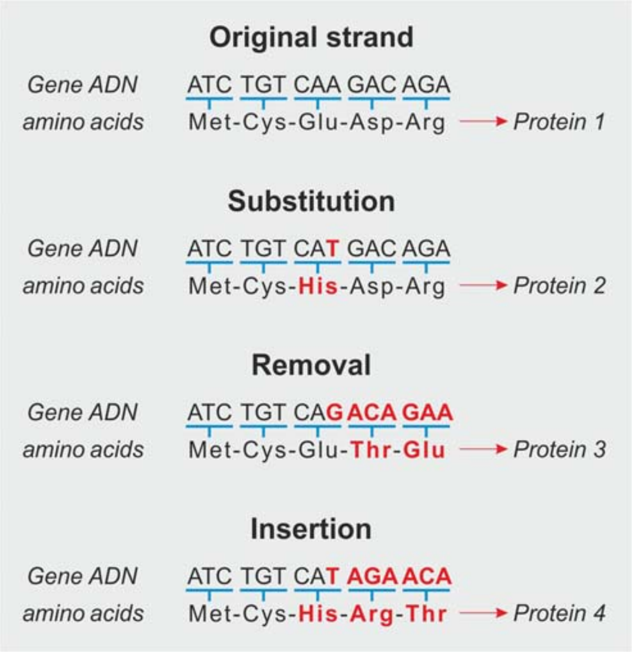

Figure 3.8 Main types of molecular or gene mutations illustrated with a hypothetical example. Genomic DNA chains are represented by the nitrogenous bases, or nucleobases—adenine (A), cytosine (C), guanine (G) and thymine (T)—of the nucleotides. A group of three bases is called a codon and encodes a specific amino acid—arginine (Arg), aspartic acid (Asp), cysteine (Cys), glutamic acid (Glu), histidine (His), methionine (Met), and threonine (Thr). Each mutation type changes the amino acid sequence and, thus, the protein. Differences relative to the original chain are marked in red. Substitution only replaces one base with another, causing a change in only one amino acid. Insertion and deletion, on the other hand, might alter the whole sequence of subsequent amino acids. In this example, we deleted the second adenine of the third codon to illustrate the effect of deletion, and we inserted a thymine at the end of the same codon to show how insertion works.

this chapter, it is more practical to use a chronological representation, where branches represent time. Therefore we need some kind of dating method to be able to transform genetic distances into time units. Fossils of the same taxonomic group under study of known age that can be linked to given nodes of the tree are the best option, but there are also indirect methods based on the so-called molecular clock. It has been observed that the number of mutations in a given gene in two species that descend from a common ancestor is proportional to their divergence time, which is the time since the two species diverged from that ancestor. Therefore there is a

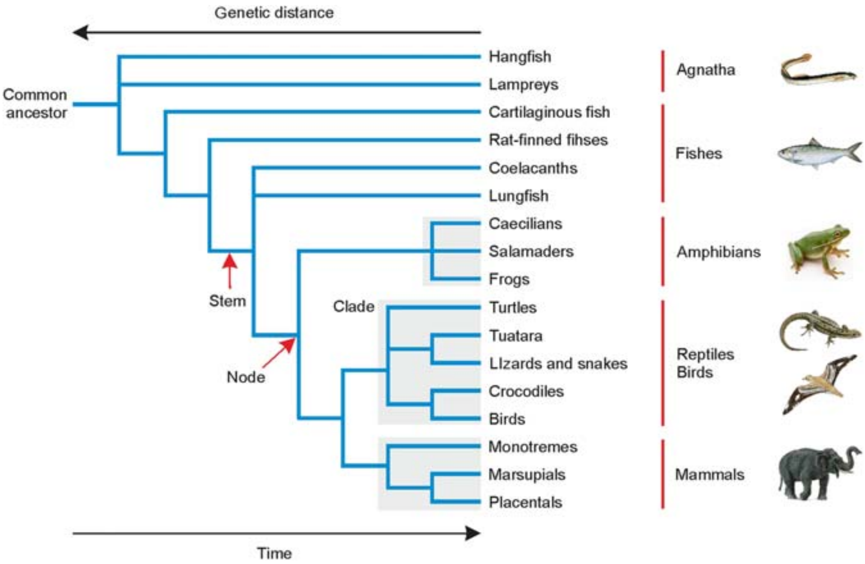

Figure 3.9 Phylogenetic tree of vertebrates based on morphological and molecular characteristics. Nodes and branches are shown, and clades (monophyletic groups) are highlighted in gray. Units are either genetic distance or time, which are inversely proportional to each other. Amphibians, reptiles–birds, and mammals are monophyletic groups, while Agnatha and fish are paraphyletic. *Redrawn and modified from Meyer and Zardoya (2003).*

direct relationship between molecular differences and the time of evolution, allowing us to estimate the second parameter from the first one (Fig. 3.10). Mutation rates vary according to the gene and the taxonomic group under study, which means that there are many molecular clocks. Molecular dating methodology is a very active field of research, which is in constant evolution. Some papers summarize the pros and cons of the different approaches (e.g., Rutschmann, 2006; Bromham, 2019).

All the information contained in phylogenetic trees can be projected onto a distribution map of the taxonomic group, which provides its phylogeography (Avise, 2000), a very useful biogeographical tool used to resolve the spatial features of the evolution of the group under study. Phylogeographical representation helps explain how and when the present distribution was reached and what evolutionary and geographical changes and reorganizations led to it. We will see some examples in Section 3.5. Undoubtedly, the combination of all the discussed disciplines (biogeography, phylogenetics, phylogeography, paleoecology, and paleontology) is

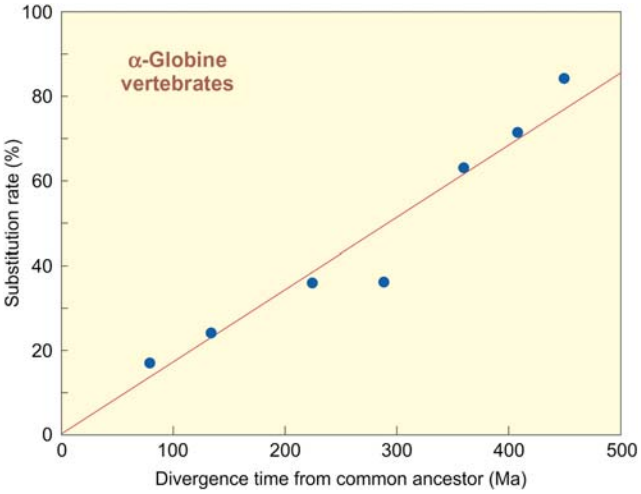

Figure 3.10 Relation between the substitution rate of amino acids in the α-globin protein of vertebrates and the time that passed since divergence from the common ancestor. The significant regression coefficient ($R^2 = 0.935$) makes it possible to calculate divergence time from the substitution rate by using the slope of the curve. In this case, the mutation rate is 5.30% per million years (Ma). *Modified and redrawn from Fontdevila and Mora (2003).*

the best strategy with which to study the origin of present-day biodiversity. And the Quaternary is especially well suited for these studies.

3.4 Heterodox theories of diversification

Everything discussed in this book thus far was based on the concepts of the niche and species idiosyncrasy, in terms of ecological relationships, and on neo-Darwinism or the modern synthesis, in terms of evolutionary processes. Nevertheless, we cannot ignore the existence of alternative hypotheses that originate from different fundaments, three examples of which are the neutral theory of biodiversity, the punctuated equilibrium, and the Red Queen hypothesis. These alternative theories sparked controversy among ecologists and evolutionists. We provide a brief review of the main points of these theories that are usually considered heterodox compared to the neo-Darwinian orthodoxy. Among the several existing hypotheses, here, we focus on only the three that had the strongest influence on current ecological and evolutionary ideas regarding the origin and continuation of biodiversity and that are referred to at some point in this book.

3.4.1 The neutral theory of biodiversity

We have already mentioned that genetic drift is based on the neutrality of genes in terms of selection, which is a fundamentally anti-Darwinian idea. Now, we should admit that molecular clocks, based on a constant temporal rate of molecular-level genetic changes, are also anti-Darwinian. Indeed, if these molecular changes were adaptive, in other words, controlled by natural selection, they would not necessarily have a constant rate because they would depend on ecological changes that do not take place at regular intervals. Based on this observation, the Japanese evolutionist Motoo Kimura (1983), put forward the neutral theory of molecular evolution. This theory holds that most molecular-level evolutionary changes are a product of genetic drift. Although this theory was considered a frontal attack against Darwinism at first, Kimura clarified that neutral and adaptive evolution are not at all incompatible with each other, although he considered the first one to be more important. Inspired by his theory, the North American ecologist Stephen Hubbell (2001) went even further and developed the neutral theory of biodiversity or, as he called it, the unified neutral theory of biodiversity and biogeography. According to Hubbell, the differences in the characteristics of the niches of species in a community are neutral, meaning that they are irrelevant to the origination and maintenance of diversity, whose patterns are generated randomly.

Both Kimura's and Hubbell's theories are based on top-down mathematical models. These models simulate general ecological and evolutionary processes and patterns at a large scale without taking into account particular details of the components (in our case, genes or species) of the analyzed system. There are two main lines of criticism against this procedure. The first one is that these models are based on unrealistic assumptions, such as the ecological equivalence of species (the claimed neutrality of niches in the generation and maintenance of diversity is especially vehemently condemned). The second one is that top-down models follow a procedure that is opposite to the conventional approach in natural sciences, where general conclusions are drawn based on regular patterns identified in particular cases (bottom-up models). Hubbell and his followers argue that their models are capable of reproducing observed reality (i.e., real diversity patterns of certain ecosystems).

We will not examine this question further here because, although very interesting, it is beyond the scope of this book. However, a word of caution is necessary regarding the use and abuse of top-down models in the study of the origin and maintenance of diversity. As pointed out by the famous North American ecologist Robert Ricklefs (2012), "Whereas the origins of ecology were firmly grounded in direct observation of nature, the emergence of strong theory in ecology appears to have changed our perspective on natural history — i.e., the direct observation of the natural world — to the point that observation is often used to serve theory rather than test predictions and find inspiration for new ideas." This author emphasized the need for a return to natural history observation and thinking for a sound understanding of the origin, maintenance, and significance of biodiversity. This remark is especially compelling coming from Ricklefs, a leading ecologist with a significant theoretical background. However, Ricklefs (2012) referred to the present component of natural history and, as is usual for most (neo)ecologists, he did not consider the past, whose contribution to understanding extant biodiversity patterns may be essential (Rull, 2012), as we demonstrate in this chapter.

3.4.2 Punctuated equilibrium

Darwinian and neo-Darwinian evolution imply a gradual, slow, and uniform transformation of species, where the transformation involves a substantial proportion of the population and takes place over a large part of the distribution area of the species. This is called phyletic gradualism. However, fossil records show quite the opposite and provide no traces of this expected gradualism. Indeed, fossil sequences are markedly discontinuous and consist of sudden substitutions of given forms by others without the evidence of intermediate morphologies. From the perspective of phyletic gradualism, these discontinuities are due to the fragmentary and partial nature of the fossil record, as a result of the selective degradation of fossils. This is why fossil sequences do not correctly represent the gradual continuity of evolution. However, according to the North American paleontologists and evolutionists Niles Eldredge and Stephen J. Gould, this is not the case. These researchers claim that the fossil record is the most important evidence for evolution and that its discontinuous nature is a faithful representation of the course of evolution, which does not proceed gradually but by abrupt changes (Eldredge and Gould, 1972; Gould and Eldredge, 1977). They state that new species emerge in a relatively short time (which is not sufficient to leave fossils behind) and then remain in a long period of stasis (the main period of fossil formation) until their extinction and their replacement by newly formed species. For Eldredge and Gould the principal method of speciation is peripatric speciation (Fig. 3.3), which takes place in small populations in limited peripheral zones.

The manner of evolution is not the only difference between punctuated equilibrium and neo-Darwinism. They also differ in the concept of natural selection. Darwinian selection operates at the level of populations, while selection under punctuated equilibrium operates at the level of species. How is this possible? According to the peripatric model, there might be several effective speciation events, which means that several new species can emerge, but that only one or a few of them survive and expand sufficiently to reach a stabilization phase or stasis (Fig. 3.11). There is still more controversy between phyletic gradualism and punctuated equilibrium. The conflict is partly due to the evident methodological differences between the two sides; phyletic gradualists mainly use genotypic and phenotypic characteristics of living organisms, while defenders of punctuated equilibrium are more interested in the fossil record. There is also a possibility that both of these options are true and that all the mechanisms are involved, depending on the case and period of time, but this view remains to be explored.

3.4.3 The Red Queen hypothesis

In Lewis Carroll's *Through the Looking-Glass*, Alice finds herself in a country reigned by the Red Queen (not to be confused with the Queen of Hearts in *Alice's Adventures in Wonderland* by the same author). Alice is amazed that, although she ran hard for a long time, she is still under the same tree where she started, and the queen's answer is "Now, here, you see, it takes all the running you can do, to keep in the same place." If somebody does not move, they will disappear from the map. The North American evolutionist Leigh Van Valen (1973) observed that extinction rates in several groups of organisms (including protists, plants, and animals) were constant at a geological scale and independent of environmental conditions and their previous history. This made him believe that extinction was an inevitable occurrence and that the only way to survive was to use all competitive advantages over other species to persist for at least some time. Otherwise, the species would vanish, like somebody who did

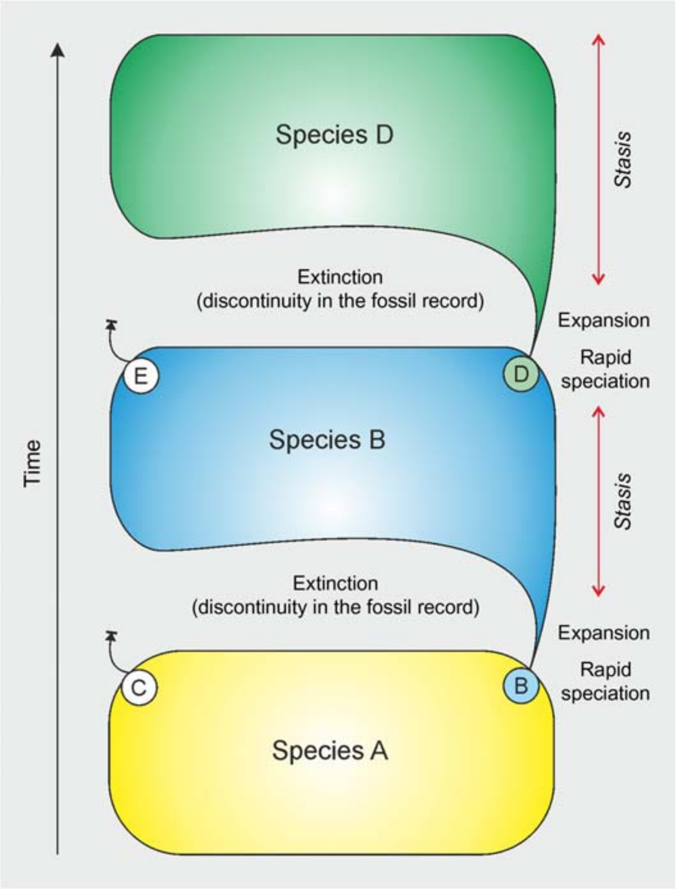

Figure 3.11 Schematic illustration of the most important processes in punctuated equilibrium. From a marginal population of species A stems species B, which prospers, and species C, which quickly goes extinct and leaves no fossils behind. When species A goes extinct, species B occupies its place until it reaches stasis, when new fossils are formed. The same process takes place for species B, D, and E, and so on. *Redrawn and modified from Price (1996).*

not move fast enough in the land of the Red Queen. In this context, genotypes would not be selected according to their reproductive superiority (as under a Darwinian perspective) but simply according to their probability of surviving. This hypothesis minimizes the importance of the environment and its changes in evolution and places the emphasis on biotic relationships in the struggle for survival. You simply have to run faster than others to survive. And this is not a simple metaphor if we consider the coevolution of predators and their prey. The theory of the Red Queen is often applied to cases of coevolution, such as the mentioned predator—prey systems or the common coevolution of plants and their pollinators. Each evolutionary innovation that occurs in one of the members must be followed by a corresponding innovation in the other member; otherwise, the system becomes unbalanced, and eventually, both members will be losers. In the cases of competition or parasitism the Red Queen hypothesis has been compared to an arms race. If one of the competing species or the parasite acquires a new character (a new arm) that gives it an advantage, it will overcome the other party. In contrast to other evolutionary mechanisms that increase diversification by enhancing speciation, the mechanism outlined by the Red Queen hypothesis does the same by minimizing extinction.

3.5 Quaternary evolution

After this short review of terms and concepts necessary to understand the origin and maintenance of biodiversity, we now ask how the different diversification mechanisms have operated during the Quaternary until reaching the current situation. In line with the objectives of the book, we concentrate on the potential influence of climatic changes on biodiversity. However, we complete the study of the Quaternary with information on earlier periods, especially the Neogene (23 to 2.6 Ma), and we extend our analysis to other environmental factors, such as topographical and paleogeographical changes provoked by plate tectonics, which have had an influence on the origin of current biodiversity. We start with the Quaternary to see some examples of its micro- and macroevolutionary changes. Afterward, we discuss the topic of LDG, considering both the Quaternary and the Neogene environmental drivers.

3.5.1 Microevolution

Species are not homogeneous from a genetic point of view. They have certain variability at the population level, which is known as population structure. Population structure also forms part of diversity (i.e., genetic diversity) and is strongly related to evolutionary capacity (Hansen, 2006). Species with higher genetic diversity have a greater possibility of adapting to diverse environments; therefore their speciation potential is higher, especially when the genetic diversity is linked to a heterogeneous geographical distribution that increases the probability of the formation of reproductive barriers among populations. Consequently, the concept of population structure comprises species richness (α-diversity) and its spatial distribution (β-diversity). According to the British evolutionist Godfrey Hewitt, most of the population structure of extant species is a Quaternary legacy (Hewitt and Butlin, 1997; Hewitt, 2000). Here, we offer two examples: the common European hedgehog (*Erinaceus* spp.) and the mare's-tale (*Hippuris vulgaris*), an aquatic plant of Asia.

The common European hedgehog is widely distributed over most of Europe and is represented by two species, one in the west (*Erinaceus europaeus*) and one in the east (*Erinaceus bicolor*) (Fig. 3.12). A study of the mitochondrial DNA (mtDNA) gene that encodes the protein called cytochrome *b* (cyt *b*) revealed the population structure of these two species (Hewitt, 1999). Each of the species is divided into two clearly distinct haplotypes (variants of the same gene). The two variants of *E. europaeus* are the Iberian (IB) and Italian (IT) variants, while *E. bicolor* can be divided into the Balkan (BC) and Turkish (TC) variants. These haplotypes diverged during glaciations by vicariance because they lived in different refugia without any gene flow between them (Section 2.2.2). During interglacial phases, all variants migrated northwards to colonize the northernmost parts of the continent, but they did not mix completely (although there were two zones of hybridization). Thus glacial haplotypes are still easily recognizable, and the corresponding population structure has remained the same. With the aid of the molecular clock of the mentioned gene (cyt *b*), which has a mutation rate of 2% per million years, the date of the divergence of the two species (*E. europaeus* and *E. bicolor*) was estimated to be approximately 6 Ma, in the Pliocene, while the haplotypes appeared more recently, mostly during the Quaternary. Both the BC—TC and IB—IT variant pairs separated approximately 3—2.7 Ma, close to the Pliocene—Pleistocene boundary, in the cooling period that initiated glaciations. The IT variant underwent a further division during its northward migration, approximately half a million years ago, probably provoked by an especially cold glaciation. The Turkish and Israeli variants, the glacial refugia of which might have been in the Caucasus or even more to the south, also separated at approximately the same time (Fig. 3.12).

The case of the mare's-tale (*H. vulgaris*), an aquatic plant of the Plantaginaceae family, illustrates well the phenomenon that Pielou called

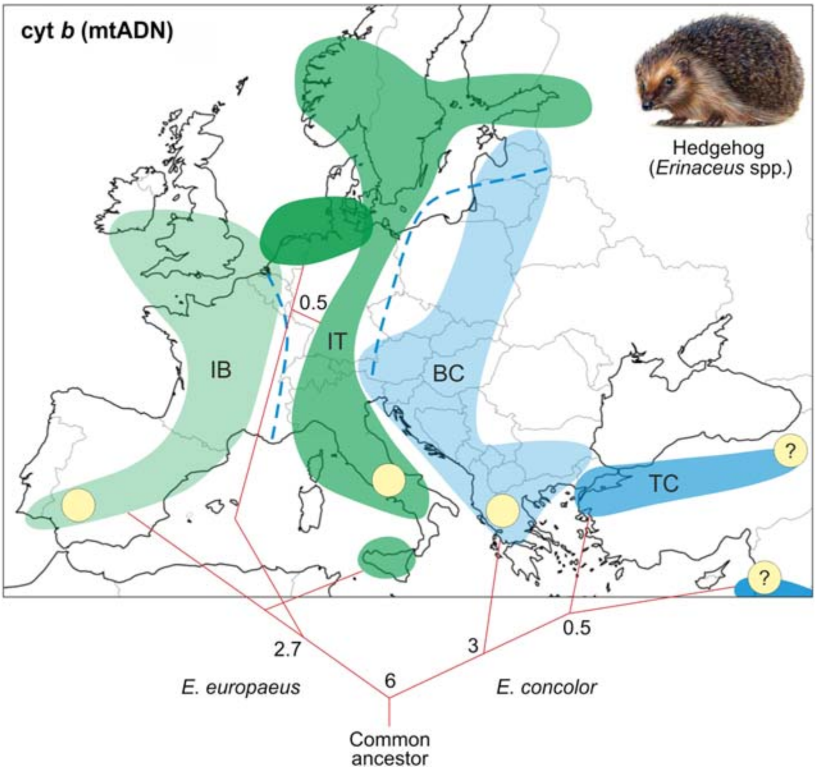

Figure 3.12 Phylogeography of the common European hedgehog (*Erinaceus* spp.) based on the gene that encodes the cytochrome b (cyt *b*) protein of mitochondrial DNA (mtDNA). The current distribution of *Erinaceus europaeus* is shown in green, and that of *Erinaceus bicolor* is shown in blue. Color intensity indicates different haplotypes (IB, IT, BL, and TC) of the two species. Dashed blue lines mark hybridization zones between haplotypes. Yellow circles show the approximate location of glacial refugia. Branches of the evolutionary tree are red, and the numbers on nodes give the divergence time in millions of years (Ma). The mutation rate is 2% per million years. *BC*, Balkan; *IB*, Iberian; *IT*, Italian; *TC*, Turkish. *Redrawn and modified from Hewitt (1999)*.

secular migration, which occurs so slowly that the migrating species undergoes intraspecific evolutionary changes (Section 2.1.2). In China, *H. vulgaris* lives in montane areas in the north (NW and NNE) and on the Qinghai–Tibet Plateau (QTP) (Fig. 3.13), but this is not its ancestral distribution area. Based on fossils found to date and a phylogeographical study of six genes of cytoplasmic DNA (cpDNA), the species emerged more to the north during the Late Pliocene or the Early Pliocene (before approximately 800 ka BP), and it migrated to China during the Middle

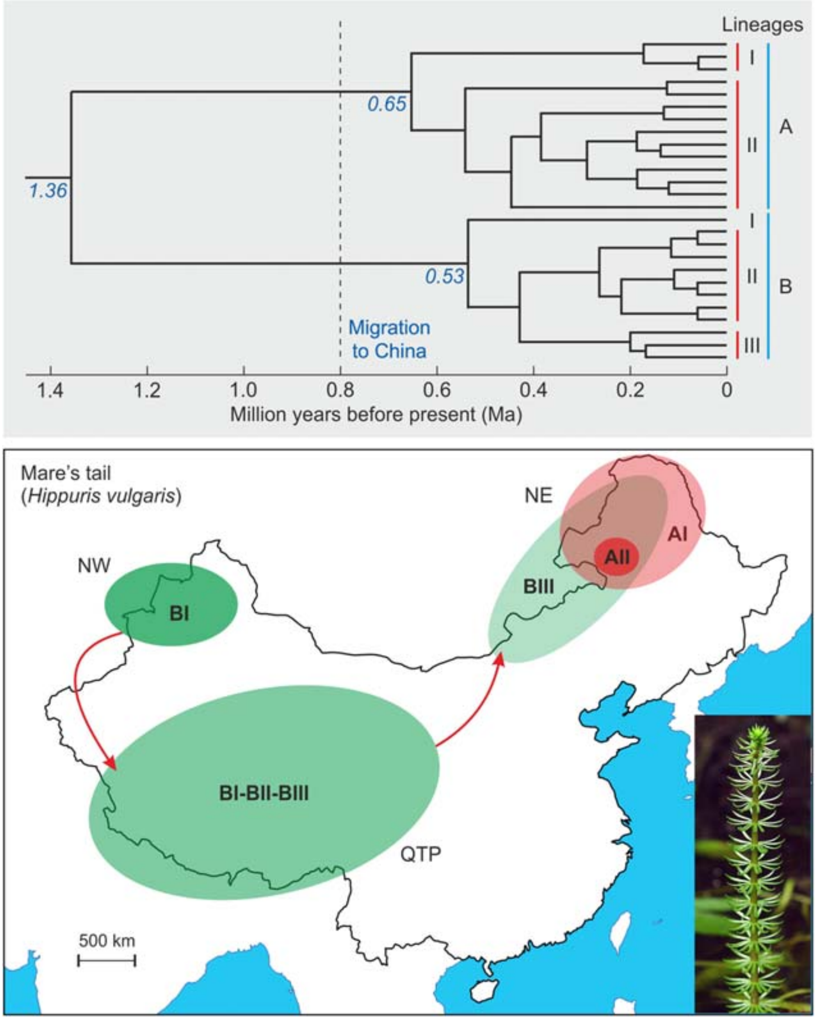

Figure 3.13 Phylogeography of mare's-tale (*Hippuris vulgaris*) in China. The phylogenetic tree shown in the upper part is based on six genes of chloroplast DNA (cpDNA) and calibrated with the corresponding molecular clock. Twenty-eight haplotypes grouped into two main lineages (A and B) and five sublineages (AI, AII, BI, BII, and BIII) can be observed. The map in the lower part shows the current geographical distribution of the lineages and sublineages. Arrows indicate migration routes during the Quaternary. *Redrawn and modified from Lu et al. (2016).*

Pleistocene (Lu et al., 2016). As discussed in the first chapter, Early Pleistocene glaciations, before 800 ka BP, were not as intense as the more recent ones, and this might have been the reason *H. vulgaris*, which prefers cold climates, did not descend latitudinally to colonize the Chinese region. When glaciations turned colder, the species, which was already divided into two lineages, entered the area through the NE (A lineage) and through the NW (B lineage) (Fig. 3.13). The following histories of the two lineages were very different. Lineage A stayed in the NE area, while lineage B expanded over most of the species' current distribution area. This southward expansion and the subsequent northward expansion did not occur in a continuous manner but followed the course of the glacial—interglacial cycles, which provoked the successive reproductive connection and disconnection of the mentioned areas. These changes favored genetic differentiation and resulted in the current population structure. Lineage A was divided into two sublineages (AI and AII) approximately 0.65 Ma without leaving its limited distribution area. Lineage B, on the contrary, colonized the area of the QTP approximately 0.53 Ma, where it diverged into three sublineages (BI, BII, and BIII). The most recent one of these three (BIII, which emerged approximately 0.2 Ma) alone colonized the NE region.

These are only two of the many examples of microevolution, or intraspecific evolution, provoked or favored by climate change in the Quaternary but there are many more (e.g., Cristescu et al., 2001; Barnosky, 2005; Bittkau and Comes, 2009; Cossíos et al., 2009; You et al., 2010; Mäder et al., 2013; Zhao et al., 2013; Dawson et al., 2014; Peres et al., 2015; Huntley and Voelker, 2016; Veríssimo et al., 2016, just to cite some). In the words of Godfrey Hewitt, no one escaped the evolutionary effects of glacial—interglacial cycles. These microevolutionary processes can be nascent speciation events if reproductive barriers are formed to separate the involved populations. Therefore the different existing lineages within species may be viewed as intraspecific ESUs (Section 3.1.1). This, however, does not mean that only intraspecific genetic variation has been generated during the Quaternary. On the contrary, a large number of species emerged during this period, as will be discussed in the following sections.

3.5.2 Macroevolution

As already mentioned, humans provide an excellent example of Quaternary macroevolution (Fig. 3.1 and Chapter 5), but we are not the only case. Most taxonomic groups of living beings include species that originated in the Quaternary, and some of them have plentiful examples.

A spectacular case is that of cycads (order *Cycadales*), which were traditionally considered living fossils, which means that they are very morphologically similar to their ancestors that go back hundreds of millions of years in history, back to the Permian or the Carboniferous. These plants, with 10 known genera and approximately 340 species, are distributed throughout the tropical zone and some subtropical areas. At first sight, they are easily mistaken for palm trees, although they are not related, at all (Fig. 3.14). Cycads were always thought to have diversified quickly after their origin and then to have remained quite similar to the way they were 280–300 million years ago, which would be an amazing case of evolutionary stasis (Section 3.4.2). Therefore we could imagine that we were looking at a genuine relic of the distant past when in front of a representative of this order. Nevertheless, a recent study dismantled this theory by proving that present-day cycad species are actually significantly more recent (Nagalingum et al., 2011). Based on the nuclear gene Phytochrome P (*PHYP*), a phylogenetic reconstruction of approximately 200 species of this group was conducted, including a well-balanced

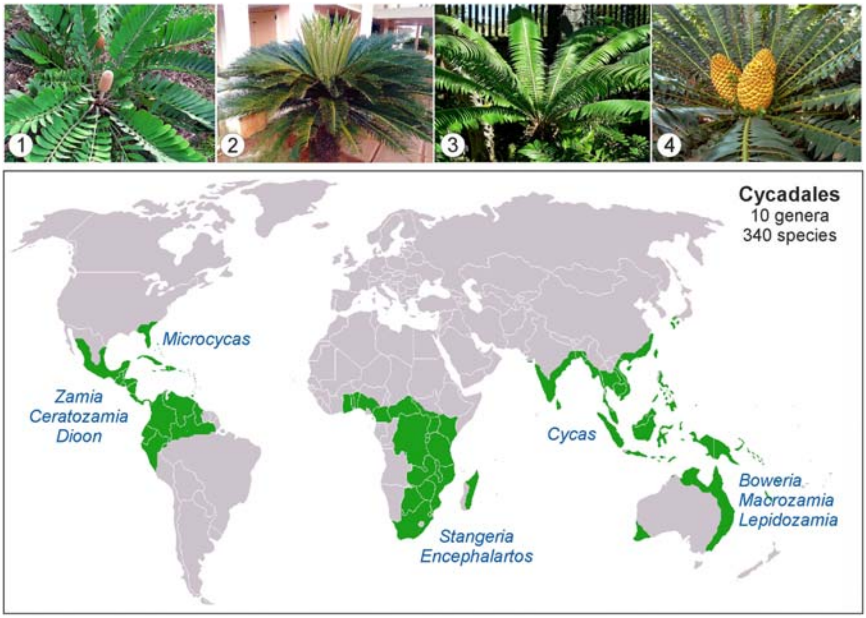

Figure 3.14 Geographical distribution of cycads (*Cycadales*), showing the genera of each continent and some examples of the most important genera. (1) *Zamia*, (2) *Cycas*, (3) *Dioon*, and (4) *Encephalartos*. *Redrawn and modified from Nagalingum et al. (2011). Plant images from Wikimedia.org.*

representation of all genera. The phylogenetic tree was calibrated to years by using fossils to set the age of certain nodes and by the corresponding molecular clock. The reconstruction confirmed that cycads, as an order, originated during the Permian (250–300 Ma) but that current genera did not appear until the Miocene (approximately 10 Ma), and that present-day species mostly emerged during the last five million years, that is, during the Pliocene and the Quaternary. The number of species that originated during the Quaternary was surprising. For instance, 24 of the 35 species (approximately 70%) of the genus *Zamia* are of Quaternary origin (Fig. 3.15). Considering the almost 200 studied species, 70 (35%) are Quaternary species. Now, we can come face to face with many cycads

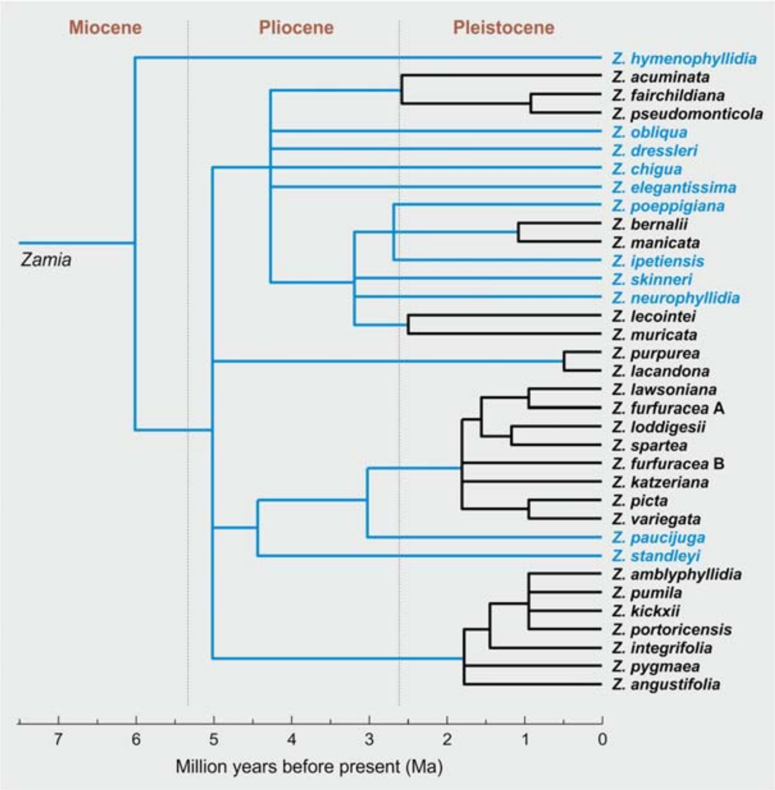

Figure 3.15 Phylogenetic tree of the *Zamia* genus based on the nuclear gene Phytochrome P (*PHYP*) and calibrated by fossils and the corresponding molecular clock. Species of Quaternary (Pleistocene) origin are marked with black, and older species, in blue. *Redrawn and modified from* Nagalingum et al. (2011).

without feeling inferior in terms of evolutionary age. This might not be as romantic as the myth of a living fossil, but it is the truth.

There are many similar cases, but we mention only a few of them here. For example, a phylogenetic study of more than 100 carnation species of the genus *Dianthus*, which are common in Eurasia and Africa, revealed that all of them originated in the Quaternary, between 1.9 and 0.7 Ma (Valente et al., 2010). Carnations, therefore, are Quaternary species. The case of garden balsams of the genus *Impatiens* is similar; 95 of the 120 species included in a phylogenetic study appeared during the Quaternary (Janssens et al., 2009). Similarly, approximately 70 of 100 species of begonias (*Begonia* spp.) from the Asian tropics emerged during the Pleistocene (Thomas et al., 2012). Another similar example is that of Andean legumes of the genus *Lupinus*, which colonized the Andes from North and Central America during the Early Pleistocene (> 1.5 Ma) and have diversified into more than 80 species since then (Hughes and Eastwood, 2006). This and many other cases of Quaternary diversification consisted of the progressive colonization of new habitats, adaption and subsequent allopatric speciation, a process that we have called adaptive radiation (Section 3.1.1). All these studies, and others involving Quaternary diversification, explicitly relate this process with Pleistocene climatic variability, although it is not always possible to assign specific evolutionary events to particular climatic changes.

There are also many Quaternary species of animals. We already talked about cichlid fishes of the great lakes of East Africa in relation to sympatric speciation (Section 3.1.1). The diversity of these fishes is astonishing in those lakes; Lake Tanganyika contains 200–250 species; in Lake Victoria, there are 500 species; and the number goes up to 1000 in Lake Malawi. Furthermore, almost all of these species are endemic to the lake where they live. The oldest of these lakes is Tanganyika, which was formed approximately 9–12 Ma. Lake Malawi appeared approximately 2–4 Ma, while Lake Victoria is less than 750,000 years old. According to phylogenetic and phylogeographical studies, the cichlids inhabiting Lakes Malawi and Victoria that belong to the Haplochromini tribe are derived from species of Lake Tanganyika (Salzburger et al., 2005). They migrated from Lake Tanganyika via the river system that connected the lakes approximately 2 Ma (Fig. 3.16). The migration benefitted from the successive reorganizations of the river network that took place due to relatively frequent tectonic movements (all of these lakes are in the tectonically active African rift). Lake Malawi was colonized approximately 1 Ma, and Lake Victoria was

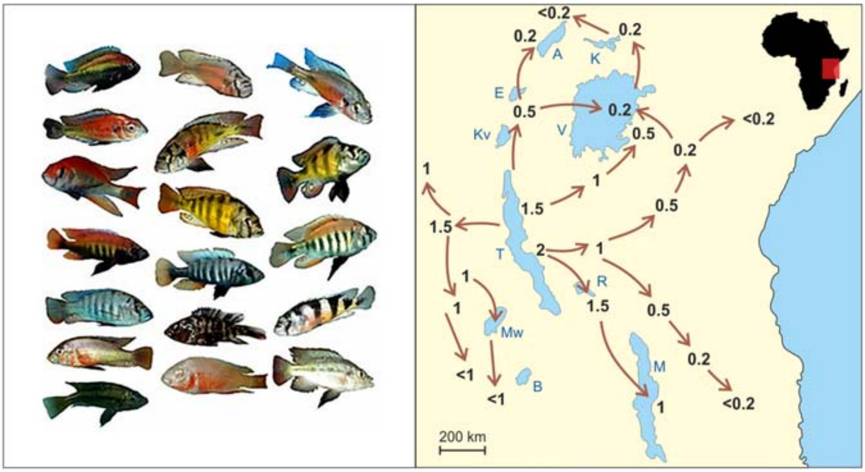

Figure 3.16 Examples of cichlids of the great lakes of the African rift (left) and their colonization routes from Lake Tanganyika during the Quaternary (right). Numbers indicate millions of years before present (Ma). Lakes: *A*, Albert, *B*, Bangweulu, *E*, Edward, *K*, Kioga, *Kv*, Kivu, *M*, Malawi, *Mw*, Mweru, *R*, Rukwa, *T*, Tanganyika, *V*, Victoria. The red rectangle shows the position of the study area on the African continent. Redrawn and modified from Salzburger et al. (2005).

colonized during the last 200,000 years (Fig. 3.16). This means that the approximately 1500 species that live in these lakes today appeared during a period of only 1 million years, which required an unparalleled speciation rate. The mechanisms that stimulated this evolutionary explosion during the Quaternary are related to climatic changes, which resulted in significant (over 100 m) decreases in the water level of the lakes. This degree of water level fall was sufficient to convert a great lake into an almost dry basin with small, isolated pools. Under these conditions, populations of the same species were separated and could differentiate, probably by means of genetic drift, and when the water level rose again, they recolonized the reunited lake already as different species. These events (mentioned above as founder effects; Section 3.1.1) may have happened repeatedly following the rhythm of glacial—interglacial oscillations, which were especially intense during the last 800,000 years. Mechanisms of sympatric speciation, as explained in Section 3.1.1, may also have been in progress within habitats and communities, thus enhancing diversification.

Another large-scale example of Quaternary speciation is that of the Zosteropidae family. These birds, known as white-eyes, live in large areas of Africa, Southeast Asia, and Australasia. According to a phylogeographical study based on mitochondrial DNA, most of the approximately 100 species of this family emerged during the last 2 Ma (Moyle et al., 2009). Similar Pleistocene speciation rates were recorded in other groups of plants, birds, mammals, reptiles and amphibians, among others. Quaternary speciation is a common phenomenon in almost all plant and animal groups widespread all over the world in both terrestrial and aquatic habitats (e.g., Richardson et al., 2001; Johnson and Cicero, 2004; Weir and Schluter, 2004; Pennington et al., 2004; Weir, 2006; Rull, 2008; Foltz et al., 2008; Chiou et al., 2011; Mullen et al., 2011; Levsen et al., 2012; Irestedt et al., 2013; Leavitt et al., 2013; Lutz et al., 2013; Turchetto-Zolet et al., 2013; Wang et al., 2013, 2017; Garzón-Orduña et al., 2014; Dolman and Joseph, 2016; Boucher et al., 2016; Pennington and Richardson, 2016; Weir et al., 2016; Bai et al., 2017; Nevado et al., 2018; Rull and Carnaval, 2019; Xu et al., 2019; and many others). In all of these taxonomic groups the number of Quaternary species ranges from a few species to all of the species in a genus or a family. Moreover, Quaternary species are sometimes extended over very large distribution areas, as discussed in the cases of carnations, garden balsams, and white-eyes. Such species can even be the only representative of a given group, such as the Andean *Lupinus* or the cichlids of the large African lakes. Therefore we must bury the myth that most current species already existed at the beginning of the Quaternary. The contribution that the Quaternary has made to present-day diversity and its spatial distribution has been crucial. Unfortunately, Quaternary speciation has not been quantified at a global level. It would be interesting to develop a global database on this subject, but the first impression, after the dated molecular phylogenetic and phylogeographical studies of the last decades, is that speciation has been outstanding.

3.5.3 Tropical biodiversity

As already mentioned (Section 3.2), the causes of LDGs are still controversial. Due to the dominant colonial view mentioned before, the debate has been focused on the explanation of the "anomalous" high tropical biodiversity instead of the depauperated extratropics. The main aspects discussed have been the balance between speciation and extinction, the environmental drivers that may have influenced speciation and the ecological mechanisms that may have favored coexistence, thus minimizing extinction. Here, we use the Neotropical region as an

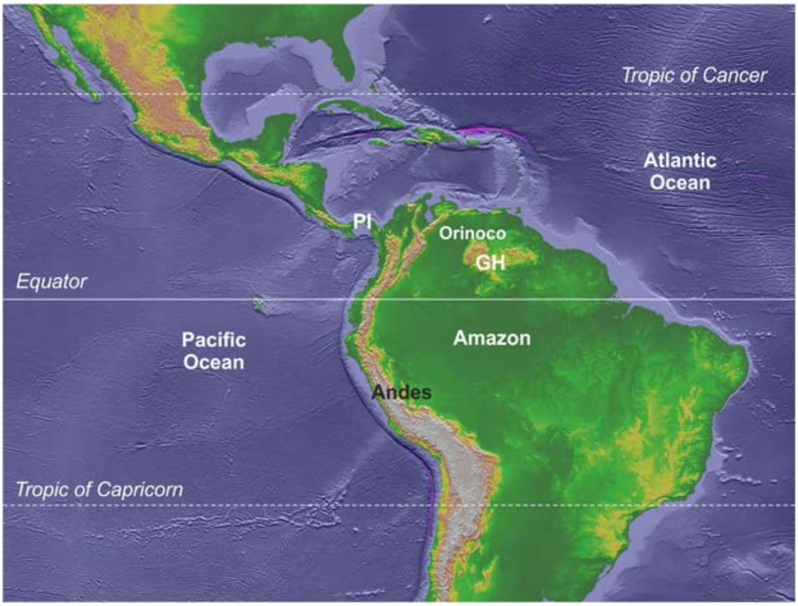

Figure 3.17 Map of the Neotropics. *IP*, Isthmus of Panama, *GH*, Guayana Highlands. *Base map courtesy SRTM Team NASA/JPL/NIMA.*

example because this part of the American continent (i.e., the zone between the Tropics of Cancer and Capricorn; Fig. 3.17) has been the most intensively studied in this sense. In addition, the American Tropics are also more diverse than their African and Asian counterparts, as they hold more vascular plants than those regions together and are also superior in amphibian, mammal, bird, butterfly, and reptile diversity (Antonelli and Sanmartín, 2011). In line with the nature of the book, we keep our focus on the influence that the Quaternary and its climatic changes may have had on Neotropical diversification. As usual for such controversial issues, there are two main opposing positions. One side argues that Quaternary diversification was of great importance, while the other one claims that most extant Neotropical species were formed earlier, during the Neogene, and that the Quaternary was principally a period of extinction. The first group emphasizes the role of climatic changes and refugia, while the second group believes that paleogeographical and paleotopographic changes driven by plate tectonics, especially the formation of mountains, favored diversification by altering the spatial patterns of migration routes and by creating new reproductive barriers.

In the former chapter (Section 2.2.2), we saw that the refuge hypothesis does not suit the Neotropics as well as it does temperate zones, at least not for the LGM, which was used as a representative of glaciations. This fact is a serious obstacle for the defenders of the Quaternary hypothesis because their main argument used to explain Neotropical diversity is the allopatric speciation that took place in the alleged refugia of rainforests between barriers formed by the dominating savannas and deserts (Haffer, 1969; Prance, 1982; Whitmore and Prance, 1987). On the other hand, followers of the Neogene hypothesis think that Neotropical species are older and offer two principal explanations for their origin. The first one is the formation of the Isthmus of Panama during the Pliocene, which made gene flow possible between the land biotas of North and South America and, at the same time, boosted the vicariance of marine organisms by the formation of a new major reproductive barrier. The Neogene hypothesis is mainly related to the rise of the Andes mountain range, which started in the Miocene and lasted until the Pliocene. This would have created new mountain habitats allowing adaptive radiation and separated the two sides of the mountain range, fostering vicariance. In addition, it changed the discharge patterns of the huge Amazonas and Orinoco basins, considerably transforming the spatial conditions of evolution (Raven and Axelrod, 1974; Gentry 1982). Fig. 3.18 shows these processes in the correct temporal context.

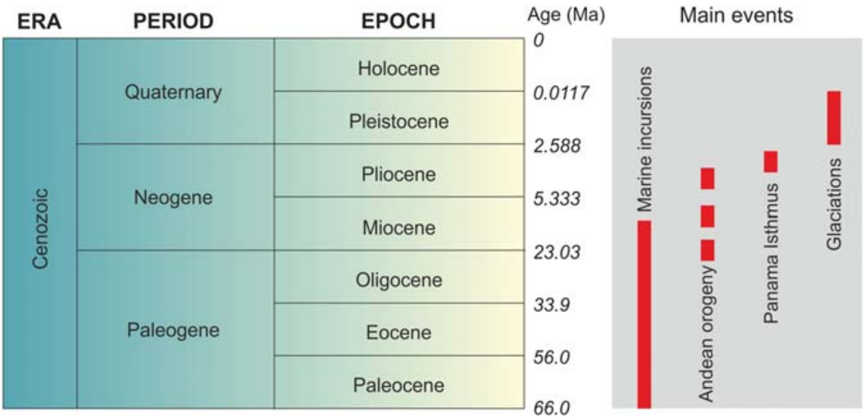

Figure 3.18 Periods and epochs of the Cenozoic Era, with the age of each limit in millions of years before present (Ma). The most important tectonic, paleogeographical and climatic events and their duration (*red bars*) are shown on the right. Redrawn from *Rull (2019)*.

Until several decades ago, these hypotheses were supported by geological, biogeographical, and paleoecological evidence, but the recent development of phylogenetics and phylogeography has provided more reliable tools to test these hypotheses by providing more accurate speciation chronologies. If the proponents of the Quaternary hypothesis were correct, most of the species would have emerged during the last approximately 2.6 million years, and the main drivers would have been climatic changes. However, if the Neogene hypothesis was correct, species would be older, and the tectonically driven reorganizations would be the more reasonable explanation. New research, however, did not have an immediate effect, as different authors used the new technology to defend their positions (e.g., Moritz et al., 2000; Hoorn et al., 2010). This continued until the arrival of the first metaanalyses that compiled all existing information and provided a synthesis as a basis for subsequent studies. The first of these analyses synthetized the available data on the age of more than 1400 Neotropical species belonging to more than 100 genera of different taxonomic groups, including amphibians, arachnids, birds, corals, echinoderms, fishes, mammals, mollusks, reptiles, and vascular plants (Rull, 2008). The results showed that these species emerged in a continuous manner (i.e., without phases of higher or lower diversification intensity) from the Miocene to the Pleistocene (Fig. 3.19). Moreover, to the utter disappointment of Quaternary and Neogene extremist parties, approximately half of the species originated before the Quaternary, and the other half originated during it. Therefore neither extreme position seemed to be correct.

Although the number of species in different groups varies according to the availability of phylogenetic and phylogeographical studies, insects, vascular plants, birds, echinoderms, and reptiles have a larger proportion of Quaternary species, while corals, amphibians, and fish have more species of Neogene origin (Rull, 2008). Several new publications and a large amount of information have come out since that first study, but the general tendencies have not changed. Subsequent metaanalyses confirmed that all chronological and causative possibilities must be taken into account, depending on the taxonomic group or the geographical area under study. In the end, as usual, inflexible positions are ruled out by empirical evidence. Now, we must accept that the high Neotropical biodiversity is the product of a large variety of environmental drivers and ecological-evolutionary processes and mechanisms that interacted in a complex spatial–temporal manner from the Neogene until the Pleistocene (Rull, 2011). Nevertheless, the importance of the Quaternary

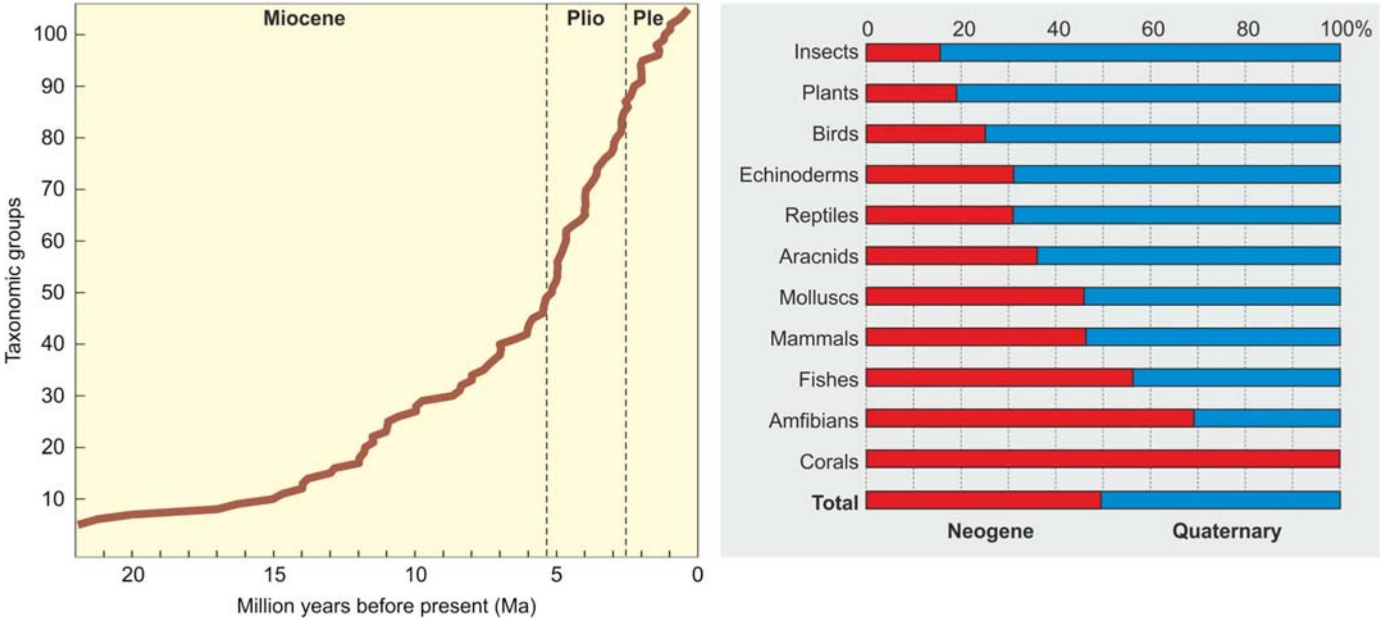

Figure 3.19 Neotropical diversification. Graph on the left illustrates the continuity of Neotropical diversification from the Miocene until the Pleistocene in terms of the number of current taxonomic groups (genera and supraspecific clades) that emerged (Plio—Pliocene, Ple—Pleistocene). The curve is cumulative and shows an exponential trend, without faster or slower phases, except for a Plio–Pleistocene acceleration. On the right the percentage of taxonomic groups that diversified in the Neogene (red) or the Quaternary (blue) is shown. The total number (last line) is very similar between the two geological periods. *Modified from Rull (2008)*.

period, our key topic, for the increase in Neotropical biodiversity is undeniable.

Quaternary speciation, however, does not necessarily imply refugial speciation (Rull, 2015). Other possible diversification mechanisms exist that are related to the recurrent waxing and waning of pathways for gene flow or reproductive barriers that might have occurred, for example, due to hydrographic network reorganizations or altitudinal fluctuations of mountain ecological belts (Fig. 2.15) provoked by climatic changes. In the first case, rivers can be effective reproductive barriers for land animals. If a river dries up, significantly decreases its flowrate, or changes course, the barrier may disappear, and gene flow between formerly isolated populations can be established. In the case of mountains the upslope shift of vegetation belts during interglacials might isolate populations of the same species on the highest peaks, where they can form new species by allopatric speciation. During glacials, mountain species can be reconnected by the descent of vegetation belts, thus facilitating gene flow and allowing speciation by hybridization to occur (Simpson, 1971). The mentioned paleogeographical, tectonic and climatic factors, and speciation mechanisms of the Neotropical region also played a role in the generation of biodiversity in other tropical regions of Earth, as did the ecological processes that impede extinction and favor coexistence. Why, then, are the Neotropics more diverse than the African and Asian tropics? Particular features of the geography, topography, climate, and biota of each region must have determined the existing differences, but this question is still open and subject to intense study.

3.6 Synthesis: net diversification

Our objective in this chapter was to discuss the nature, magnitude, and possible causes of biological diversification during the Quaternary. It is undeniable that evolution was highly active in this period and created intraspecific population variability in every species (population structure), together with a multitude of new species in most organismal groups. This affected biogeographical and global macroecological patterns, such as the latitudinal gradients of biodiversity. There are even genera and families of exclusively or almost exclusively Quaternary origin. Quaternary speciation played a fundamental role in several taxonomic groups and has exceeded extinction. This is especially obvious in the case of plants since only one global and some local, regional, or continental extinctions were recorded, the number of which is significantly smaller than the number of newly formed species (Section 2.2.3). More extinction events of animal species took place, especially of megamammals, but extinct species are still not more numerous than newly formed species. Therefore all the available evidence points toward the Quaternary as a period of net diversification for many taxonomic groups and of global net diversification.

However interesting it may be, a quantitative demonstration of this idea is still lacking because of incomplete quantitative data on extinction. The most reliable method is still based on the fragmentary and incomplete fossil record, and extinction is therefore probably still largely underestimated. Hopefully, the abovementioned biomarkers (Section 3.1.2) will contribute to improving this situation. Molecular phylogenetic trees are based on living organisms and, therefore, have been of limited use in estimating extinction, but experts continue working on the problem (Sanmartín and Meseguer, 2016). It was precisely thanks to genomics that a new, very useful type of fossil, the biomarker called ancient DNA (aDNA), was discovered. With the new technology of genetics, it is possible to detect the aDNA of extinct organisms in rocks and sediments and to produce a much more complete extinction record. Regarding the causes of Quaternary diversification, it seems obvious that climatic changes had an important role to play, but chronological coincidence between a given diversification event and a particular environmental change is not enough to demonstrate causal relationships. More in-depth analyses are necessary to identify the evolutionary processes and ecological mechanisms involved and their geographical expression.

References

Antonelli, A., Sanmartín, I., 2011. Why are there so many plant species in the Neotropics? Taxon 60, 403–414.

Avise, J.C., 2000. Phylogeography. The History and Formation of Species. Harvard University Press, Cambridge.

Bai, W.-N., Yan, P.-C., Zhang, B.-W., Woeste, K.E., Lin, K., Zhang, D.-Y., 2017. Demographically idiosyncratic responses to climate change and rapid Pleistocene diversification of the walnut genus *Juglans* (Juglandaceae) revealed by whole-genome sequences. New Phytol. 217, 1726–1736.

Barnosky, A.D., 2005. Effects of Quaternary climatic change on speciation in mammals. J. Mammal Evol. 12, 247–264.

Bennett, K.D., 2004. Continuing the debate on the role of Quaternary environmental change for macroevolution. Philos. Trans. R. Soc. B 359, 295–303.

Bittkau, C., Comes, H.P., 2009. Molecular inference of a Late Pleistocene diversification shift in Nigella s. la. (Ranunculaceae) resulting from increased speciation in the Aegean archipelago. J. Biogeogr. 36, 1346–1360.

Boucher, F.C., Zimmermann, N.E., Conti, E., 2016. Allopatric speciation with little niche divergence is common among alpine primulaceae. J. Biogeogr. 43, 591–602.

Bromham, L., 2019. Six impossible things before breakfast: assumptions, models, and belief in molecular dating. Trends Ecol. Evol. 34, 474–486.

Brown, J.H., 2014. Why are there so many species in the tropics? J. Biogeogr. 41, 8–22.

Chiou, K.L., Pozzi, L., Lynch Alfaro, J.W., Di Fiore, A., 2011. Pleistocene diversification of living squirrel monkeys (*Saimiri* spp.) inferred from complete mitochondrial genome sequences. Mol. Phylogenet. Evol. 59, 736–745.

Cohen, K.M., Finney, S.C., Gibbard, P.L., Fan, J.-H., 2013. The ICS International Chronostratigraphic Chart. Episodes 36, 199–204.

Cossíos, D., Lucherini, M., Ruíz-García, M., Angers, B., 2009. Influence of ancient glacial periods on the Andean fauna: the case of the pampas cat (*Leopardus colocolo*). BMC Evol. Biol. 9, 68.

Coyne, J.A., Orr, H.A., 2004. Speciation. Oxford University Press, Oxford.

Cracraft, J., 1985. Biological diversification and its causes. Ann. Missouri Bot. Gard. 72, 794–822.

Cristescu, M.E.A., Hebert, P.D.N., Witt, J.D.S., MacIsaac, H.J., Grigorovich, I.A., 2001. An invasion history for *Cercopagis pengoi* based on mitochondrial gene sequences. Limnol. Oceanogr. 46, 224–229.

Dawson, N.G., Hope, A.G., Talbot, S.L., Cook, J.A., 2014. A multilocus evaluation of ermine (*Mustela erminea*) across the Holarctic, testing hypotheses of Pleistocene diversification in response to climate change. J. Biogeogr. 41, 464–475.

Delord, J., 2007. The nature of extinction. Stud. Hist. Philos. Biol. Biomed. Sci. 38, 656–667.

Dolman, G., Joseph, L., 2016. Multi-locus sequence data illuminate demographic drivers of Pleistocene speciation in semi-arid southern Australian birds (*Cinclosoma* spp.). BMC Evol. Biol. 16, 226.

Eldredge, N., Gould, S.J., 1972. Punctuated equilibria: an alternative to phyletic gradualism. In: Schopf, T.J.M. (Ed.), Models in Paleobiology. Freeman Cooper, San Francisco, CA, pp. 193–223.

Foltz, D.W., Nguyen, A.T., Kiger, J.R., Mah, C.L., 2008. Pleistocene speciation of sister taxa in a North Pacific clade of brooding sea stars (*Leptasterias*). Mar. Biol. 154, 593–602.

Fontdevila, A., Mora, A., 2003. Evolución. Origen, Adaptación y Divergencia de las Especies. Síntesis, Madrid.

Forster, J.R., 1778. Observations Made During a Voyage Made Round the World, on Physical Geography. Natural History and Ethic Philosophy. G. Robinson, London.

Garzón-Orduña, I.J., Benetti-Longhini, J.E., Brower, A.V.Z., 2014. Timing the diversification of the Amazonian biota: Butterfly divergences are consistent with Pleistocene refugia. J. Biogeogr. 41, 1631–1638.

Gaston, K.J., Spicer, J.I., 2004. Biodiversity: and Introduction. Wiley-Blackwell, Hoboken, NJ.

Gentry, A.H., 1982. Neotropical floristic diversity: phytogeographical connections between Central and South America, Pleistocene climatic fluctuations, or an accident of the Andean orogeny? Ann. Missouri Bot. Gard. 69, 557–593.

Gould, S.J., Eldredge, N., 1977. Punctuated equilibria: the tempo and mode of evolution reconsidered. Paleobiology 3, 115–151.

Haffer, J., 1969. Speciation in Amazonian forest birds. Science 165, 131–137.

Hall, B.G., 2011. Phylogenetic Trees Made Easy. A How-To Manual. Oxford University Press, Oxford.

Hansen, T.E., 2006. The evolution of genetic architecture. Annu. Rev. Ecol. Evol. Syst. 37, 123–157.

Hewitt, G.M., 1999. Post-glacial re-colonization of European biota. Biol. J. Linn. Soc. 68, 87–112.

Hewitt, G.M., 2000. The genetic legacy of the Quaternary ice ages. Nature 405, 907–913.

Hewitt, G.M., Butlin, R.K., 1997. Causes and consequences of population structure. In: Krebs, J., Davies, N. (Eds.), Behavioural Ecology: An Evolutionary Approach. Blackwell, Oxford, pp. 350–372.

Hofreiter, M., Collins, M., Stwrat, J.R., 2012. Ancient biomolecules in Quaternary palaeoecology. Quat. Sci. Rev. 33, 1–13.

Hoorn, C., Wesselingh, F.P., ter Steege, H., Bermúdez, M.A., Mora, A., Sevink, J., et al., 2010. Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. Science 330, 927–931.

Hubbell, S.P., 2001. The Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press, Princeton.

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. U.S.A. 103, 10334–10339.

Huntley, J.W., Voelker, G., 2016. A tale of the nearly tail-less: the effects of Plio-Pleistocene climate change on the diversification of the African avian genus *Sylvietta*. Zool. Scr. 46, 523–535.

Irestedt, M., Fabre, P.-H., Batalha-Filho, H., Jønsson, K.A., Roselaar, C.S., Sangster, G., et al., 2013. The spatio-temporal colonization and diversification across the Indo-Pacific by a 'great speciator' (Aves, *Erythropitta erythrogaster*). Proc. R. Soc. Lond. B 280, 20130309.

Jablonski, D., 2000. Micro- and macroevolution: scale and hierarchy in evolutionary biology and paleobiology. Paleobiology 26, 15–52.

Janssens, S.B., Knox, E.B., Huysmans, S., Smets, E.F., Merckx, V.S.F.T., 2009. Rapid radiation of *Impatiens* (Balsaminaceae) during Pliocene and Pleistocene: result of global climate change. Mol. Phylogenet. Evol. 52, 806–824.

Johnson, N.K., Cicero, C., 2004. New mitochondrial DNA data affirm the importance of Pleistocene speciation in North American birds. Evolution 58, 1122–1130.

Jorgensen, T.H., Olessen, J.M., 2001. Adaptive radiation of island plants: evidence from *Aeonium* (Crassulaceae) from the Canary Islands. Perspect. Plant. Ecol. Evol. Syst. 4, 29–42.

Kim, S.-C., McGowen, M.R., Lubinsky, P., Barber, J.C., Mort, M.E., Santos Guerra, A., 2008. Timing and tempo of early and successive radiative adaptions in Macaronesia. PLoS One 3, e2139.

Kimura, M., 1983. The Neutral Theory of Molecular Evolution. Cambridge University Press, Cambridge.

Kutschera, U., Niklas, K.J., 2004. The modern theory of biological evolution: an expanded synthesis. Naturwissenschaften 91, 255–276.

Leavitt, S.D., Lumbsch, H.T., Stenroos, S., Clair St., L.L., 2013. Pleistocene speciation in North American lichenized fungi and the impact of alternative species circumscriptions and rates of molecular evolution on divergence estimates. PLoS One 8, e85240.

Levsen, N.D., Tiffin, P., Olson, M.S., 2012. Pleistocene speciation in the genus *Populus* (Salicaceae). Syst. Biol. 61, 401–412.

Lomolino, M.V., Riddle, B.R., Whittaker, R.J., 2016. Biogeography. Oxford University Press, Oxford.

Lu, Q., Zhu, J., Yu, D., Xu, X., 2016. Genetic and geographical structure of boreal plants in their southern range: phylogeography of *Hippuris vulgaris* in China. BMC Evol. Biol. 16, 34.

Lutz, H.L., Weckstein, J.D., Patané, J.L., Bates, J., Aleixo, A., 2013. Biogeography and spatio-temporal diversification in *Selenidera* and *Andigena* Toucans (Aves: Ramphastidae). Mol. Phylogenet. Evol. 69, 873–883.

Mäder, G., Fregonezi, J.N., Lorenz-Lemke, A.P., Bonatto, S.L., Freitas, L.B., 2013. Geological and climatic changes in Quaternary shaped the evolutionary history of *Calibrachoa heterophylla*, an endemic South-Atlantic species of petunia. BMC Evol. Biol. 13, 178.

Magurran, A.E., 1996. Ecological Diversity and Its Measurement. Chapman and Hall, London.

Mannion, P.D., Upchurch, P., Benson, R.B.J., Goswami, A., 2014. The latitudinal diversity gradient through deep time. Trends Ecol. Evol. 29, 42–50.

Mayr, E., 1982. Speciation and macroevolution. Evolution 36, 1119–1132.

Mayr, E., 1996. The modern evolutionary theory. J. Mammal. 77, 1–7.

McGlone, M.S., 1996. When history matters: scale, time, climate and tree diversity. Glob. Ecol. Biogeogr. Lett. 5, 309–314.

Meyer, A., Zardoya, R., 2003. Recent advances in the (molecular) phylogeny of vertebrates. Annu. Rev. Ecol. Evol. Syst. 34, 311–338.

Mittelbach, G.G., Schemske, D., Cornell, H.V., Allen, A.P., Brown, J.M., Bush, M.B., et al., 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. Ecol. Lett. 10, 315–331.

Moritz, C., 1994. Defining "evolutionarily significant units" for conservation. Trends Ecol. Evol. 9, 373–375.

Moritz, C., 2002. Strategies to protect biological diversity and the evolutionary processes that sustain it. Syst. Biol. 51, 238–254.

Moritz, C., Patton, J.L., Schneider, C.J., Smith, T.B., 2000. Diversification of rainforest faunas: an integrated molecular approach. Annu. Rev. Ecol. Syst. 31, 533–563.

Moyle, R.G., Filardi, C., Smith, C.E., Diamond, J., 2009. Explosive Pleistocene diversification and hemispheric expansion of a "great speciator". Proc. Natl. Acad. Sci. U.S.A. 106, 1863–1868.

Mullen, S.P., Savage, W.K., Wahlberg, N., Willmott, K.R., 2011. Rapid diversification and not clade age explains high diversity in neotropical *Adelpha* butterflies. Proc. R. Soc. B 278, 1777–1785.

Mutke, J., Barthlott, W., 2005. Patterns of vascular plant diversity at continental to global scales. Biologiske Skrifter 55, 521–531.

Nagalingum, N.S., Marshall, C.R., Quental, T.B., Rai, H.S., Little, D.P., Mathews, S., 2011. Recent synchronous radiation of a living fossil. Science 334, 796–799.

Nei, M., Kumar, S., 2000. Molecular Evolution and Phylogenetics. Oxford University Press, Oxford.

Nevado, B., Contreras-Ortiz, N., Hughes, C., Filatov, D.A., 2018. Pleistocene glacial cycles drive isolation, gene flow and speciation in the high-elevation Andes. New Phytol. 219, 779–793.

Orlando, L., Cooper, A., 2014. Using ancient DNA to understand evolutionary and ecological processes. Annu. Rev. Ecol. Evol. Syst. 45, 573–598.

Parducci, L., Bennet, K.D., Ficetola, G.F., Alsos, I.G., Suyama, Y., Wood, J.R., et al., 2017. Ancient plant DNA in lake sediments. New Phytol. 214, 924–942.

Pennington, J.E., Richardson, R.T. (Eds.), 2016. Origin of Tropical Diversity: From Clades to Communities. Frontiers Media, Lausanne.

Pennington, J.E., Lavin, M., Prado, D., Pendry, C.A., Pell, S.K., Butterworth, C.A., 2004. Historical climate change and speciation: neotropical seasonally dry forest plant show patterns of both Tertiary and Quaternary diversification. Philos. Trans. R. Soc. B 359, 515–538.

Peres, E.A., Sobral-Souza, T., Perez, M.F., Bonatelli, I.A.S., Silva, D.P., Silva, M.J., et al., 2015. Pleistocene niche stability and lineage diversification in the subtropical spider *Araneus omnicolor* (Araneidae). PLoS One 10, e0121543.

Pielou, E.C., 1975. Ecological Diversity. John Wiley and Sons, New York.

Pontarp, M., Bunnefeld, L., Cabral, J.S., Etienne, R.S., Fritz, S.A., Gillespie, R., et al., 2019. The Latitudinal Diversity Gradient: novel understanding through mechanistic eco-evolutionary models. Trends Ecol. Evol. 34, 211−223.

Prance, G.T. (Ed.), 1982. Biological Diversification in the Tropics. Columbia University Press, New York.

Price, P.V., 1996. Biological Evolution. Saunders, Philadelphia, PA.

Raby, M., 2017. The colonial origins of tropical field stations. Am. Sci. 105, 216−223.

Raven, P.H., Axelrod, D.I., 1974. Angiosperm biogeography and past continental movements. Ann. Missouri Bot. Gard. 61, 539−673.

Richardson, J.E., Pennington, R.T., Pennington, T.D., Hollingsworth, P.M., 2001. Rapid diversification of a species-rich genus on Neotropical rain forest trees. Science 293, 2242−2245.

Ricklefs, R.E., 2012. Naturalists, natural history, and the nature of biological diversity. Am. Nat. 179, 423−435.

Rosenzweig, M.L., 1995. Species Diversity in Space and Time. Cambridge University Press, Cambridge.

Rull, V., 2008. Speciation timing and neotropical biodiversity: the Tertiary-Quaternary debate in the light of molecular phylogenetic evidence. Mol. Ecol. 17, 2722−2729.

Rull, V., 2011. Neotropical biodiversity: timing and potential drivers. Trends Ecol. Evol. 26, 508−513.

Rull, V., 2012. Past natural history and ecological biodiversity modeling. Syst. Biodivers. 10, 261−265.

Rull, V., 2015. Pleistocene speciation is not refuge speciation. J. Biogeogr. 42, 602−609.

Rull, V., 2019. Neotropical diversification: historical overview and conceptual insights. In: Rull, V., Carnaval, A. (Eds.), Neotropical Diversification: Patterns and Processes. Springer, Berlin.

Rull, V., Carnaval, A. (Eds.), 2019. Neotropical Diversification: Patterns and Processes. Springer, Berlin.

Rutschmann, F., 2006. Molecular dating of phylogenetic trees: a brief review of current methods that estimate divergence times. Divers. Distrib. 12, 35−48.

Ryder, O.A., 1986. Species conservation and systematics: the dilemma of subspecies. Trends Ecol. Evol. 1, 9−10.

Salzburger, W., Mack, T., Verheyen, E., Meyer, A., 2005. Out of Tanganyika: genesis, explosive speciation, key-innovations and phytogeography of haplochromine cichlid fishes. BMC Evol. Biol. 5, 17.

Sanmartín, I., Meseguer, A.S., 2016. Extinction in phylogenetics and biogeography: from timetrees to patterns of biotic assemblage. Front. Genet. 7, 35.

Simpson, B., 1971. Pleistocene changes in the flora and fauna of South America. Science 173, 771−780.

Slatkin, M., Racimo, F., 2016. Ancient DNA and human history. Proc. Natl. Acad. Sci. U.S.A. 113, 6380−6387.

Stebbins, G.L., 1974. Flowering Plants: Evolution Above the Species Level. Belknap Press, Cambridge.

Steeves, T.E., Anderson, D.J., Friesen, V.L., 2005. The Isthmus of Panama: a major physical barrier to gene flow in a highly mobile pantropical seabird. J. Evol. Biol. 18, 1000−1008.

Templeton, A.R., 1980. The theory of speciation *via* the founder principle. Genetics 94, 1011−1038.

Thacker, C.E., 2017. Patterns of divergence in fish species separated by the Isthmus of Panama. BMC Evol. Biol. 17, 111.

Thomas, D.C., Hughes, M., Phuttai, T., Ardi, W.H., Rajbhandary, S., Rubite, R., et al., 2012. West to east dispersal and subsequent rapid diversification of the mega-diverse genus *Begonia* (Begoniaceae) in the Malesian archipelago. J. Biogeogr. 39, 98–113.

Turchetto-Zolet, A.C., Pinheiro, F., Salgueiro, F., Palma-Silva, C., 2013. Phylogeographical patterns shed light on evolutionary process in South America. Mol. Ecol. 22, 1193–1213.

Valente, L.M., Savolainen, V., Vargas, P., 2010. Unparalleled rates of species diversification in Europe. Proc. R. Soc. B 277, 1687.

Van Doorn, G.S., Noest, A.J., Hogeweg, P., 1998. Sympatric speciation and extinction driven by environment dependent sexual selection. Proc. R. Soc. B 265, 1915–1919.

Van Valen, L., 1973. A new evolutionary law. Evol. Theory 1, 1–30.

Veríssimo, J., Znari, M., Stuckas, H., Fritz, U., Pereira, P., Teixeira, J., et al., 2016. Biol. J. Linn. Soc. 119, 943–959.

von Humboldt, A., 1850. Views of Nature: or Contemplation on the Sublime Phenomena of Creation. Harrison and Sons, London.

Wang, Q., Abbott, R.J., Yu, Q.S., Lin, K., Liu, J.-Q., 2013. Pleistocene climate change and the origin of two desert plant species, *Pugionium cornutum* and *Pugionium dolabratum* (Brasssicaceae), in northwest China. N. Phytol. 199, 277–287.

Wang, Y.-H., Comes, H.P., Cao, Y.-N., Guo, R., Mao, Y.-R., Qiu, Y.-X., 2017. Quaternary climate change drives allo-peripatric speciation and refugial divergence in the *Dysosma versipellis-pleiantha* complex from different forest types in China. Sci. Rep. 7, 40261.

Weir, J.T., 2006. Divergent timing and patterns of species accumulation in lowland and highland neotropical birds. Evolution 60, 842–855.

Weir, J., Schluter, D., 2004. Ice sheets promote speciation in boreal birds. Proc. R. Soc. Lond. B 271, 1881–1887.

Weir, J.T., Haddrath, O., Robertson, H.A., Colbourne, M.N., Baker, A.J., 2016. Explosive ice age diversification of kiwi. Proc. Natl. Acad. Sci. U.S.A. 113, E5580–E5587.

Whitmore, T.C., Prance, G.T., 1987. Biogeography and Quaternary History in Tropical Latin America. Oxford University Press, New York.

Whittaker, R.H., 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecol. Monogr. 30, 279–338.

Wiley, E.O., Lieberman, B.S., 2011. Phylogenetics. The Theory of Phylogenetic Systematics. Wiley-Blackwell, Hoboken, NJ.

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

Woese, C.R., Kandler, O., Wheelis, M.L., 1990. Towards a natural system of organisms: proposal for the domain Archaea, Bacteria and Eucarya. Proc. Natl. Acad. Sci. U.S.A. 87, 4576–4579.

Xu, X.-X., Cheng, F.-Y., Peng, L.-P., Sun, Y.Q., Xu, J.-G., Li, S.Y., et al., 2019. Late Pleistocene speciation of three closely related tree peonies endemic to the Qinling-Daba Mountains, a major glacial refugium in Central China. Ecol. Evol. 9, 7528–7548.

You, Y., Sun, K., Xu, L., Wang, L., Jiang, T., Lu, G., 2010. Pleistocene glacial cycle effects on the phylogeography of the Chinese endemic bat species, *Myotis davidii*. BMC Evol. Biol. 10, 208.

Zhao, J.-L., Zhang, L., Dayanandan, S., Nagaraju, S., Liu, D.-M., Li, Q.-M., 2013. Tertiary Origin and Pleistocene Diversification of Dragon Blood Tree (*Dracaena cambodiana*—Asparagaceae) Populations in the Asian Tropical Forests.

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CHAPTER FOUR

Communities: adjustments, innovations, and revolutions

Contents

As mentioned before (Chapter 2), this chapter is focused on synecology, which is also called community ecology or ecosystem ecology because it is the study of ecology at the levels of communities and ecosystems (Walter and Hengeveld, 2000). In ecology the classic definition of a community is a group of populations of different species that occupy the same area at a particular time (Vellend, 2010). The last factor, time, is not always included in definitions of an ecological community, but based on what we saw in earlier chapters, we can deduce that it is of fundamental importance. This aspect will be further discussed. There is yet another important detail for the concept of the community, as coexistence in space and time is not sufficient; an intrinsic functional condition must be fulfilled so that we can talk about an ecosystem, the basic functional unit of the biosphere. For an ecosystem to be functional, populations of species that live in the same community must interact with each other (biotic interactions) and with the environment (abiotic interactions). Of course,

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ecosystem functioning depends on the taxonomic composition of the community, which determines its structure (or architecture), and on diversity, not only in terms of the number of species (species richness) but also in terms of species abundance (or equitability), which is an indicator of the ecological complexity and functionality of the ecosystem (Raffaelli, 2006). More diverse communities have more complex ecological relations. Fig. 4.1 shows a hypothetical example of two communities with the same biodiversity (species richness) but different ecological diversities. This difference leads to completely divergent structures and functionalities. Margalef (1997) compared biodiversity to a dictionary in which we can find all the words of a language together with their meanings, while ecological diversity is similar to a novel, where only a selection of these words are used and combined to form meaningful sentences and ideas.

Community ecology includes the study of patterns of diversity, abundance and species composition in a community, and of processes that are responsible for the formation of those patterns. In other words, community ecology studies what communities are like and why they are so (Vellend, 2010). These two questions, together with ecological functioning, which include ecological relationships and corresponding matter and energy flows, make up ecosystem ecology. The apparently simple concept of the community has varied over time. At the beginning of the 20th century the so-called Clementsian theory dominated. This theory of the American plant ecologist Frederic Clements (1916) considered the community as a superorganism that is able to regulate and manage its own dynamics through ecological succession, which always leads to a stable state in equilibrium with the environment, known as the climax, that remains unchanged over time. Some time later, another American ecologist, Henry Gleason (1926), suggested that defining relatively permanent units, such as communities, did not make much sense given that species are idiosyncratic, that is, they have an individual relationship with the environment. This idea was ignored until the middle of the past century, when a third American plant ecologist, Robert Whittaker, used Gleason's ideas to develop the concept of the spatial continuum. According to this concept, the presence and abundance of species vary along complex environmental gradients; therefore it is not possible to identify characteristic associations of species, such as communities (Fig. 4.2) (Whittaker, 1951).

The concept of species' idiosyncrasy led to the idea of communities as artificial units defined by ecologists rather than as biological realities (Palmer and White, 1994; Scheiner and Willig, 2008). At the end of the

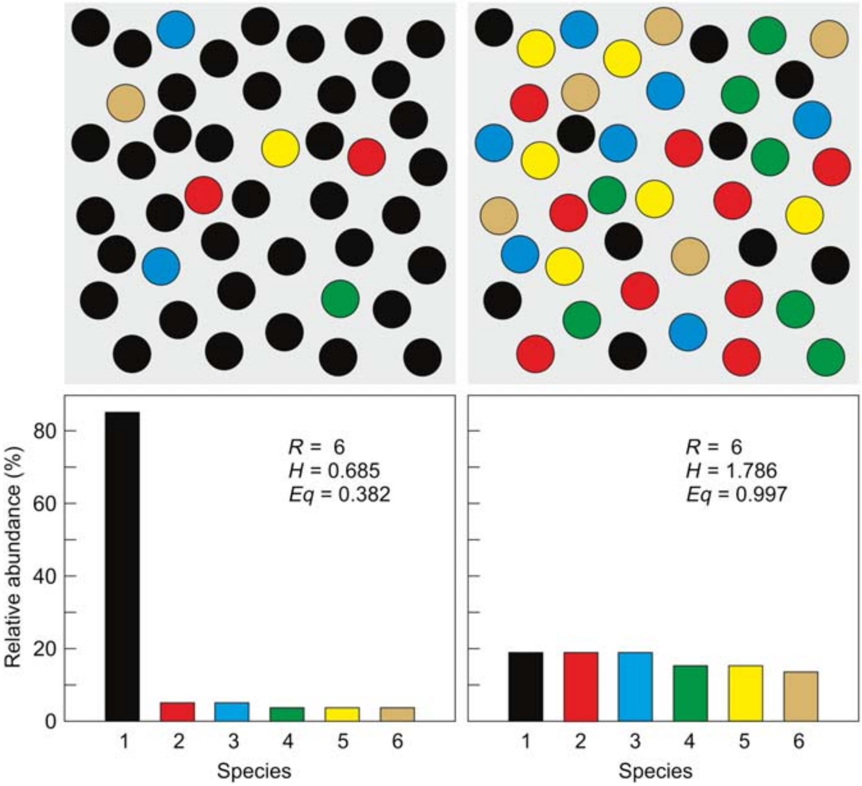

Figure 4.1 Illustration of the difference between species richness and ecological diversity. Boxes at the top represent the hypothetical distributions of six species in a given geographical area. Apparently, diversity looks higher in the right box, but both boxes have the same number of species (six), so the species richness is equal ($R = 6$). The relative abundances of the species are different, however. In the box on the left the black species is dominant (80% of the individuals belong to it). On the right the species are evenly represented. Indexes of ecological diversity take into account the relative abundance of species. In this case the Shannon–Weaver index (H) was used. It expresses the higher ecological diversity of the box on the right ($H = 1.786$) than of that on the left ($H = 0.685$) due to the greater equitability of the former ($Eq = 0.997$ and $Eq = 0.382$, respectively) in the division of individuals among species. Equitability varies between 0 (when all individuals belong to the same species) and 1 (when all species are equally represented).

20th century, these theories led to a level of frustration among ecologists that resulted in statements such as "all this begs the question of why ecologists continue to devote so much time and effort to traditional studies on community ecology" and "community ecology is a mess" (Stott, 1998; Lawton, 1999). At the beginning of the 21st century, there was a wave of

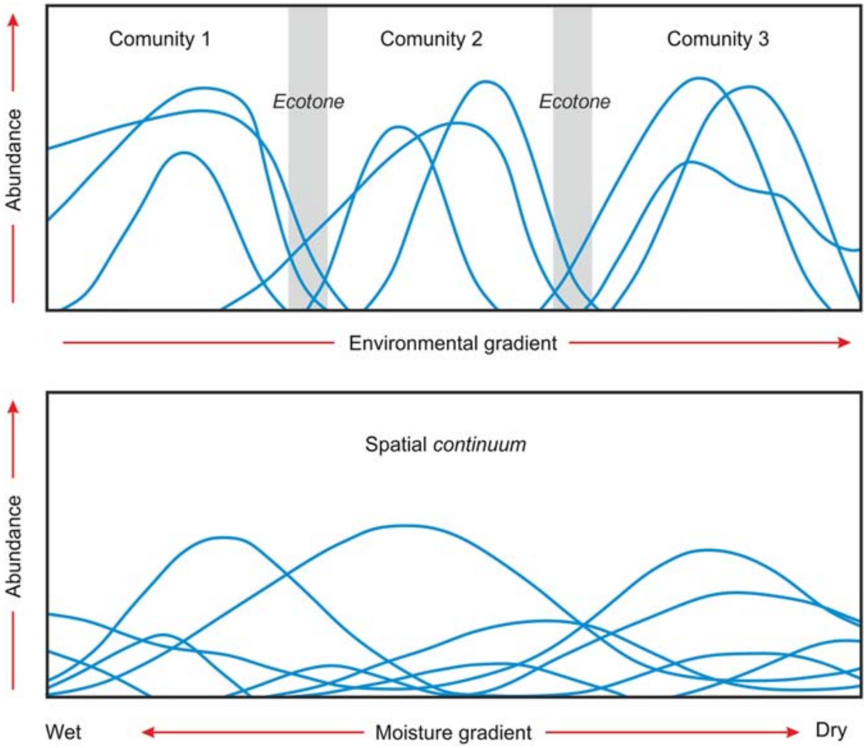

Figure 4.2 Relative abundances of various species (*blue lines*), considering two different concepts of species' responses to environmental gradients. Above: hypothetical model of community formation in discrete units, showing the boundaries (ecotones) along an environmental gradient according to Clements's theory (1916), in which interactions between species are determining factors in community composition and development. Below: spatial continuum of tree species, without obvious formation of communities, along a real wetland gradient on Santa Catalina Mountain (Arizona, United States). This setup fits Gleason's model (1926) of species' individual (idiosyncratic) responses to environmental gradients. *Redrawn from Whittaker (1951)*.

optimism led by Simberloff (2004) and Ricklefs (2008), among others, that resulted in community ecology being redefined to take into account not only local community features but also regional patterns. According to this reformulation, inspired by the theory of island biogeography of MacArthur and Wilson (1963) (Section 4.4.1), what we need to understand is how the factors that condition species distributions at a regional scale determine their local coexistence in particular communities. In this context the primary entities of community ecology are not species but their populations, and the main question is how these populations may coexist in different communities at a regional scale. Under this view, historical and biogeographical factors such as speciation and dispersal matter more than local processes.

This will be better understood by using the concepts of the metapopulation and metacommunity (Hanski, 1999; Holyoak et al., 2005; Alexander et al., 2012). A metapopulation is a population of populations, that is, a group of populations of the same species scattered across a given region that are genetically linked by dispersal. For example, in a Neotropical forest—savanna mosaic, each local forest patch may have its own sloth populations, and the assemblage of all these populations across the whole forested area may form the regional sloth metapopulation, provided that sloths can disperse among forest patches across the savanna matrix. A metacommunity is a multispecies metapopulation, that is, a set of communities linked by multiple interacting species. In the same forest—savanna mosaic the assemblage of all forest patches is the regional forest metacommunity, which includes multiple metapopulations of different plant and animal species. In this framework a particular community results from the local coexistence of samples (i.e., populations) of the different species' metapopulations available in the metacommunity. Using the same example of the forest—savanna mosaic, the composition of a particular forest patch results from the local coexistence of populations representing the regional metapopulations of sloths, trumpet trees (where sloths used to thrive), and all other species of the forest metacommunity that participate in ecological dynamics at a regional level.

This approach to community ecology is better suited to understanding how local communities are and which biotic and abiotic factors influence their composition and dynamics. However, it gives no answer as to how this assemblage of species has formed and how it can develop in the future. Communities do not come instantaneously from nothing as if there were a pool of species in a foyer waiting for the signal to get on stage and form a community. Ecological communities follow a process, so-called ecological succession, to generate their structure, and it can be of a shorter or longer duration according to community type. For example, plankton communities of a high-mountain lake become structured a few weeks after the ice melts, while it can take a fir forest centuries or millennia to establish its configuration. We call this process community assembly, and to understand it, we need to study time frames that are significantly longer than the decades usually considered by (neo)ecologists. Therefore we need paleoecology, which at the same time can provide information about the permanence or transience of communities to verify either the hypothesis of Clements or that of Gleason and Whittaker. It would also be interesting to check whether Whittaker's concept of a space continuum could be transferred to time and with what results.

In the second chapter, we observed how species were idiosyncratic in their responses to environmental changes and what consequences this has had during the Quaternary for individual biogeographical reorganizations. In the third chapter, we showed that a significant part of the current biodiversity emerged during the Quaternary by means of various evolutionary mechanisms. In this chapter, we will analyze the influence that the biogeographical reorganizations of the existing species and the formation of new species have had on the assembly of communities and their developments until they reached the current situation. We will mostly rely on the methods of paleoecology, more precisely on palynology, to understand the dynamics of vegetation, which is of fundamental importance to the structure of terrestrial communities. As always, we will start with an introduction of the terms and concepts necessary to situate paleoecological evidence in a general ecological context able to link paleoecology and (neo)ecology in a single narrative. Palynological methods of vegetation reconstruction are explained in detail by Birks and Birks (1980), Faegri et al. (1989), and Bennett and Willis (2001), among others.

4.1 Long-term ecology

In the introduction, we commented briefly on how several ecological processes need more time than the periods routinely considered in ecological studies, which usually do not exceed decades. There is no precise definition of what "long term" means in ecology, as it varies according to the organisms and communities under study. However, it is usually considered to range between the centennial and millennial timescales. We have also mentioned that this type of study is not undertaken out of simple historical curiosity to find out about past events (museum syndrome) but emerges from the need to understand processes that gave rise to the current situation (living syndrome). In the words of the British paleoecologist Keith Bennett, we must learn to consider the millennial scale as part of our modern world and not as part of its history (Bennett, 1997). To cite just a few examples, if we did not take into account the centennial or millennial timescale, we would not be able to find enough evidence to study processes such as the following (Rull, 2010, 2012a):

- the origin and age of species of extant communities,
- species coexistence or extinction and their ecological causes,
- the origin of biodiversity patterns,
- the constancy (or not) of the species niche over time,
- the roles of migration and dispersal in the assembly of extant communities,
- the micro- and macroevolutionary patterns and processes within communities,
- ecological succession and its biotic and abiotic drivers,
- the constancy (or not) of ecological communities over time,
- the ecological stability of communities and its resilience and associated processes,
- community-level biotic responses to climatic changes, and
- preanthropogenic ecosystems and their modification processes.

It seems obvious that proper knowledge of these aspects and others is not only useful to increase and improve our cultural heritage as intelligent beings but also necessary to forecast possible future scenarios of global change with more confidence and, thus, take proper steps. It is equally evident that these topics are of considerable interest to ecologists, in general. Once, after a talk on time in ecology, a fellow ecologist who specialized in biogeochemical cycles approached the author of this book to manifest that he had never wondered about questions such as those stated earlier. However, this was only one occasion in almost 40 years.

As mentioned in the introduction, time is a continuum, and the past, present, and future are but human inventions that only serve to classify ecological patterns and processes—and, as a consequence, those who study these patterns and processes—into exclusive categories. We have created boundaries among these disciplines and their practitioners that are so difficult to cross that eventually the categories become independent entities with hardly any communication between them, similar to a speciation process (Section 3.1.1). From a strictly scientific point of view that is based on empiricism, only the past is real because it has already happened and has left observable and measurable traces. The future is still only a concept that emanates from our mind based on cyclic—that is, predictable—phenomena. Days, years, centuries, millennia, and so on go on repeatedly, and there is no reason to believe that it will not always be so. The present, on the other hand, is similar to a point that advances on the continuous curve of time (a derivative, in mathematical terms) that transforms the future into the past as it passes by. Another way to imagine this situation is to picture time as an infinite container that is gradually filled up with a liquid (i.e., reality). In this metaphor the past is the amount of liquid already in the container, and the present is the surface of the liquid. It seems quite logical that if we want to find out something about reality, we should look at the whole available amount of liquid and not only the surface, as if the latter were a crystal ball.

True long-term ecology should break down the boundaries between the past, present and future and merge the corresponding disciplines into a single ecology. The word "true" is introduced to differentiate the concept used here, which incorporates the past, from the current version of long-term ecology, which considers only the present and future since it is based on recently created ecological stations that measure current parameters and intend to continue doing the same in the near future (e.g., Müller et al., 2010). If we included the past, the obtained time series could be much longer and more informative. However, we still need to overcome several psychological and methodological obstacles to get there. We will not go into detail here, but a major handicap is how to combine past and present (and future) data into one continuous series with the same time resolution. For this, we need to find a resolution level that is common for past and present-future measurements. In Fig. 4.3, we can observe that this resolution level ranges from decades to seasons and that the optimal resolution is the annual scale. The study that provided this figure also analyzed other difficulties and proposed some solutions, which suggest that the possibility of achieving true, long-term ecology seems to be simply a question of time and good intentions from all sides (Rull, 2014).

4.2 Succession and community assembly

Based on what we discussed in the last chapter about the origins of species and their chronology, it is easy to understand that the species within a given community did not originate at the same time and, therefore, did not always coexist in the same ecosystem. This raises a number of questions as to how present-day communities were assembled or how

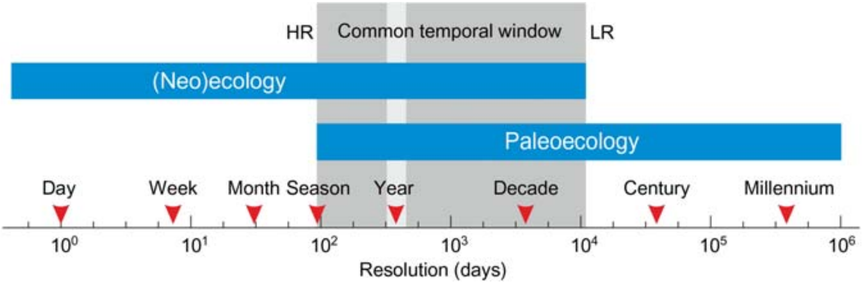

Figure 4.3 Temporal scales of (neo)ecology and paleoecology (blue) and their overlap (gray). The highest resolution (HR) is reached in the seasonal range, and the lowest resolution (LR) is reached in the decadal range. The optimal resolution for real, long-term ecological series is annual resolution. *Redrawn and modified from Rull (2014)*.

niches of different species evolved so that precisely those species would end up forming a given community. Defenders of the neutral theory of biodiversity (Section 3.4.1) would not hesitate to declare that the assembly of a community is the result of a random process based on the regional metacommunity species pool and the respective migratory and dispersal capacities of those species, independent of the ecological requirements—that is, the particular niche features—of each species (Hubbell, 2001). Gleason (1926) and his followers would consider community assembly to be the result of a spatiotemporally transient coincidence of several species with similar environmental requirements. According to Clements (1916), community assembly is the result of a process called ecological succession, which ends in a steady climax community, which is in equilibrium with the regional climate. In plant ecology the concept of the climax has been expressed as Potential Natural Vegetation (PNV), which has been defined in several ways but basically refers to the vegetation that "corresponds" to a given climatic context, without human influence (review in Chiarucci et al., 2010). Under this view, if a community is different from what would be expected in a given environment, it is interpreted as a degraded community, as a result of human disturbance, or an intermediate state toward the target PNV, which will establish sooner or later. Therefore the PNV seems to be an inescapable destiny determined from the beginning, regardless of the intermediate steps that lead there.

This notion is similar to the ancient Greek mythological idea of destiny. The Moirai (known in English as The Fates) were the incarnations of destiny that controlled the thread of life of humans and gods from birth to death (Fig. 4.4). No mortal or deity, not even Zeus, escaped their pre-established destiny under the control of the Fates. Gods were entitled to intervene in only minor human affairs. There were three Fates, the "spinner" (Clotho), the "allotter," (Lachesis) and the "unturnable" (Atropos). Clotho spun the thread of life on her spindle, which represents birth. Lachesis measured the thread of life allotted to each person, and Atropos cut the thread of life with her shears at the moment of death. But all of this was predetermined. In Clementsian ecological succession, Clotho would control the initiation of the process (pioneer communities), Lachesis would decide the length and main features of community development (perhaps with some lesser interference from the gods), and Atropos would have been in charge of finishing the process once the inexorable end (i.e., the climax community) arrived.

The classic concept of ecological succession is fundamentally Clementsian. According to Clements (1916), succession is the process of climax formation and is comparable to the development of an organism as it arises, grows, matures, and dies. Moreover, a succession leading to a climax community is able to reproduce itself by repeating the same stages again and again. This is the Clementsian idea of ecological succession, or climax formation, as a superorganism. In general, succession is a process of community change, both in structure and taxonomic composition, and

Figure 4.4 The three Moirai (Clotho, Lachesis, and Atropos) of ancient Greek mythology. *Reproduction from Giorgio Ghisi, Italian artist of the 16th century (publicly available at fineartamerica.com).*

goes through several stages called seral communities (the term "sere" refers to all of these communities together). To understand this concept, we should imagine a terrain, a water body, or any other environment that, for some reason, is uninhabited, although the conditions are suitable for life. The first organisms to arrive and establish populations are the pioneers, which are usually organisms with a high dispersal capacity, high reproductive rate, and relatively short life cycle (in the case of plants, these are usually annuals). This is the first seral stage, colonization. The growth of pioneer populations alters the environment (e.g., by the formation of soil or by changing the physicochemical conditions of water), thus providing a more accessible milieu for other species that would have been unable to colonize a wasteland or clearer water. With the progressive arrival of new inhabitants, the physicochemical and biological conditions continue developing, as do the seral stages, until an equilibrium is reached with the local climate and environment. This is the climax community, and the most common example is a mature forest (Fig. 4.5). The British ecologist Arthur Tansley slightly changed this concept when he proposed

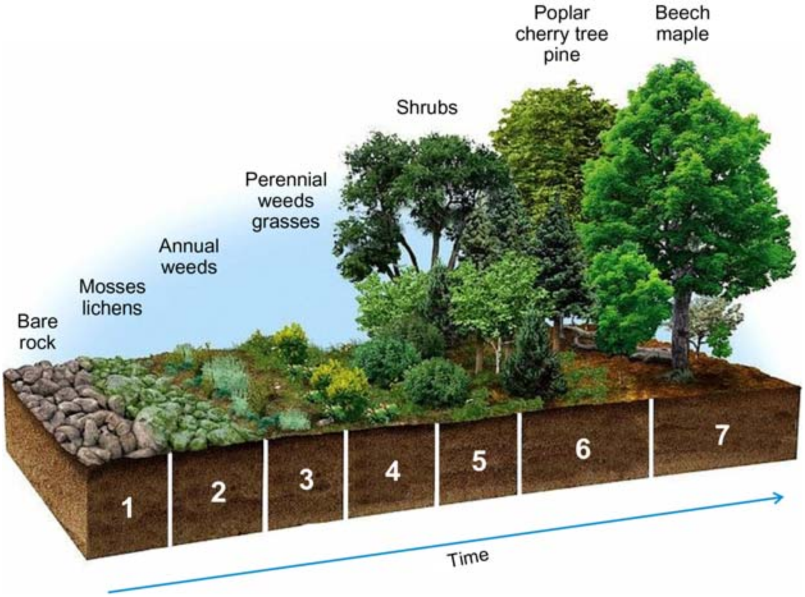

Figure 4.5 Formation of a beech and maple forest as an example of ecological succession. Seral stages are indicated by numbers, and their main components are shown in the upper part. *Base image used under Creative Commons license (en.wikipedia.org).*

the polyclimax theory, according to which there are more than one climax community for any given climate depending on the soil, topography, and other local factors, including the influence of animals (Tansley, 1935). In contrast to initial colonizing species, species of the climax community do not reproduce very actively, and their success is instead linked to their individual longevity. With few modifications, this is the concept of ecological succession, as a deterministic, directional, and predictable process, commonly used in ecological literature (e.g., Odum, 1969; Connell and Slatyer, 1977) (Table 4.1).

Successions are considered primary when they initiate in substrates recently formed by natural processes and that have not yet been inhabited. These conditions could exist, for example, when glacial ice retreats from an area, when a volcanic island is formed, or when a lake is filled with water for the first time (Walker and del Moral, 2011). Secondary successions take place in previously inhabited areas where communities have been partially erased by natural catastrophes or anthropogenic deforestation (in the case of vegetation), but where species and their propagules are still available for recolonization in the surrounding areas (Shugart, 2012). This would also be the case for the ocean floor where bottom trawling has partly destroyed benthic communities. Secondary successions are faster since colonizing propagules are already present in the neighboring

Table 4.1 Main features of early and mature stages in ecosystem development.

Ecosystem attributes	Developmental stages	Mature stages
Production/respiration ratio (P/R)	Greater or less than 1	Approaches 1
Production/biomass ratio (P/B)	High	Low
Net community production	High	Low
Food chains	Linear	Web-like
Total organic matter	Small	Large
Species diversity/equitability	Low	High
Spatial heterogeneity	Poorly organized	Well organized
Niche specialization	Broad	Narrow
Size of organisms	Small	Large
Life cycles	Short and simple	Long and complex
Mineral cycles	Open	Closed
Growth form	Rapid (*r*-selection)	Slow (*K*-selection)
Nutrient conservation	Poor	Good
Resistance to external perturbations	Poor	Good
Entropy	High	Low

Source: Simplified from Odum (1969).

substrates and quickly occupy the disturbed area. Primary successions are more difficult to observe directly, especially in terrestrial ecosystems, because they are usually longer than a human lifetime. This is the reason succession studies that are mostly based on direct monitoring of the much-faster secondary successions.

The longest, but still incomplete, case of primary succession that has been directly observed to date is the natural colonization of an island and the development of the first successional stages of its vegetation within a recent natural experiment. In 1883 a volcanic eruption occurred in the Krakatau Islands, in the region of Indonesia between Sumatra and Java (Fig. 4.6), approximately 35 km from the first and 45 km from the second. The eruption drastically changed the land configuration and covered the islands with an ash layer more than 100 m thick that erased all traces of life. We could say that the islands were sterilized. The area was virtually free from human influence both before and after the eruption, which allowed the progressive colonization and community assembly to evolve under natural conditions for more than a century (Whittaker et al., 1989). Under these conditions—that is, complete sterilization and a lack of human intervention—primary succession is the right term. To reach Krakatau, new species had to find a way to disperse across marine barriers that separated the islands from the rest of the Indonesian archipelago. A year after the eruption, blue-green algae (Cyanophyta) formed pioneer communities in the volcanic ash. They were followed by herbaceous plants, and in 1900, meadows with scattered trees and shrubs could be observed (Fig. 4.6). Trees invaded the meadows to form open forests until, in approximately the 1920s, the canopy density increased enough to exclude herbaceous plants from the understory by preventing light penetration. From that moment on the forest continued to grow, although with few variations in composition. Today, the forest reaches 40 m in height and is formed by trees more than 1 m in diameter.

A little more than a century has passed, and the islands have been colonized by approximately 300 plant species. However, similar areas of nearby islands (Sumatra and Java) host 1200–1400 species, which makes us think that succession is far from complete. The estimated time for the succession to be completed is 1000 years (Bush, 2003). The closed forest type makes it more difficult for new species to establish, which predicts a smaller rate of forest development in the future than in earlier stages of succession. With the available evidence, we do not know where this succession is heading. We will have to watch what happens in the next

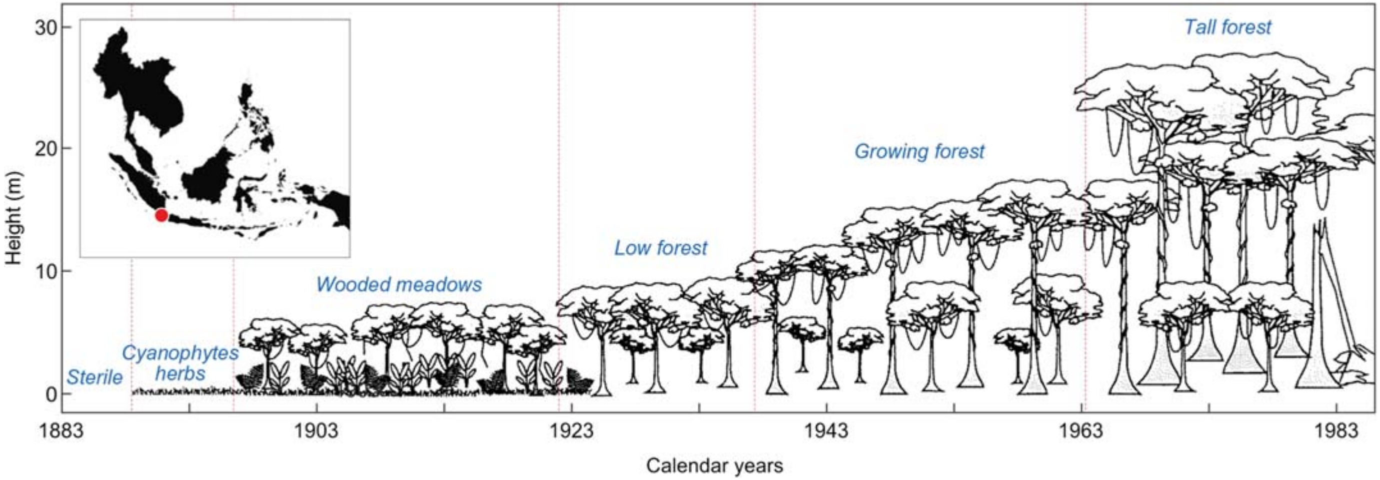

Figure 4.6 Primary succession and community structure formation of a tropical forest of the Krakatau Islands, after the volcanic eruption of 1883. Krakatau is shown as a red dot on the map of Southeast Asia. *Modified and redrawn from* Bush (2003).

centuries or, in the case of extreme hurry, ask the Fates, especially Lachesis and Atropos. For now, as humans, we may predict that the succession on Krakatau will not be exactly the same as the succession of the Sumatran and Javan forests (where most of the species come from) because their environmental histories have been, and will continue to be, different. Environmental changes (especially global warming but also changes in atmospheric composition and human activities) will introduce stochastic factors that convert the succession of Krakatau into a random, unpredictable process. Of course, these environmental variations will be felt by the communities of Sumatra and Java as well, but the effect of environmental changes on different communities varies, especially if the communities are at different stages of succession. Here, we have an excellent example of the colonization and assembly of new communities on islands that can serve as a model for the interpretation and reconstruction of similar processes that occurred earlier in the Quaternary. Hopefully, "civilization" will never reach these islands, and future ecologists will be interested in following the successional process on Krakatau to resolve some of the mysteries of ecological succession.

Another approach to studying ecological succession using extant communities is the so-called space-for-time substitution (Pickett, 1989). This approach assumes that different communities situated along spatial gradients are seral stages of the same ecological succession. A set of seral stages of this type arranged along a given environmental gradient is called a chronosequence (Walker et al., 2010). Classic examples of chronosequences are the progressive colonization of meander areas formed by sediment deposition during the lateral migration of a river and the zonal distribution of vegetation in prograding coastal areas (Snedaker, 1982; Salo et al., 1986). For example, sediments deposited on the riverbanks build point bars that are eventually colonized by pioneer plant communities (Fig. 4.7). As the bars grow, the pioneer communities get farther away from the water and are successively replaced by more advanced (or mature) communities until the establishment of climax communities on dry land. This chronosequence reproduces primary succession in space and, in time, will reach the stage of the climax community. If this is true, chronosequences are the key to discovering the secret plans of the Fates for a given community.

Climatic stability—at least for the duration of the process—is an inherent condition of succession and climax. Under constant climatic conditions the community itself is in control of the succession process;

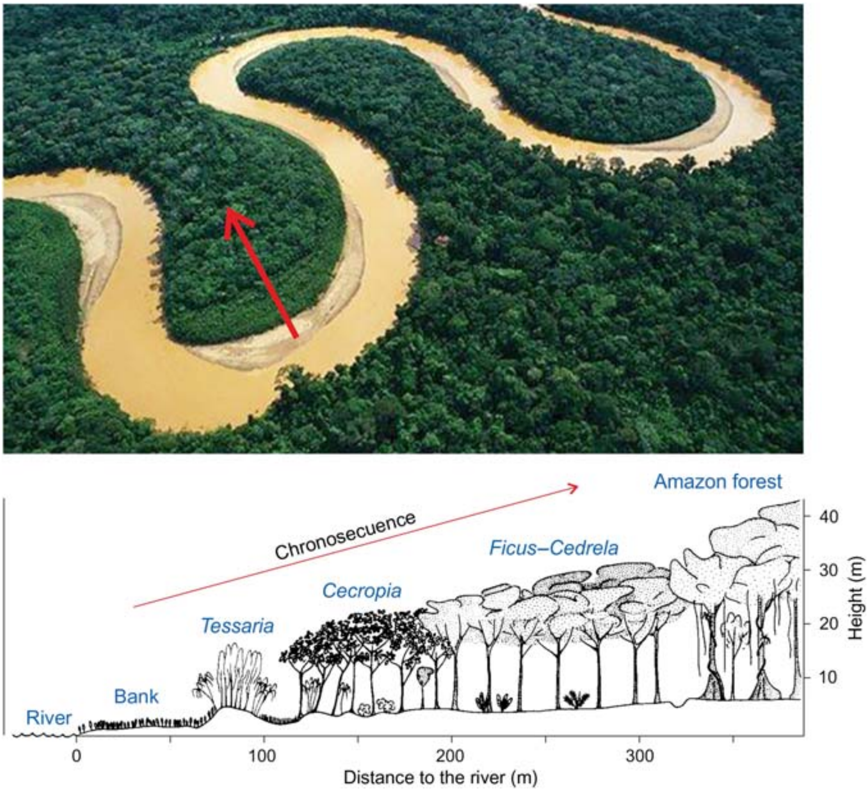

Figure 4.7 Chronosequence of a river meander in Peruvian Amazonia. Above: aerial view of the meander. The chronosequence direction is shown by a red arrow. Below: longitudinal section of the chronosequence, showing five seral stages from the meander bar (practically uninhabited sand deposits in the upper image) to the mature Amazonian rainforest, which is the end member of the succession. *Redrawn and modified from Salo et al. (1986).*

this is what we call autogenic succession (Tansley, 1953). However, if the climate or any other external environmental agent disturbs the process, the succession changes its direction and is called allogenic. As discussed in the first chapter, during the Quaternary, climate changes occurred constantly and at all timescales. This raises the question of how the process of community assembly has led to the present situation. What has been more important: the deterministic plans of the Fates, as Clements or Tansley thought; species idiosyncrasy, in line with Gleason's or Whittaker's vision; or Hubbell's neutral theory? We will analyze this in Section 4.4, but first, a clarification of the concept of ecological stability seems pertinent.

4.3 Stability, resilience, and domains of attraction

The stability of communities and of corresponding ecosystems has long been debated in ecology. In the beginning the concepts of climate stability and communities' equilibrium with the climate were considered axiomatic. They were based on the observation of phenomena at a human timescale, similar to secondary succession, which as discussed earlier, induced the Clementsian dogma of the climax. We call this idea the hypothesis of static equilibrium. However, earlier ecologists, such as George E. Hutchinson, already foretold the possible influence of environmental variability on community assembly. In his famous plankton paradox, Hutchinson (1957) asked why plankton communities were so diverse. According to this author, in such an isotropic (or homogenous) medium as water, only the species with the highest competitive capacity was expected to persist and form monospecific assemblages, with other species being driven to extinction by competitive exclusion. Hutchinson himself provided the explanation that competitive exclusion required a stable environment and that water does not fulfill this requirement. Small environmental changes in physicochemical characteristics, however short lived, may be enough to change competitive relations instantaneously, which in turn would contribute to spatiotemporal niche segregation and enable the existence of surprisingly high biological diversity. This idea is known as the hypothesis of nonequilibrium dynamics, as communities are constantly trying to adjust to environmental oscillations without reaching a true stable equilibrium due to the higher rates of environmental change in comparison with the reaction capacity of the constituent species (Section 2.1.2).

There exists a series of intermediate options between the static equilibrium and nonequilibrium dynamics, which have been given a complex terminology in relation to ecological stability (Grimm et al., 1992). Here, we will look at the most influential concepts with regard to the assembly of ecological communities (Table 4.2). For decades, these concepts have been debated from a purely theoretical perspective by applying short-term ecological observations and derived mathematical models. Similar to other modeling practices, such as the neutral theory of biodiversity (Section 3.4.1), these models usually follow a top-down approach, commonly based on unwarranted ecological assumptions—for example, species' equivalence in terms of age of origin, niche features, and responses to

Table 4.2 Main terms and concepts related to ecosystem stability (Grimm et al., 1992).

Stability concept	Definition	Related measures
Constancy	Staying essentially unchanged	Standard deviation, annual variability
Resistance	Staying essentially unchanged despite external disturbances	Sensitivity, buffer capacity
Resilience	Returning to the referential state after a temporal external disturbance	Return time, size of the attraction domain
Persistence	Persistence of populations through time	Mean time to extinction

environmental change—and they use "elegant" but oversimplified and reductionist mathematical constructions reproducing physical, rather than biological, processes (Rull, 2012b). In contrast, under an inductive, bottom-up reasoning framework, the first step is to observe and/or measure natural phenomena and try to provide the best explanation by hypothesis testing. In this framework, general theories emerge from the modeling of eventual regularities in the behavior of communities rather than from preexisting theoretical assumptions. Regardless of which stability concept we wish to study (Table 4.2), time frames can be long enough to befit long-term ecology, which, as mentioned earlier, depends upon paleoecology for a proper empirical basis. We insist on top-down versus bottom-up approaches, not to criticize modelers but to offer them a sounder empirical basis for the creation of more powerful, nonreductionist models based on realistic biological assumptions. The Quaternary provides us with a proper empirical basis for analyzing the stability of current or former ecosystems, which are exactly what we are interested in. The Quaternary is a real treasure trove for those interested in faithfully modeling long-term ecological processes and using those models to predict the ecological future of our changing world (Anderson et al., 2006). But, as Ricklefs (2012) pointed out, modeling approaches should be based on natural history observations and at the service of ecology, not the reverse (Section 3.4.1).

Returning to stability concepts, resilience, a term introduced by Holling (1973), is the one that is most in use today. Ecosystems hardly remain unchanged when facing external disturbance, and the factor that decides whether an ecosystem endures or not is its capacity to return to the initial state, or at least to a similar one, after the disturbance. By saying

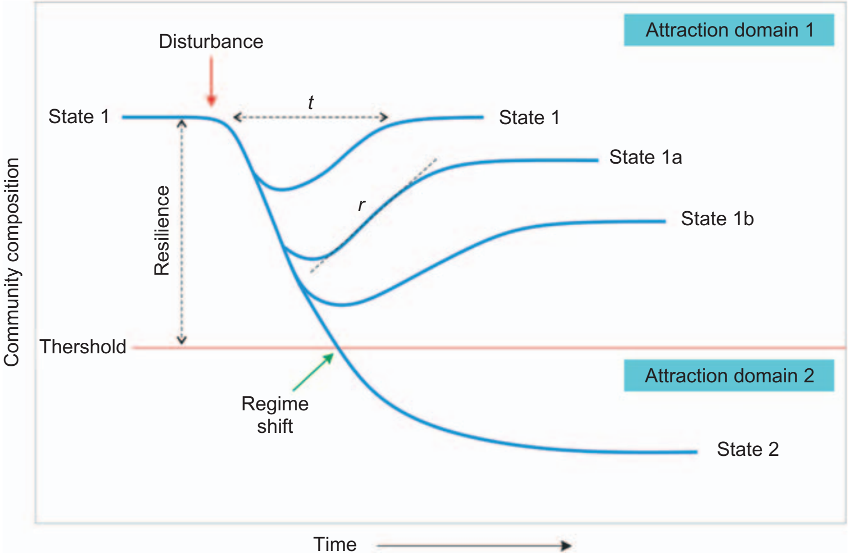

Figure 4.8 Changes in the composition of a hypothetical community (*blue lines*) provoked by a disturbance (*red arrow*). A small, short-term disturbance allows the community to return to its initial state (1) in a short time (*t*) with a fast recovery rate (*r*). Major disturbances lead to slower recovery and adaption to other possible stages within the domain of attraction (1a, 1b). When the disturbance is very large and/or long term (or there is a positive feedback effect) and the change goes beyond the resilience threshold of the community (*red line*), a regime shift takes place, and the community is replaced by another belonging to a different domain of attraction (2).

"a similar one," we are referring to a similar structure, identity, and function, although there can be certain differences in taxonomic composition. This capacity is what we call resilience, and it varies according to the type of community (Gunderson, 2000). The intensity and duration of the disturbance also play a key role in the expression of resilience by a given community. Small and/or short-term disturbances can be relatively quickly overcome with a high recovery rate (Fig. 4.8). More intense or long-term disturbances have a more powerful effect on the community, which will need more time to recover, and the final composition of the community may be different (but without a loss of the essential characteristics). Each community has a variety of alternative stable states in which it is recognizable. The complete set of these varieties has been called the community's domain of attraction (Holling, 1973). When modifications produced by a disturbance cross a given threshold, the community can no longer recover and enters another domain of attraction, which means that it is replaced by another community (Fig. 4.8). We also call this change a regime shift. Regime shifts can occur in two ways: by a major disturbance (i.e., both intense and long term) or by minor disturbances that are amplified by feedback mechanisms causing a nonlinear response, that is, a response of disproportionate magnitude in comparison with the intensity of the disturbance (Scheffer et al., 2001; Biggs et al., 2009).

An illustrative example of a regime shift due to a nonlinear response is deforestation caused by fire. A large-scale, long-term wildfire may completely erase a forest, which will then be replaced by a savanna, for example. However, smaller fires can have the same final effect if they are amplified. An initial fire destroys part of the forest and makes it more open, that is, less dense, which favors evaporation and creates a drier microclimate. The new microclimate is more suitable for herbaceous plants and shrubs that are more inflammable than the original forest. These changes, together with soil degradation by erosion, hinder the recovery of the forest and stabilize the drier vegetation, which increases the wildfire risk. In this manner, vegetation inflammability gradually increases, as does the speed at which wildfires spread. In the end the degree of deforestation will be significantly higher than expected after a small fire, and eventually, the whole forest might disappear. A deforestation process of this type may also be accelerated by an aridification trend.

4.4 Quaternary community ecology

All the modifications that species and populations have experienced during the Quaternary and that we have analyzed in former chapters have had an impact on communities at local, regional, and global levels. Obviously, communities and biomes already existed before the Quaternary, but due to two easily deducible reasons, they were quite different from what they are today. The first of the reasons is that many species did not exist yet; they emerged only during the Quaternary. The second is that species had individual (i.e., idiosyncratic) responses to Quaternary climatic changes in terms of extinctions and geographical redistributions; as a result, the taxonomic composition of communities and the abundance distribution of their species have been changing in a contingent manner. In this section, we will see how these community shifts have actually occurred. One of the conclusions of the former chapter was that practically all current species, including some that we previously considered living fossils, have a Quaternary evolutionary footprint either because they originated during this period or because the genetic structure of their populations developed at this time. Communities display a similar situation; some did not even exist before the Quaternary, while others of pre-Quaternary origin established their composition and ecological diversity during the Quaternary.

4.4.1 Typical Quaternary communities

Strictly speaking, the age of a community is given by the age of the youngest species it includes, if evolved in situ, or the last to establish, if established by migration or dispersal. Nevertheless, the same community, or a very similar one (within its domain of attraction), could have existed previously without that youngest species or later colonizer; thus, in reality, its age could be greater. We can apply this rule in the case of species that are not indispensable for the existence of the community. However, some species—that is, keystone species (Barua, 2011)—are of key importance, and the community could not exist as it actually is without them. This is the case, for example, of *Fagus sylvatica* (beech) in a beech forest or *Quercus ilex* (oak) in an oak grove. However, a species does not have to be dominant, in structural or quantitative terms, to be considered a keystone species. For example, large carnivores, although less abundant than other species, could be keystones for community dynamics (even for their own existence) due to their controlling role in the trophic web. In the Quaternary, this would be the case for the already extinct Late Pleistocene megafauna (Section 2.2.3) (Malhi et al., 2016).

Evidently, if a keystone species in a community is of Quaternary origin, the age of that community is also Quaternary. This is the case for a characteristic high-Andean community dominated by several species of the genus *Chimantaea* (Asteraceae), locally known as frailejones, which form a rosette of living leaves on a trunk of variable length covered with dead leaves (Fig. 4.9). A recent phylogeographical study discovered that frailejones are Quaternary species and that they all originated from the same common ancestor that started to diversify at the beginning of the Pleistocene, approximately 2.3 Ma (Pouchon et al., 2018). Similar to *Lupinus* (Section 3.5.2), diversification occurred by adaptive radiation as

Figure 4.9 *Espeletia* community of the Ocetá Páramo (Colombia). A red dot shows its approximate position on the map of South America. *Photo by Javier Vargas, used under the Wikimedia Commons license (es.wikipedia.org).*

the distribution area of the species expanded by migration, and reproductive barriers were formed by topography and elevational oscillations of glaciers and ecological belts as a consequence of glacial cycles (Section 2.2.2). Other typical Quaternary communities include the already mentioned cichlid fishes of the lakes of the African rift (Section 3.5.2). These are just two examples; there are many more.

Other genuinely Quaternary communities are those that, despite being composed of a mixture of Quaternary and pre-Quaternary species, were not assembled until the Quaternary. This is the case for several volcanic islands that emerged from the sea during this period and have been colonized by species that arrived from everywhere, but especially from the nearby continents and/or islands, whose biotas acted as metapopulations and metacommunities. According to the theory of island biogeography of the American ecologists Robert H. MacArthur and Edward O. Wilson, the diversity and composition of island communities are the result of long-term equilibrium between the dispersal of species toward the island and local extinction (MacArthur and Wilson, 1963). This equilibrium determines the species richness that the island can hold depending on its size and the distance to the source of colonization (Fig. 4.10).

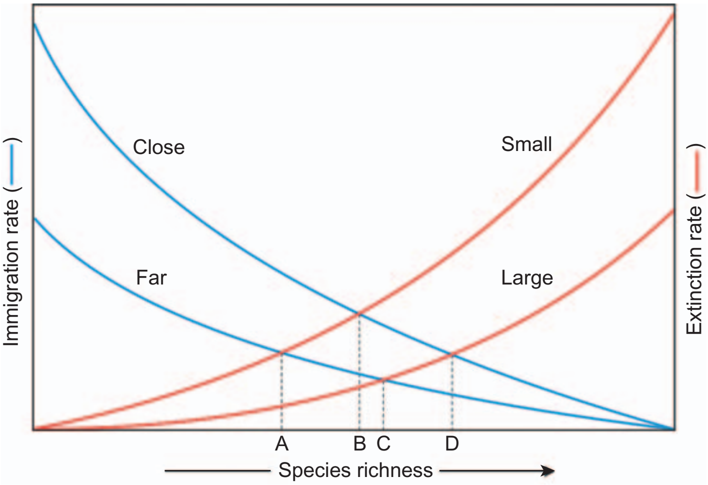

Figure 4.10 Island biogeography model of MacArthur and Wilson (1963), according to which the biodiversity of an island (and thus of every component of its communities) represents an equilibrium between immigration and extinction. The highest biodiversity (D) is expected on islands with the largest area and the closest proximity to the continent that provides colonizing species. The lowest biodiversity (A) is usually found on small, faraway islands.

Easter Island represents an extreme case (illustrated as situation A in Fig. 4.10). This island has an area of slightly more than 160 km^2 (with the longest straight-line distance being hardly greater than 20 km) and is considered the most remote inhabited island in the world (Fig. 4.11). It is actually the peak of a submarine volcano 3000 m in height, the eruption of which started about a million years ago, but the island, which is approximately 500 m in height, rose above sea level only approximately 750 ka BP. Ever since, it has been colonized by species that originated from other islands of Oceania and from South America (the closest continent). This mixture resulted in the formation of novel communities compared to the communities of the places of origin. Studies of plants revealed that 75% of colonizing species would have been transported by birds, while 25% would have arrived by ocean drift. Wind transport did not seem to have been effective on this island (Carlquist, 1967; Zizka, 1991). Something similar may have happened to the hundreds or thousands of volcanic islands formed during the Quaternary, although the dispersal mechanisms might have varied. Today, the flora and fauna of most islands are completely or partly modified by human activity, which has also created (either by design or

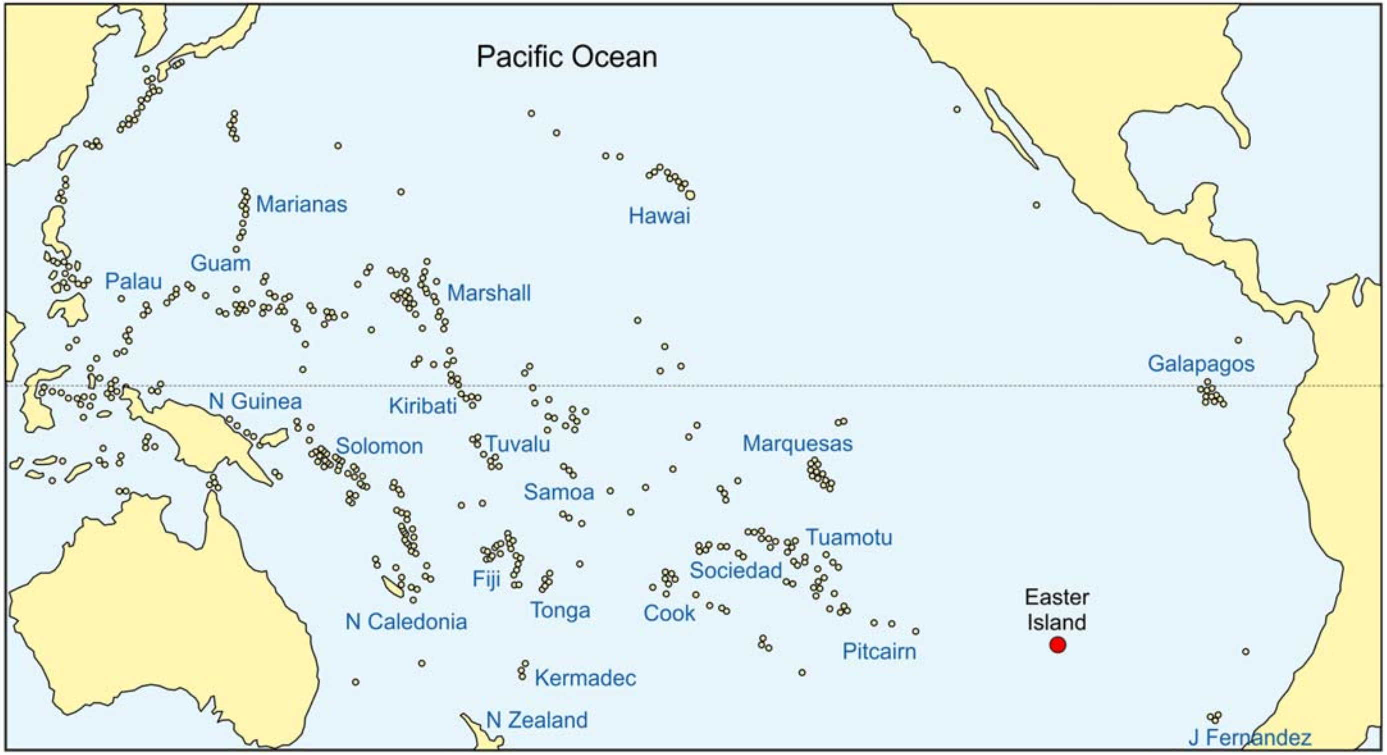

Figure 4.11 Easter Island (*red circle*), in the south Pacific Ocean, is more than 2000 km away from the closest ocean island (Pitcairn) and approximately 3500 km from the American continent and the Galapagos Islands. *Redrawn from Rull (2016).*

by accident) completely new associations of species with highly varying origins that form independent, functional communities. We will elaborate on this topic in the next chapter. Pollen analysis of Easter Island reveals that before the arrival of humans, the dominating communities were palm tree forests of an unknown but probably endemic species, with an undergrowth of small trees and shrubs such as *Sophora* (Fabaceae), *Triumfetta* (Tiliaceae), *Macaranga* and *Acalypha* (Euphorbiaceae), *Coprosma* (Rubiaceae), and several unidentified Asteraceae, Myrtaceae, and Urticaceae/Moraceae species (Flenley and King, 1984; Flenley et al., 1991). This community type is unique; it has not been documented on any other island or continent. The species are of variable geographical origin, and some of them are endemic, which suggests that not only the community itself but also some of its species are of Quaternary origin, as they have evolved in situ from their colonizing ancestors during this period. Alternatively, endemic species would have gone extinct in their places of origin after dispersal to Easter Island.

4.4.2 Chronosequences and Quaternary successions

As already explained, chronosequences are based on space-for-time substitution and used to reproduce successional trends (Section 4.2). One way to check this analogy between a chronosequence and succession would be to observe a real succession event and compare it to the corresponding chronosequence (Johnson and Miyanishi, 2008; Damgaard, 2019). However, as we know, terrestrial successions can last for centuries or millennia, which makes their observation rather difficult. One way to break this circle is to make use of paleoecological methods, especially pollen analysis. A classic study that compared a chronosequence based on present-day vegetation patterns with a paleoecologically reconstructed succession process was conducted by the British palynologist John Birks in the Yukon area, by the Canada-Alaska border (Fig. 4.12). In this area the Klutlan Glacier advanced in a significant manner until 1200 years ago, leaving a large terminal moraine behind, which is called Harris Creek and is composed of all the material that was mechanically eroded and transported by the ice tongue. Since that time, the glacier has retreated approximately 20 km but not in a constant manner, as evidenced by the existence of five levels of minor moraines (I to V) within the Harris Creek area, corresponding to smaller glacier readvances (Wright, 1980). Following the retreating glacier, the uncovered land was progressively

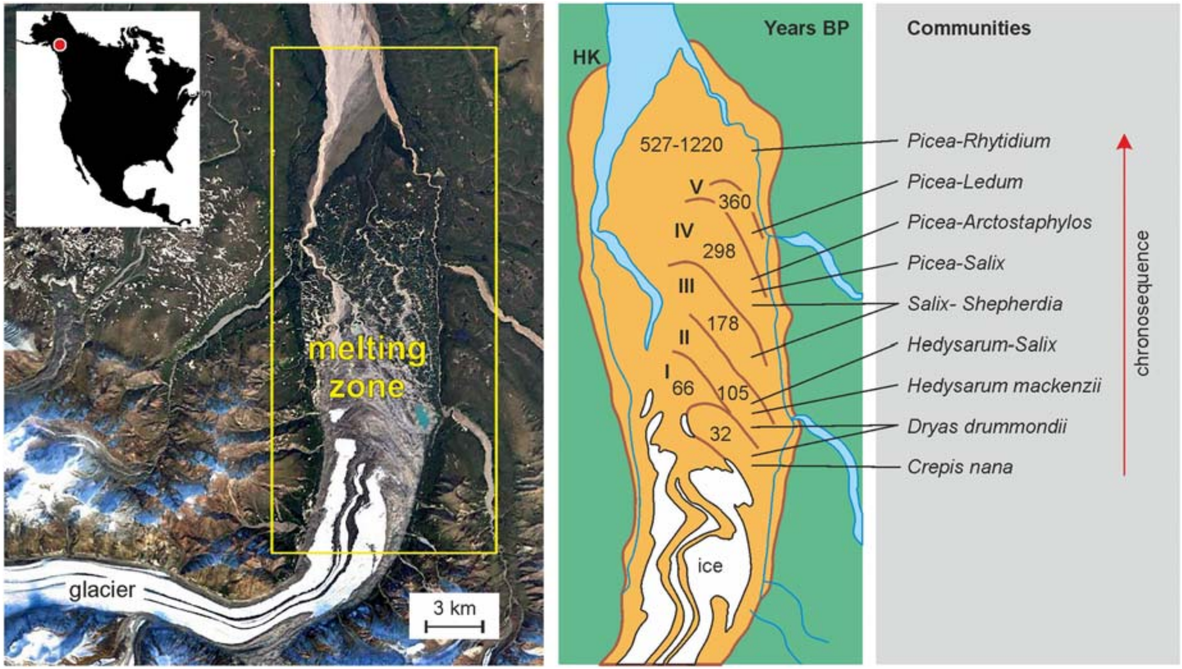

Figure 4.12 The terminal zone of the Klutlan Glacier, where glacier retreat due to progressive melting can be observed. Minor readvances are represented by moraines I to V. The terminal moraine of Harris Creek indicates the maximum glacier extension approximately 1200 years ago. Numbers on the minor moraines give their respective ages in years BP. On the right, dominant species of the communities of each stage are shown in order of their age and approximate position in the chronosequence. The approximate position of the Klutlan Glacier is indicated by a red dot on the map of North America. *Based on Google Earth (left image) and redrawn and modified from Birks (1980)*.

colonized by plant communities, in a typical example of primary succession. The oldest of these communities is situated in the moraine of Harris Creek, the intermediate ones are in the smaller moraines, and the most recent ones are right in front of today's glacier front. Birks (1980) decided to check whether this pattern fit the description of a chronosequence and, if so, whether that chronosequence truly represented succession from pioneer communities to more mature ones.

To date the chronosequence, Birks (1980) calculated the age of each community using growth rings of the oldest woody plants in each of them. This method is way more objective and evidence-based than the approach usually adopted in this type of study, which relies on assumptions based on community composition, structure, and physiognomy to define different seral stages and their hypothetical succession over time. In this way the author managed to accurately define the real temporal sequence of colonization and obtained a gradient from the Harris Creek moraine, which supported communities established more than 500 years ago, to moraine I, where plant communities established between 30 and 70 years ago (Fig. 4.12). In this sequence, pioneer communities (moraines I and II) were made up of herbaceous plants, such as *Crepis nana* (dwarf alpine hawksbeard) or *Dryas drummondii* (Drummond's mountain-avens), which are able to grow on sand or gravel substrates without any well-developed soil. *D. drummondii* fixes nitrogen very effectively and helps other plants develop, which favors humus accumulation and initiates soil formation. This boosted the rooting of other plants, such as *Hedysarum mackenzii* (MacKenzie's sweetvetch), that gradually became dominant in the still herbaceous community until a mixed community of *Hedysarum* and shrubs of *Salix* (willow) established. This mixed community was then replaced by a shrub community dominated by *Salix* and *Shepherdia* (buffaloberry), which reach heights of 1–2 m. In this stage, seeds of trees such as *Picea glauca* (white spruce) can start to germinate, and eventually, a community dominated by *Picea* and *Salix* was formed, in which *Picea* trees stand out (they can reach up to 6 m in height) but without developing a true forest. Later, *Salix* was replaced by *Arctostaphylos uva-ursi* (bearberry), and *Picea* increased in height (8–12 m) and in density to form an open forest. The next stage involved a closed forest dominated by *Picea* and the shrub *Ledum palustre* (marsh Labrador tea). The oldest and, in theory, most mature stage of this chronosequence (i.e., the one found in Harris Creek) is an even taller (14 m) but less dense *Picea* forest with the moss *Rhytidium rugosum* in the understory.

This properly dated chronosequence already represented a leap forward in empirical reconstruction of successions spanning centuries or millennia. But Birks (1980) went further and verified that this chronosequence represented real succession by studying the pollen preserved in lake sediments and organic soils of the oldest white spruce communities. First, he studied modern analogs in surface samples to learn how to characterize each community by the pollen composition that was deposited in the local soil and sediments. Even moss samples were used, in which pollen and spores had accumulated in a similar manner as in surface sediments and provided a faithful representation of the surrounding vegetation. The results of this study were used to deduce past vegetation from the composition of pollen accumulated in the soils and lake sediments, which made it possible to follow the succession of vegetation over time. The result obtained was that, despite small differences due to local microtopographic and microclimatic conditions, the chronosequence provided a good general representation of the succession that took place over the last 1200 years. One outcome that was rather surprising at the time was that the *Picea-Rhytidium* community was less diverse than the *Picea* forests of earlier seral stages, which could be interpreted as degradation of these forests (actually, Birks talked about an impoverished *Picea* forest). It seems that they did not follow the law of increasing diversity with succession, which is inconsistent with the concept of a climax community (Table 4.1). Observing the diversity trends closely (following the chronological order of seral stages), we find that maximum diversity was reached at approximately 150 years with the *Picea-Arctostaphylos* community. After that point, diversity was significantly reduced and then stabilized (Fig. 4.13). Although Birks did not analyze this tendency in depth, it is possible that environmental changes played a part in the ecological change and, in reality, that the *Picea-Ledum* and *Picea-Rhytidium* communities were not climax communities but seral stages induced by allochthonous factors (allogenic succession). In this case, it could be said that it was possible to uncover the secret plans of the Fates.

In other cases the agreement between the interpreted chronosequence and the true ecological succession falls short. Curiously, one of the best known examples of this disagreement was found at one of the sites where Clements and his colleagues came up with the principles of succession based on chronosequences: the coastal dunes of Lake Michigan, in the United States. These coasts have a temporal sequence of sediment bars parallel to the coastline; the youngest bars are closest to the coast, and the

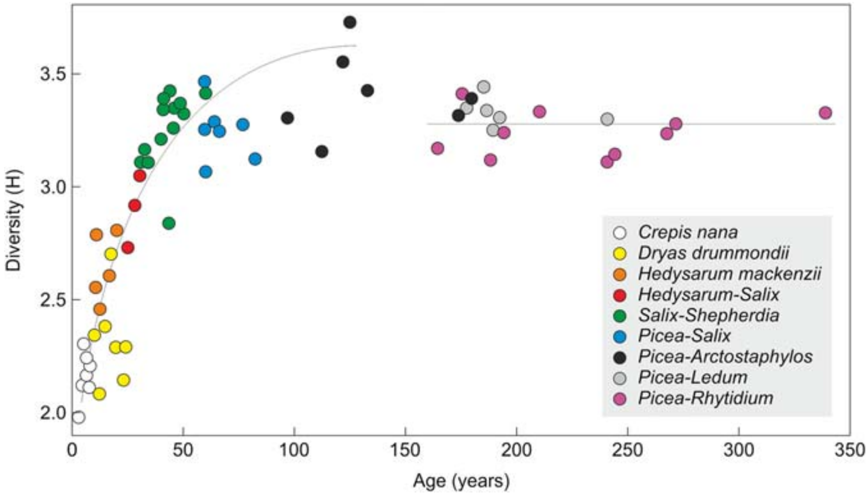

Figure 4.13 Diversity trends in the chronosequence of the Klutlan Glacier. The Shannon index of ecological diversity (H) is applied (Fig. 4.1). Each color represents a community type, as described in the main text. *Modified and redrawn from Birks (1980)*.

oldest ones are farther inland (Fig. 4.14). These dune bars are the result of the progressive coastal advance linked to the continued decrease in water level initiated 2000 years ago, when the lake attained its maximum Holocene water level. The dune bars are separated by depressions with numerous ponds that follow the same time sequence. Today, communities of the youngest bars are dominated by *Populus* (poplar), which is gradually replaced by *Pinus* (pine) as we proceed inland and, then, by *Quercus* (oak). A parallel sequence can be observed in the aquatic environments, which starts with submerged aquatic plants in the youngest depressions and ends with wetland shrubs in the oldest ones. In intermediate stages, we can find floating and emergent aquatic plants (Fig. 4.14). Thus we have two different sequences: one on land and one in water. The American scientist Victor Shelford, Clements's colleague, suggested that both sequences were chronosequences, representing two parallel ecological successions that started approximately 2000 years ago; the terrestrial sequence culminated in a *Quercus* forest, while the aquatic sequence, in a wetland of *Cephalanthus* (Shelford, 1911).

Shelford's interpretation held for almost 80 years, until Jackson et al. (1988) started to study the pollen and plant macrofossils of the sediments that were deposited during the last 2700 years in a lagoon between two of

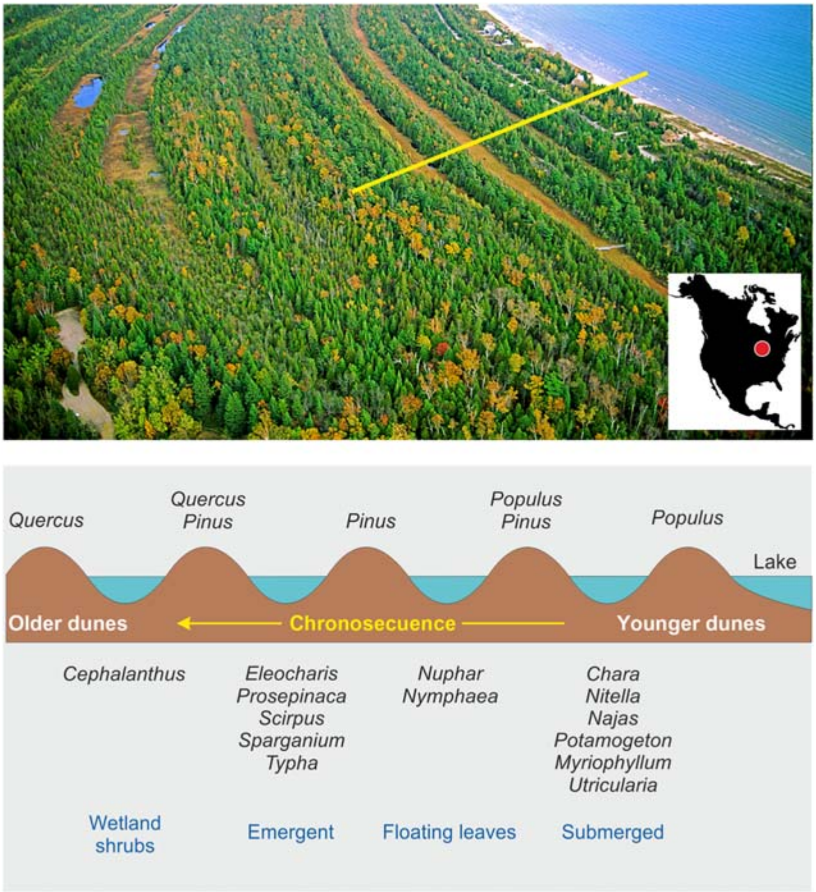

Figure 4.14 Dune sequence parallel to the southwestern coastline of Lake Michigan (the *red dot* marks the approximate position). The lower part shows a transverse section of the dune complex (*yellow line* in the photo), where the land and water chronosequences defined by Shelford (1911) can be seen. *Photo by D. Sherman (publicly available at pbase.com), chronosequence redrawn and modified from Shelford (911).*

the oldest dune bars. These sediments should have contained a record of all the changes in vegetation that occurred in this period and, thus, should have offered the first-hand evidence of the true succession. However, the researchers found that neither the terrestrial nor the aquatic vegetation had changed during the last 2700 years. In this period, forests were always dominated by *Pinus* and *Quercus*, and in the aquatic vegetation, most of the species were present from the beginning. There were no signs of long-term succession, as previously "read" in the chronosequence. The big change, both on land and in water, had come approximately 150 years ago with the deforestation caused by the first Euro-American colonists. This was the reason why pine trees had grown scarcer on or even disappeared from the oldest dunes and why *Quercus* had taken over. At the same time the formerly very diverse aquatic vegetation suffered notable impoverishment, which led to a significant increase in *Typha* and *Cephalanthus* and a decrease in or the disappearance of most submerged and floating aquatic plants. Therefore in this case, the current spatial distribution of plants does not represent different stages of succession but results from changes in the type and intensity of human disturbances to initially homogeneous terrestrial and aquatic vegetation. This time, the designs of Clementsian Fates were not written in the spatial arrangement of modern communities.

4.4.3 Community disassembly and reassembly

Communities not only assembled during the Quaternary but also disassembled (usually during glaciations) and then reassembled (usually during interglacial periods). Therefore present-day communities are a product of many recurrent processes of assembly, disassembly, and reassembly. The question is whether this repetitive process caused changes in the communities or left them the same as they were in the beginning, as the Clementsian concept of the superorganism predicts. The compositional changes of the forest communities of the British Isles during the last four glacial cycles provide us with a good example to analyze this phenomenon. As we can see in Fig. 1.11, these islands were physically connected to the continent during the last glaciation, while today they are separated from it by the English Channel (La Manche, in French). The same situation was repeated in the last four glacial cycles; during glaciations, ice almost completely covered the British Isles, except for the south, where treeless tundra dominated. Thus each glaciation completely erased the forests of the archipelago, which subsequently had to recolonize the islands starting from their European refugia (Section 2.2.2) at the beginning of each interglacial period, when it was still possible for them to cross the channel. After arriving at the archipelago, forests reassembled. Present-day forests assembled during the Holocene, and the first phases were dominated by boreal forests of birch (*Betula*) and pine (*Pinus*) (Fig. 4.15). Components of temperate forests—elm (*Ulmus*), oak (*Quercus*), and hazel (*Corylus*)—arrived afterwards, almost together, at the time when boreal forests shifted northwards. *Corylus* was the first component to substantially

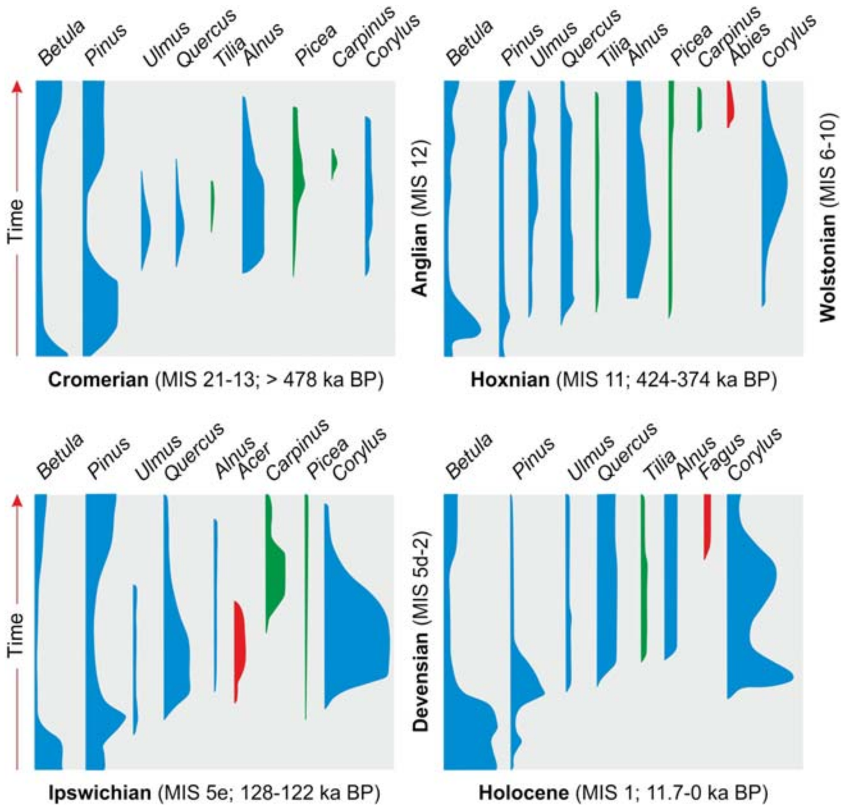

Figure 4.15 Reassembly of boreal and temperate forests of the British Isles during the last four interglacial phases based on pollen studies. Interglacials (Cromerian, Hoxnian, Ipswichian, and Holocene) are ordered chronologically from left to right and top to bottom (see the dates in ka BP). Intermediate glaciations (Anglian, Wolstonian, and Devensian) are also indicated. Because of the local British terminology, MISs (Chapter 1) and their ages are also given. Within each interglacial, time is represented in a stratigraphic manner, in the direction of the red arrow. Taxa that were common in the four interglacial periods are shown in blue; those that appeared in two or more interglacials are shown in green; and those that were present in only one are shown in red. *MISs*, Marine isotope stages. *Modified and redrawn from Wright (1977).*

increase its populations. The next colonizers were lime (*Tilia*) and alder (*Alnus*), which together with hazel, dominated the great Holocene expansion of British temperate forests. Beech (*Fagus*) arrived only at the end of the Holocene, when hazel began to decline (Wright, 1977).

The Holocene process of British forest assembly differs significantly from how the same forest communities were assembled in earlier interglacial periods. For example, in the boreal forests of the Ipswichian interglacial (128—122 ka BP), birch and pine were present in similar quantities, in contrast to the Holocene, when birch was dominant. Components of the temperate forest also arrived in a different manner because elms and oaks appeared before the expansion of hazel and because alder was much less abundant than in the Holocene (Fig. 4.15). Moreover, during the Ipswichian, three elements (*Acer*, *Carpinus*, and *Picea*) entered that are not present in the Holocene, and beech did not appear at all. Thus Holocene and Ipswichian boreal and temperate forests were different, not only in the process of assembly but also in the final result in the terms of taxonomic composition and relative abundances. The same thing happened in earlier interglacials (Hoxnian and Cromerian), namely, that forests reassembled in a different way each time (Fig. 4.15). The differences can be attributed to differences in the response to climatic changes among species. Random factors related to environmental changes and the distribution of European refugia of the given species may also have played a role in specific differences in response lag, migration routes, and migration speed. In summary the action of random factors and processes managed to produce different types of boreal and temperate forests using the same elements. In other words, these interglacial forests shifted within their respective attraction domains without crossing any regime-shift threshold. This result is incompatible with the idea of a superorganism able to manage its own development and reproduce in the same manner again and again. In this case, Clementsian Fates loosened control of the process at least four times, which reveals that ecological successions may be highly contingent rather than predetermined. In this case, Lachesis was unable to reproduce the same succession with the elements provided by Clotho, and Atropos cut the thread of life for four different community compositions. It seems that the influence of gods, in the form of environmental changes, prevented the Fates from successfully completing their job.

4.4.4 Continuous changes in composition

As already discussed in Chapter 2, the influence of idiosyncratic factors of species on the development of communities is evident in the postglacial colonization of North America (Section 2.2.2). In that chapter, we described the individual migration of species and genera (Fig. 2.9), and here, we analyze the consequences that it had on the community composition of North American forests. We apply the following logic: if the main components of boreal and temperate forests migrated from different glacial refugia, with different response lags, at different speeds, and following different migration paths, we can hardly expect the forest community composition of a given area to be homogeneous during the Holocene. This hypothesis could be tested by reconstructing the temporal dynamics of dominant trees of these forests using pollen analysis. A study of this type was undertaken in Michigan (United States) based on pollen found in the sediments of the last 8000 years of Tower Lake, which is in the region of the Great Lakes between the United States and Canada (Fig. 2.9). In the obtained pollen diagram the changes in the abundance of the most important local and regional forest trees can be clearly observed (Fig. 4.16). It was even possible to differentiate four forest types that followed each other in time (Jackson et al., 2014).

Today, *Fagus*, *Tsuga*, *Acer*, and *Betula* dominate the forests in the Tower Lake basin, with the minor presence of *Pinus*, but it was not always so. This combination started 1.4 ka (Zone T-4 in Fig. 4.16), when *Fagus*—the last genus to arrive due to its longer migration lag (Fig. 2.9)—started to arrive and reach its present importance. The first Holocene

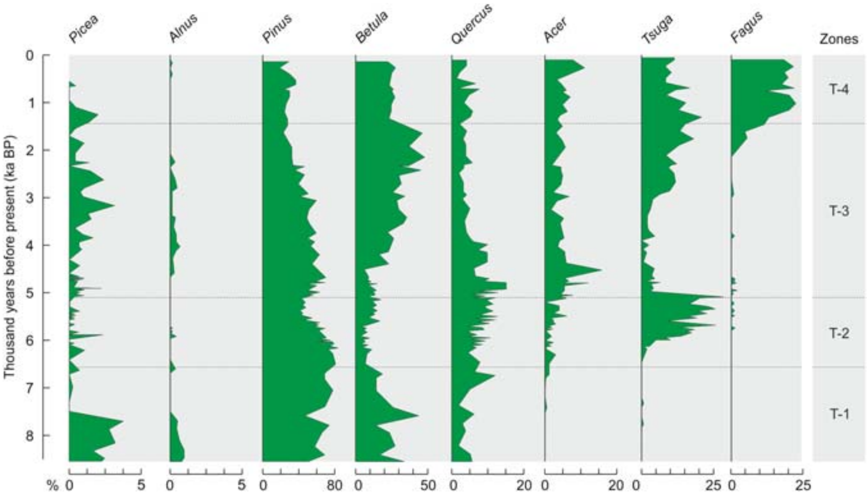

Figure 4.16 Holocene pollen diagram of the main forest trees surrounding Tower Lake, in the region of the Great Lakes, between the United States and Canada (Fig. 2.9). The vertical axis represents age in thousands of years before present (ka BP). The horizontal axis shows the pollen percentage of each taxon at the given scales. Pollen zones mark phases of different taxon compositions of the forest. *Redrawn and modified from Jackson et al. (2014).*

forests were very different since they were dominated by *Picea*, *Pinus*, and *Betula* (Zone T-1). This changed approximately 6.5 ka BP into another type dominated by the recently arrived *Tsuga* and *Acer*, due to which *Picea* practically disappeared (Zone T-2). There was another change approximately 5 ka BP: *Tsuga* decreased and handed dominance over to *Pinus* and *Betula* (T-3). In conclusion, the composition of forest communities in this region constantly changed due to environmental factors (mainly climatic changes), and the process was governed by the idiosyncratic particularities of the affected species (Jackson et al., 2014). Therefore although the forest type remained unchanged, it was never exactly the same. This is just one example of many that prove that this process is a rather general phenomenon in both temperate and tropical areas.

These temporal sequences are similar to the distribution of species along spatial gradients, as Robert Whittaker described approximately 70 years ago (Fig. 4.2). Similar to the spatial continuum of Whittaker (1951), communities can be regarded as transient associations of species along temporal gradients. Once again, paleoecological evidence seems to contradict the concept of communities as relatively permanent entities in equilibrium with the environment. Available evidence is more compatible with the concept of Ricklefs (2008) and Simberloff (2004), which considers communities to be a result of the spatial and temporal coalescence of population samples of species from a regional pool of metapopulations and metacommunities. This continuous change in community composition is also compatible with Hutchinson's (1957) concept of nonequilibrium dynamics, which was adapted to terrestrial ecosystems by Margaret Davis, on the basis of paleoecological evidence. According to Davis (1981), constant environmental variations at diverse spatial and temporal scales produce a dynamic disequilibrium (or nonequilibrium dynamics), in which plant communities undergo permanent alterations without ever reaching equilibrium with the environment because the high rates of environmental change exceed what they can manage as communities.

4.4.5 Stability, resilience, and nonlinear responses

Upon close examination of the Quaternary paleoecological record, we find that phases of ecological stability have been an exception rather than a rule. However, some significant time intervals of apparent constancy in community composition are worth mentioning. The Neotropical region of Guiana, in the north of South America, provides us with an outstanding example. This region contains a complex of table mountains with elevations of up to 3000 m, locally called tepuis. The assemblage of flat tops of these mountains forms a biogeographical province (known as Pantepui) thanks to the uniqueness of their highly diverse and endemic biota (Fig. 4.17). The communities that form this biota are equally unique: they are composed of and/or dominated by species that do not exist on any other part of the planet, and they have singular physiognomic and structural characteristics (Rull et al., 2019). The exceptional nature and remoteness of Pantepui—it is thousands of kilometers away from what we call civilization and cannot be reached by foot, except in a couple of cases—inspired the celebrated British writer Arthur Conan Doyle to write his popular adventure story, *The Lost World*, in which dinosaurs live together with ancient human civilizations. The origin of the Pantepui biota and communities is still debated, but we have some paleoecological reconstructions of the Holocene of these high plateaus, which describe two apparently contradictory situations.

On some of these flat tepui summits, communities underwent changes in their composition and altitudinal distribution due to Holocene climatic variations, whereas in others, there are no traces of vegetation change during the last 6000 years, although the climate was far from stable (Fig. 4.18). This could be considered an example of resistance, as indicated in Table 4.1, and at first sight, could be taken as a case of climax communities that have reached a stable equilibrium with the environment (i.e., the PNV for the Pantepui bioclimatic conditions). However, the fact that ecological changes provoked by climatic oscillations were detected on other tepuis of the same region with similar vegetation and in the same time period proves that Pantepui communities were not indifferent to environmental changes. In these cases, plant communities underwent altitudinal shifts due to temperature variations, similar to the communities of the tropical Andes (Section 2.2.2; Fig. 2.15). Therefore the vegetation constancy recorded on some tepui summits during the last 6000 years could be a sampling artifact (Rull, 2015). Indeed, sampling site has a strong influence on whether climatic and ecological oscillations are detected. Paleoecological records from, or from close to, the altitudinal ecotone between two neighboring communities make it easier to find traces of ecological change, regardless of how small the change is. The reason is that the altitudinal setting of the ecotones is highly sensitive to elevational shifts of vegetation types provoked by climatic changes. On

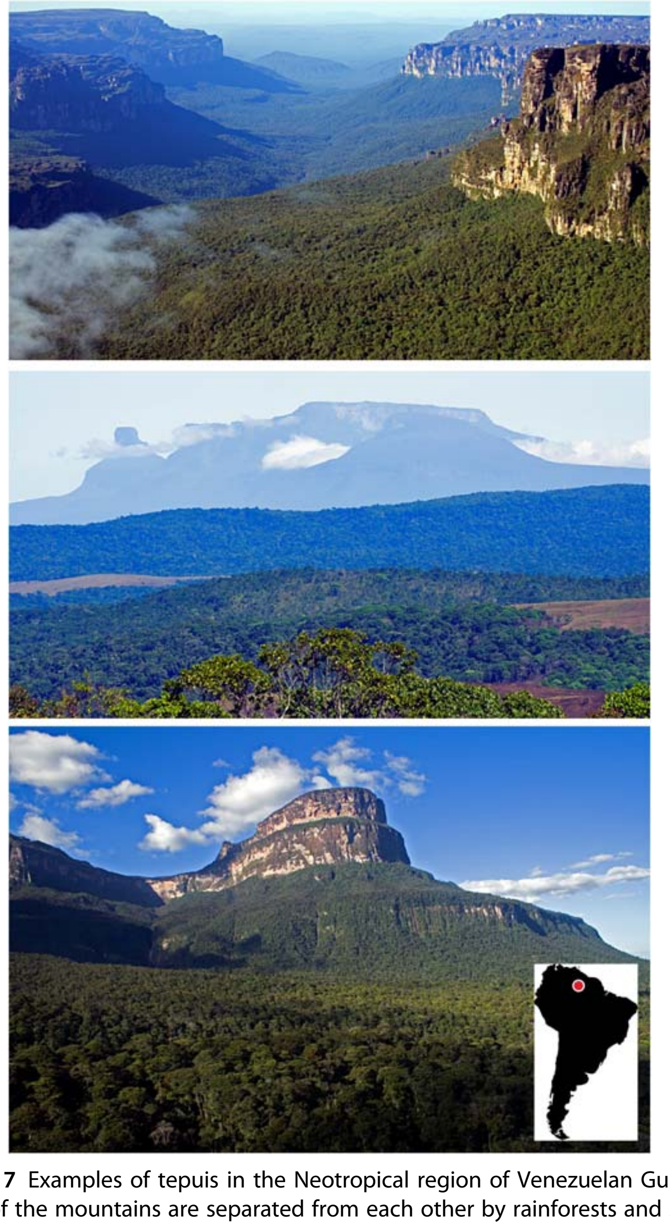

Figure 4.17 Examples of tepuis in the Neotropical region of Venezuelan Guiana. The flat tops of the mountains are separated from each other by rainforests and savannas as if they were islands floating in the air. A red dot shows their position on the map of South America. *Photos by V. Rull.*

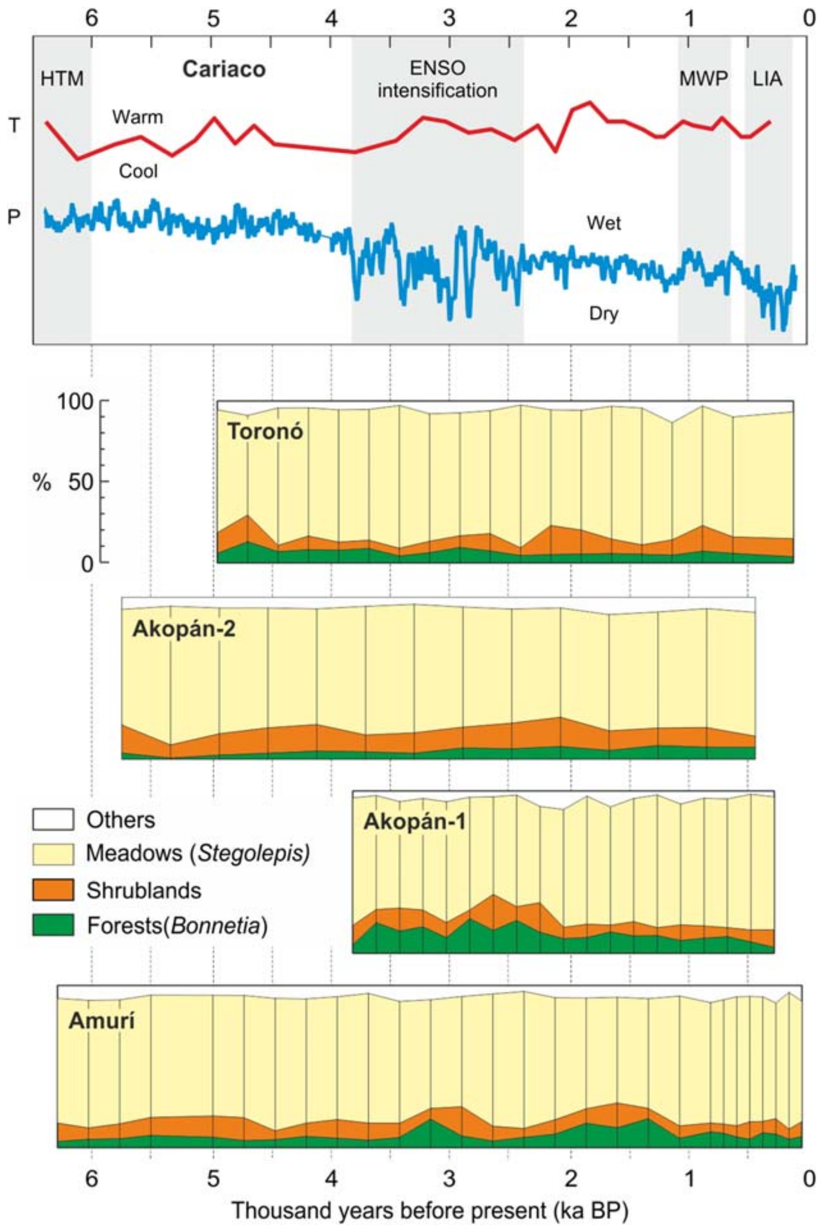

Figure 4.18 Stability of plant communities on three tepuis of the Pantepui Neotropical region (Fig. 4.17) during the last 6000 years. In this period the studied communities on top of the Toronó, Akopán (2 sites) and Amurí tepuis were always characterized by *Stegolepis* communities (Rapateaceae), with a minor presence of *Bonnetia* (Bonnetiaceae) forest and shrubs. In the upper part of the graph, regional (i.e., the northern part of South America) temperature (T) and rainfall (P) variations are shown together with the main events described in Chapter 1. *ENSO*, El Niño-Southern Oscillation; *HTM*, Holocene Thermal Maximum; *LIA*, Little Ice Age; *MWP*, Medieval Warm Period. *Redrawn and modified from Rull (2005).*

the contrary, if the paleoecological record is obtained in the altitudinal center of a given community, the chance of detecting community replacements provoked by altitudinal migration is significantly lower. This could be an explanation for the apparent ecological stability of certain tepuis during the Holocene. Another possibility is that paleoecological changes are of a smaller temporal scale than can be detected with the resolution of paleoecological studies. For example, the first paleoecological study of the Galapagos Islands was of a millennial resolution and seemed to support vegetation stability during the whole Holocene, but further studies conducted at a decadal resolution revealed ecological changes induced by climatic oscillation, including variations in El Niño-Southern Oscillation (ENSO) frequency and intensity (Bush et al., 2010). In summary, millennial-scale ecological stability is a rare feature in paleoecological records, even in the tropics (both Pantepui and the Galapagos are close to the Equator), and methodological problems cannot be disregarded. Therefore even in the case of apparent long-term ecological constancy, the concepts of the climax and PNV may be subject to serious criticism.

As a norm, communities undergo continuous changes induced by never-ceasing environmental, mainly climatic, variations. We have already seen an example, illustrated by Fig. 4.16, where the rate of community change is high, and the forest existed for only 1400 years in its present ecological state. However, the same example can be used to demonstrate that, despite environmental pressure, the forest was not replaced by another community. It was resilient enough to absorb climatic changes by adopting other states (T-1 to T-4) within its domain of attraction. This phenomenon has been called modulated succession (Rull, 1992) and can be considered an intermediate phase between autogenic and allogenic successions (Section 4.2). In other cases, however, environmental pressure is sufficiently large to overcome the community's resilience and remove it from its domain of attraction (Fig. 4.8), in which case the community is replaced by another one. As already mentioned, this is called a regime shift or induced replacement. We find an example of both processes (i.e., modulated succession and induced substitution) in the region known as the Gran Sabana (Venezuela), on the uplands situated below the easternmost Pantepui highlands (Fig. 4.17). Three main types of communities coexist in the Gran Sabana: mixed forests (especially montane forests and riparian forests), treeless savannas (dominated by grasses), and morichales (monospecific palm communities of *Mauritia flexuosa*) (Fig. 4.19). The dynamics of these communities, in terms of spatial distribution and

Figure 4.19 Main vegetation types in the Neotropical region of the Gran Sabana uplands in the easternmost part of the Pantepui highlands (Fig. 4.17). Left: riparian forest (rainforest). Middle: treeless savanna (with silhouettes of two tepuis in the background). Right: *Mauritia flexuosa* palm stand around a lagoon. *Photos by V. Rull.*

composition, vary over time as a function of climate, especially moisture, and anthropogenic fire regime.

In a study on the origin of morichales in the Gran Sabana, two paleoecological records [Divina Pastora (DV) and Urué (UR)] documenting the development of this community were obtained that covered the time period from the mid-Holocene to the present (Rull, 1992). Based on pollen analysis, diagrams similar to those in Fig. 4.16 were used to illustrate the dynamics of succession. By means of multivariate statistical methods, the domains of attraction and the course of succession were plotted for each drilling site (Fig. 4.20). Surprisingly, the study revealed that the two palm forests had completely different origins in terms of ecological succession, despite currently being part of the same domain of attraction. The longer of the two sequences (DV), which represents the last 4 ka, started with a dry savanna community. However, the increase in moisture approximately 2.7 ka BP overcame the resilience of the savanna, changed the course of succession, and provoked a shift into the domain of attraction of the morichal (this community needs permanent or seasonal water cover to survive), which eventually resulted in the current community at site DV. The history of the other palm forest (UR) was completely different. It started with a mixed forest community (1.7 ka BP) that crossed the threshold of the morichal domain of attraction slightly after 1.4 ka BP because of recurrent fires. These fires continued to occur until the beginning of the last millennium and impeded the recovery of the forest. In this case, Clotho provided two different threads of life, but Lachesis, probably with the help of gods (i.e., climatic changes and anthropogenic disturbance), managed to drive both successions to the same point, allowing Atropos to cut both threads within the same domain of attraction.

In this example, community replacements (or regime shifts) were induced by well-defined, concrete events, but gradual, long-term environmental changes can also lead to regime shifts. This is the case for nonlinear responses. Fig. 4.21 shows a simplified pollen diagram obtained for the sediments of Lake Osborne (Tasmania, Australia). Here, a humid forest of *Nothofagus* suffered a complete and sudden collapse and was replaced by sclerophyll (hard-leaved) forests of *Eucalyptus* approximately 6 ka BP (Fletcher et al., 2018). During the Holocene the number of fires increased gradually, and a progressive reduction in the *Nothofagus* forests, rather than their sudden irreversible collapse, could have been expected. As we can see in Fig. 4.21, there was a strong fire event approximately 8 ka BP—related to an El Niño event, which controls drought conditions and, thus,

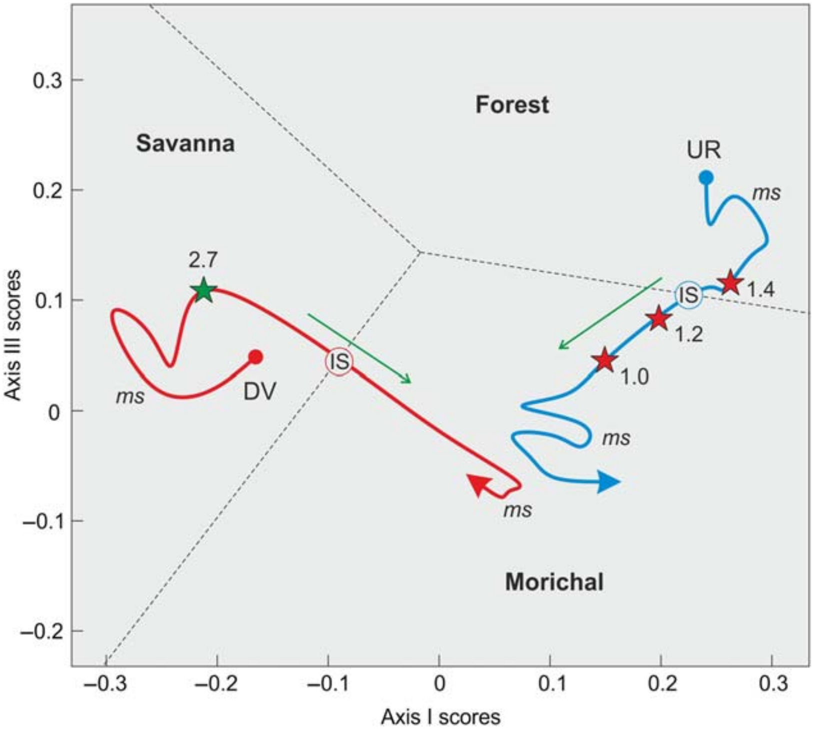

Figure 4.20 Biplot of a principal component analysis based on pollen data of two paleoecological sequences obtained in *Mauritia* palm forests of the Neotropical Gran Sabana region (Venezuela, Fig. 4.17). Domains of attraction were defined on the basis of surface samples after modern analog studies. Thresholds between domains are marked with dashed lines. The course of succession at site DV is shown in red; that at site UR is shown in blue. In both cases, succession onset is indicated by a circle, and the end stage is indicated by an arrowhead. At DV the green star shows a climatic change toward more humid conditions, and the number next to it gives its age in thousands of years before present (ka BP). At UR, red stars indicate fire events, and the numbers give their respective ages. Green arrows show the direction of the succession that crosses the threshold of the domain of attraction. *DV*, Divina Pastora; *IS*, induced substitution or regime shift; *ms*, modulated succession; UR, Urué. *Redrawn and simplified from Rull (1992).*

the risk of fire in Australia (Section 1.2.7)—that reduced the *Nothofagus* forest to a minimum. Nevertheless, the forest recovered and reached an extent similar to that before the fire. This was probably due to a long (almost 2000-year) period with a humid climate due to the low intensity of the ENSO and the consequent scarcity of El Niño events. However, the frequency and intensity of these events increased again beginning

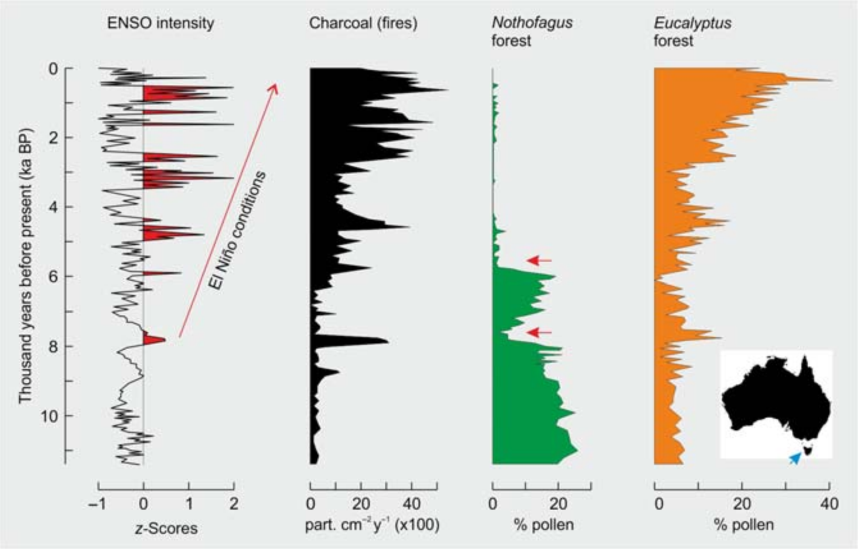

Figure 4.21 Diagram illustrating the collapse of *Nothofagus* humid forests of Tasmania (Australia) and their replacement by sclerophyll forests of *Eucalyptus* due to the interactions of climate and fire. Red peaks on the ENSO intensity curve indicate El Niño phases. Red arrows on the curve of the *Nothofagus* forest mark major reduction phases in the community. The first one was reversible, and the second one was irreversible. A blue arrow shows Tasmania on the map of Australia. *ENSO*, El Niño-Southern Oscillation. *Simplified and redrawn from* Fletcher et al. (2018).

from 6 ka BP, leading to a double negative effect on the *Nothofagus* forest. On the one hand, the dry El Niño events impeded the forest's recovery; on the other hand, they boosted the intensity and frequency of wildfires in a vicious cycle that abruptly removed these humid forests, which were replaced by sclerophyll forests of *Eucalyptus* that were well adapted to the dry climates and resistant to fire. This is an example of how two environmental factors (drought and fire) that increase gradually can enhance each other, generating a positive feedback mechanism that causes instantaneous and catastrophic biotic responses.

4.4.6 Communities without modern analogs and ghost communities

With all the changes that occurred during the Quaternary, both in climate and in the biota, it is logical to think that today's communities are but a sample of all Quaternary communities that have ever existed. For example, as we are living in an interglacial phase, present-day communities must be very different from the communities during glaciations. We can find an evident and spectacular example in the communities of the last glaciations, before the extinction of the megafauna (Section 2.2.3). These communities, with the now-extinct great mammals as keystone species (Section 4.4.1), will never return, and the only evidence we will ever find for them is in the fossil record, that is, their ghosts. Similarly, communities formed by species of Quaternary origin must have been different in the past. For example, communities of the Andean highlands—an area with especially active Quaternary diversification, as we saw in Chapter 3—must have undergone progressive changes as new species appeared, either by evolution or by immigration, especially in the case of species that dominate the communities today (Fig. 4.9). But we do not need to go far back in time to find communities without contemporary analogs; variations, in terms of both the composition and relative abundance of species, in the communities from the Last Glacial Maximum (LGM) until today provide ample evidence. We have seen several important examples from the Holocene: the modulated succession of the temperate forests of Great Britain (Fig. 4.15) and of North America (Fig. 4.21) and the shifts in domains of attraction in the Neotropics (Fig. 4.20) and in Tasmania (Fig. 4.21).

Not even the tropical rainforests of the Amazonian lowlands, which used to be considered communities that did not change over thousands and millions of years (Section 3.2), were free from changes in composition and ecological diversity. Several examples prove this, but we will mention only the most recent discovery. In the Ecuadorian Amazonas, in a lagoon near the El Pindo locality, sediments dating back 50,000 years, near the middle of the last glaciation (Fig. 1.8), were analyzed (Montoya et al., 2018). In contrast to what would be expected based on the refuge hypothesis (Section 2.2.2), the glacial vegetation did not belong to a savanna or a desert but to a real Amazonian rainforest with high ecological diversity. On the face of it, this forest did not look very different from the present-day rainforests of the region, but its composition was very different. It contained species that still live there, species that, although present in the rainforests of the region, cannot be found at this site today, and various tree species that, today, live on Andean hillsides at significantly higher altitudes. In other words the Amazonian rainforests of the last glaciation consisted of a mixture of species of the lowlands and of the Andean mountain rainforests (Fig. 4.22). Today, this combination is nowhere to be found in the Amazonian region, so it is a community without contemporary analogs. The fact

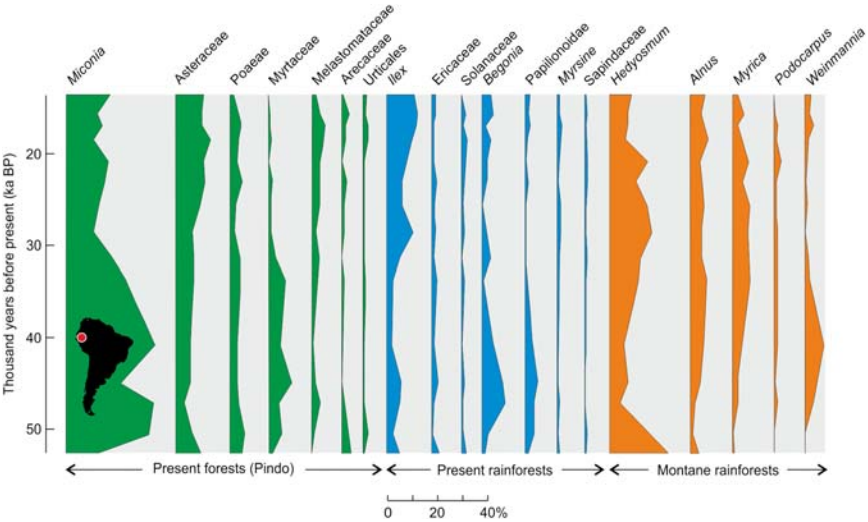

Figure 4.22 Pollen diagram showing the composition of the Amazonian rainforests of Ecuador during the last glaciation, between 50,000 and 15,000 years BP. Taxa are divided into three groups: in green the ones that can be found today in the rainforest of the study site (El Pindo); in blue, components found in other parts of the rainforest but not at the site today; and in orange, trees of the Andean mountain rainforest that do not live in the lowlands today. A red dot shows the position of El Pindo on the map of South America. *Redrawn and modified from Montoya et al. (2018).*

that mountain species descended to the level of El Pindo suggests that a significant temperature decrease made their downhill migration possible. The temperature decrease was demonstrated in other parts of Amazonia by means of independent paleoclimatic methods, such as stable isotope analysis in speleothems (Chapter 1). This is one more proof that altitudinal migrations of species happen at an individual level, according to species' individual tolerances of climatic changes. In Chapter 2 (Section 2.2.2, Fig. 2.15), we saw an example of the vertical shift of Andean vegetation belts during the last glaciation. The Ecuadorian example discussed here proves that these shifts did not take place in an analogous manner for all the species at each altitudinal level. Some species are more sensitive than others and may ascend and/or descend more, in accordance with the properties of their niche. Here is another fact to corroborate species' ecological idiosyncrasy. Interestingly, the *Miconia* species that dominated glacial rainforests (Fig. 4.22) are still very abundant, which demonstrates their plasticity in response to temperature changes.

4.5 Recent developments

Two important conceptual and methodological developments have recently been added to the study of community ecology with a long-term perspective. The use of paleoecological evidence to develop long-term explanatory and predictive models is an old demand of paleoecologists (Davis, 1994) that has not yet been properly exploited (Anderson et al., 2006) but now seems to be on the right track. In addition, the molecular phylogenetic methods explained in Chapter 3, are potentially useful for studying community assembly and dynamics. These methods are still in an incipient phase of development, but they are worth mentioning as their future also looks promising.

4.5.1 Paleoecological modeling

In recent years, some advances have been made regarding paleoecological modeling and its potential to understand past/present ecosystem dynamics and to predict future trends. As noted earlier, when dealing with true long-term ecology (Section 4.1), efforts are needed to integrate (neo)ecological and paleoecological data into continuous and homogeneous time series, for which seasonal to annual resolutions seem to be the best options (Fig. 4.3). Other challenges to be addressed are the fragmentary nature of paleoecological evidence, the difficulty in identifying fossils at the species level (taxonomic resolution) and the difficulty in equating past and present measures of abundance and diversity, among others. Some paleoecologists are working hard to overcome these handicaps, but further interdisciplinary initiatives are needed (Anderson et al., 2006). One proposal is to take advantage of the already existing "long-term" station networks based on present and future measurements—for example, the Long-Term Ecological Research Network (https://lternet.edu/) or similar networks—and upgrade them to true long-term past—present—future ecological observatories (PPFEOs) by including lakes with varved sediments (i.e., sediments with seasonal/annual laminations, Section 1.2), which may provide the resolution required to combine (neo)ecological and paleoecological data into continuous time series. This would be similar to the use of tree rings from fossil and extant species to build a single paleoclimatic curve for the last millennia, as shown in Fig. 1.12, but this time using other ecological parameters that may be proxies for population dynamics, community assembly, ecological succession, biodiversity changes, range shifts, vegetation cover, land-use patterns, fire incidence, and many others (Rull, 2014).

Among the recent developments in this direction, the PalEON (Paleo-Ecological Observatory Network; http://www.paleonproject.org/) project is worth mentioning. This project has been launched by an interdisciplinary team of paleoecologists, ecological statisticians, and ecosystem modelers to reconstruct the forest composition, fire regime, and moisture balance in northern North America over the past 2000 years and then use this to drive and validate terrestrial ecosystem models. Raw data for PalEON include pollen, charcoal, tree rings, and associated fire scars as proxies for the past distribution and dynamics of vegetation, with a focus on competition, dispersal, species declines, and their causes and the stability of species assemblages. An important point is that modeling is based on empirical paleoecological observations rather than on unsupported biological assumptions and the dynamics of physical systems. Some problems listed earlier, including the lack of paleoecological proxies of sufficient temporal and taxonomic resolution, remain. However, the initiative seems to be headed in the right direction to take advantage of paleodata for long-term explanatory and predictive ecological inferences. More initiatives of this type are needed, hopefully including varved lake sediments to attain a true network of long-term PPFEOs.

4.5.2 Molecular phylogenetics and community assembly

As already mentioned in Chapter 3, paleoecology relies on the occurrence of suitable archives (lakes, bogs, outcrops, etc.), which are randomly scattered across communities, thus hampering a thorough view of community development. Molecular phylogenetic methods can complement paleoecological records by providing a more suitable spatial and temporal context for community assembly processes (Emerson and Gillespie, 2008). To date, phylogenetic methods have been mainly used to understand the formation of large-scale regional biotas and biomes (e.g., Pennington et al., 2006; Byrne et al., 2008), which occur at the deep-timescale and, hence, transcend intracommunity interactions and assembly at Quaternary timescales. Attempts have been made to use molecular phylogenetics to address problems such as the influence of niche features or neutral processes on community assembly. For example, Cavender-Bares et al. (2009) review the pertinent literature on this subject and conclude that the phylogenetic structure of communities—

which is similar to the previously analyzed concept of population structure (Section 3.5.1) but at a community level—would be a key factor in understanding community assembly and highlight the importance of in situ evolution versus dispersal. These authors also emphasize the potential of molecular phylogenetics for reconciling microevolutionary and macroevolutionary studies and for predicting future developments in a changing world. Unfortunately, Cavender-Bares et al. (2009) consider the past to be a homogeneous dimension in which only evolution occurs and do not distinguish between deep-time and Quaternary processes (actually, the Quaternary is never mentioned by these authors). This makes it difficult to discuss their results and conclusions in the context of this book. This significant gap between deep time and present time (or between evolutionary and ecological processes), ignoring the Quaternary time dimension and the processes that occur in it (including micro- and macroevolution), is usual in classic ecological literature and seems to have been inherited by those using molecular phylogenetic approaches to understand community ecology. Some exceptions exist that consider the Quaternary time frame in phylogeographical studies about community assembly and argue for more close collaboration between ecologists and phylogeographers (e.g., Marske et al., 2013). However, no mention is made of the significance of paleoecological data, which are completely ignored, as straightforward evidence for past communities, or of the past of modern communities. In summary the incorporation of phylogenetic and phylogeographical methods into the study of ecological communities has not changed the former (neo)ecological view that ignored the Quaternary time frame, paleoecological evidence, or both. This topic is further discussed in the epilog.

A more useful approach, in the context of this book, has been recently developed by van der Merwe et al. (2019), who proposed a phylogenetic method to estimate the age of species' populations in a community and then developed an assemblage accumulation curve (AAC) that describes and characterizes the assembly of this community over time. The authors applied this method to three Australian rainforest communities and obtained three different AACs that were explained in terms of differential functional traits of the involved species. In all cases a recent acceleration in AACs is consistent with the increase in suitable habitats for rainforests following the LGM. The potential for this methodology, along with paleoecology and bottom-up modeling based on empirical data, seems high.

4.6 Synthesis: “everything flows; nothing remains”

Rather that the idea of a predestined fate under the surveillance of the Fates, the quote of the Greek philosopher Heraclitus of Ephesus (535–475 BCE) “everything flows, nothing remains” might be the best and briefest summary of this chapter. For a classic (neo)ecologist, this could seem even more frustrating than Gleason’s idiosyncrasy and Whittaker’s continuum concepts, as it includes both and extends the uncertainty to the time dimension. But this is what empirical observations tell us, and we should deal with it. Fortunately, we have Quaternary paleoecology, from which we can learn the real history of communities and ecosystems that live today or that have long disappeared, based on evidence, without any unfounded extrapolations of present-day observations. In this way, we can follow the evolutionary and ecological histories that produced the configuration of the living world that we live in, and we can also gain some understanding of the possible causes. In this chapter, we reviewed the topics of community assembly, disassembly, and reassembly in the Quaternary and saw that environmental (and especially climatic) changes have been very important, even crucial, in these processes. This does not mean that any change in the community must be due to external causes because environmental variations have different effects on different species, according to the species’ ecological niche parameters, which might affect their interactions with other components of the community. In other words, environmental change acts at two levels: it directly influences the autecology of each species based on the degree of individual sensitivity, and at the same time, it affects biotic relationships and, thus, ecosystem functioning. Therefore the niche characteristics of each species are determinant in the development of communities exposed to environmental variations, in contrast to what Hubbell (2001) suggested in his neutral theory of biodiversity.

Nevertheless, the concept of nonequilibrium dynamics, which is closely related to the individual migration capacity of species, introduces a random element into the system, which is compatible with the neutral theory of biodiversity, where dispersal is a fundamental process. If we regard communities as associations of species undergoing continuous change along spatial and temporal gradients, which is compatible with the Quaternary paleoecological record, the particular features of the niche of each species seem to be less important in the assembly of the community.

This means that species would not have preferences for other species in the formation of communities but that concurrence in space and time would determine the assembly. Discussing the topic of succession, we saw that the Clementsian idea of a superorganism is hardly compatible with most Quaternary evidence regarding community development. However, it is equally hard to imagine that a simple coincidence in time and space is enough to form a community without certain functional links between populations of species that are thrown together. In other words, neither strict determinism nor pure randomness seems to be the answer. A combination of random factors and niche compatibility seems more consistent with paleoecological observations. Random factors determine the combination of species drawn from a metacommunity that is mainly a product of migratory responses of the affected species to climatic changes (this also includes differential elements of the niche). In addition, niche compatibility decides whether this attempt at community assembly succeeds, according to the functional compatibilities of the species (or part of them) that co-occur in space and time. In conclusion, even if many followers of the two hypotheses (i.e., neutral theory and niche compatibility) claim that the two are incompatible with each other, it does not have to be so (e.g., Svenning et al., 2011; Jackson and Blois, 2016). The development of long-term ecological bottom-up models based on paleoecological evidence by transdisciplinary teams of (neo)ecologists, paleoecologists, and modelers is envisaged as the best way of obtaining more realistic outputs, not only in community ecology but also in ecology more generally.

But this is not all, as another fundamental and highly disturbing actor is missing: the genus *Homo*. We have not yet discussed this in detail, but without humans, the world would not be the same as it is today. Quaternary paleoecology, together with other disciplines such as archeology and anthropology, is fundamental in understanding how humans have interacted with the environment and with existing communities in the creation of the current situation. We will discuss this in the next chapter.

References

Alexander, H.M., Foster, B.L., Ballantyne, F., Collins, C.D., Antonovics, J., Holt, R.D., 2012. Metapopulations and metacommunities: combining spatial and temporal perspectives in plant ecology. J. Ecol. 100, 88–103.

Anderson, H.J., Bugmann, H., Dearing, J.A., Gaillard, M.-J., 2006. Linking palaeoenvironmental data and models to understand the past and to predict the future. Trends Ecol. Evol. 21, 696–704.

Barua, M., 2011. Mobilizing metaphors: the popular use of keystone, flagship and umbrella species concepts. Biodivers. Conserv. 20, 1427.

Bennett, K.D., 1997. Evolution and Ecology: the Pace of Life. Cambridge University Press, Cambridge.

Bennett, K.D., Willis, K.J., 2001. Pollen. In: Smol, J.P., Birks, H.J.B., Last, W.M. (Eds.), Tracking Environmental Change Using Lake Sediments. Vol. 3: Terrestrial, Algal, and Siliceous Indicators. Kluwer, Dordrecht, pp. 5–32.

Biggs, R., Carpenter, S.R., Brock, W.A., 2009. Turning back from the brink: detecting and impeding regime shift in time to advert it. Proc. Natl. Acad. Sci. U.S.A. 106, 826–831.

Birks, H.J.B., 1980. Modern pollen assemblages and vegetational history of the moraines of the Klutlan Glacier and its surroundings, Yukon Territory, Canada. Quat. Res. 14, 101–129.

Birks, H.J.B., Birks, H.H., 1980. Quaternary Palaeoecology. Edward Arnold, London.

Bush, M.B., 2003. Ecology of a Changing Planet. Prentice Hall, Upper Saddle River, NJ.

Bush, M.B., Colinvaux, P.A., Steinitz-Kannan, M., Overpeck, J.T., Sachs, J., Cole, J., et al., 2010. Forty years of paleoecology in the Galapagos. Galapagos Res. 67, 55–61.

Byrne, M., Yeates, D.K., Joseph, L., Kearney, M., Bowler, J., Williams, M.A.J., et al., 2008. Birth of a biome: insights into the assembly and maintenance of the Australian arid zone biota. Mol. Ecol. 17, 4398–4417.

Carlquist, S., 1967. The biota of long-distance dispersal. V. Plant dispersal to Pacific Islands. Bull. Torrey Bot. Club 44, 129–162.

Cavender-Bares, J., Kozak, K.H., Fine, P.V.A., Kembel, S.W., 2009. The merging of community ecology and phylogenetic biology. Ecol. Lett. 12, 693–715.

Chiarucci, A., Araújo, M.B., Decocq, G., Beierkuhnlein, C., Fernández-Palacios, J.M., 2010. The concept of potential natural vegetation: an epitaph? J. Veg. Sci. 21, 1172–1178.

Clements, F.E., 1916. Plant Succession, an Analysis of the Development of Vegetation. Carnegie Institute, Washington, DC.

Connell, J.H., Slatyer, R.O., 1977. Mechanisms of succession in natural communities and their role in community stability and organization. Am. Nat. 111, 1119–1144.

Damgaard, C., 2019. A critique of the space-for-time substitution practice in community ecology. Trends Ecol. Evol. 34, 416–421.

Davis, M.B., 1981. Quaternary history and the stability of forest communities. In: West, D.C., Shugart, D.B., Botkin, D.B. (Eds.), Forest Succession, Concepts and Applications. Springer, New York, pp. 132–153.

Davis, M.B., 1994. Ecology and paleoecology begin to merge. Trends Ecol. Evol. 9, 357–358.

Emerson, B.C., Gillespie, R.G., 2008. Phylogenetic analysis of community assembly and structure over space and time. Trends Ecol. Evol. 23, 619–630.

Faegri, K., Kaland, P.E., Krywinski, K., 1989. Textbook of Pollen Analysis. Wiley, Chichester.

Flenley, J.R., King, S., 1984. Late Quaternary pollen records from Easter Island. Nature 307, 47–50.

Flenley, J.R., King, A.S.M., Jackson, J., Chew, C., 1991. The Late Quaternary vegetational and climatic history of Easter Island. J. Quat. Sci. 6, 85–115.

Fletcher, M.-S., Bowman, D.M.J.S., Whitlock, C., Mariani, M., Stahle, L., 2018. The changing role of fire in conifer-dominated temperate rainforest through the last 14,000 years. Quat. Sci. Rev. 182, 37–47.

Gleason, H.A., 1926. The individualistic concept of the plant association. Bull. Torrey Bot. Club 53, 7–26.

Grimm, V., Schmidt, E., Wissel, C., 1992. On the application of stability concepts in ecology. Ecol. Model. 63, 143–161.

Gunderson, L.H., 2000. Ecological resilience — in theory and application. Annu. Rev. Ecol. Syst. 31, 425—439.

Hanski, I., 1999. Metapopulation Ecology. Oxford University Press, New York.

Holling, C.S., 1973. Resilience and stability of ecological systems. Annu. Rev. Ecol. Syst. 4, 1—23.

Holyoak, M., Leibold, M.A., Holt, R.D., 2005. Metacommunities: Spatial Dynamics and Ecological Communities. Chicago University Press, Chicago, IL.

Hubbell, S.P., 2001. The Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press, Princeton, NJ.

Hutchinson, G.E., 1957. Concluding remarks. Cold Spring Harb. Symp. Quant. Biol. 22, 415—427.

Jackson, S.T., Blois, J.L., 2016. Community ecology in a changing environment: perspectives from the Quaternary. Proc. Natl. Acad. Sci. U.S.A. 112, 4015—4021.

Jackson, S.T., Futyma, R.P., Wilcox, D.A., 1988. A paleoecological test of a classical hydrosere in the Lake Michigan dunes. Ecology 69, 928—936.

Jackson, S.T., Booth, R.K., Reeves, K., Andersen, J.J., Minckley, T.A., Jones, R.A., 2014. Inferring local to regional changes in forest composition from Holocene macrofossils and pollen of a small lake in central upper Michigan. Quat. Sci. Rev. 98, 60—73.

Johnson, E.A., Miyanishi, K., 2008. Testing the assumptions of chronosequences in succession. Ecol. Lett. 11, 419—431.

Lawton, J.H., 1999. Are there general laws in ecology? Oikos 84, 177—192.

MacArthur, R.H., Wilson, E.O., 1963. An equilibrium theory of insular biogeography. Evolution 17, 373—387.

Malhi, Y., Doughty, C.E., Galetti, M., Smith, F.A., Svenning, J.-C., Terborgh, J.W., 2016. Megafauna and ecosystem function from the Pleistocene to the Anthropocene. Proc. Acad. Sci. U.S.A. 113, 838—846.

Margalef, R., 1997. Our Biosphere. Ecology Institute, Oldendorf/Luhe.

Marske, K.A., Rahbeck, C., Nogués-Bravo, D., 2013. Phylogeography: spanning the ecology-evolution continuum. Ecography 36, 1169—1181.

Montoya, E., Keen, H.F., Luzuriaga, C.X., Gosling, W.D., 2018. Long-term vegetation dynamics in a megadiverse hotspot: the Ice Age record of a pre-montane forest of central Ecuador. Front. Plant Sci. 9, 196.

Long-term ecological research. In: Müller, F., Baessler, C., Scubert, H., Klotz, S. (Eds.), Between Theory and Application. Springer, Dordrecht.

Odum, E.P., 1969. The strategy of ecosystem development. Science 164, 262—270.

Palmer, M.W., White, P.S., 1994. On the existence of ecological communities. J. Veg. Sci. 5, 279—282.

Pennington, R.T., Richardson, J.E., Lavin, M., 2006. Insights on the historical construction of species-rich biomes from dated plant phylogenies, neutral ecological theory and phylogenetic community structure. N. Phytol. 172, 605—616.

Pickett, S.T.A., 1989. Space-for-time substitution as an alternative to long-term studies. In: Likens, G.E. (Ed.), Long-Term Studies in Ecology. Springer, New York, pp. 110—135.

Pouchon, C., Fernández, A., Nassar, J.M., Boyer, F., Aubert, S., Lavergne, S., et al., 2018. Phylogenomic analysis of the explosive adaptive radiation of the *Espeletia* (Asteraceae) complex in the tropical Andes. Syst. Biol. 67, 1041—1060.

Raffaelli, D.G., 2006. Biodiversity and ecosystem functioning: issues of scale and trophic complexity. Mar. Ecol. Prog. Ser. 311, 285—294.

Ricklefs, R.E., 2008. Disintegration of the ecological community. Am. Nat. 172, 741—750.

Ricklefs, R.E., 2012. Naturalists, natural history, and the nature of biological diversity. Am. Nat. 179, 423—435.

Rull, V., 1992. Successional patterns of the Gran Sabana (southeastern Venezuela) vegetation during the last 5000 years, and its responses to climatic fluctuations and fire. J. Biogeogr. 19, 329–338.

Rull, V., 2005. Vegetation and environmental constancy in the Neotropical Guayana Highlands during the last 6000 years? Rev. Palaeobot. Palynol. 135, 205–222.

Rull, V., 2010. Ecology and palaeoecology: two approaches, one objective. Open Ecol. J. 3, 1–5.

Rull, V., 2012a. Community ecology: diversity and dynamics over time. Commun. Ecol. 13, 102–116.

Rull, V., 2012b. Past natural history and ecological biodiversity modeling. Syst. Biodivers. 10, 261–265.

Rull, V., 2014. Time continuum and true long-term ecology: from theory to practice. Front. Ecol. Evol. 2, 75.

Rull, V., 2015. Long-term vegetation stability and the concept of potential natural vegetation in the Neotropics. J. Veg. Sci. 26, 603–607.

Rull, V., 2016. Natural and anthropogenic drivers of cultural change on Easter Island: review and new insights. Quat. Sci. Rev. 150, 31–41.

Rull, V., Vegas-Vilarrúbia, T., Huber, O., Señaris, C. (Eds.), 2019. Biodiversity of Pantepui: the pristine "Lost World" of the Neotropical Guiana Highlands. Elsevier-Academic Press, London.

Salo, J., Kalliola, R., Häkkinen, I., Näkinen, Y., Niemelä, P., Puhakka, M., et al., 1986. River dynamics and the diversity of Amazon lowland forest. Nature 322, 254–258.

Scheffer, M., Carpenter, S., Foley, J.A., Walker, B., 2001. Catastrophic shifts in ecosystems. Nature 413, 591–596.

Scheiner, S.M., Willig, M.R., 2008. A general theory of ecology. Theor. Ecol. 1, 21–28.

Shelford, V.E., 1911. Ecological succession. II. Ponds fishes. Biol. Bull. 21, 127–151.

Shugart, H.H., 2012. Secondary succession. eLS. Wiley, Chichester. Available from: https://doi.org/10.1002/9780470015902.a0003182.pub2.

Simberloff, D., 2004. Community ecology, is it time to move on? Am. Nat. 163, 787–799.

Snedaker, S.C., 1982. Mangrove species zonation, why? In: Sen, D.N., Rajpurohit, K.S. (Eds.), Tasks for Vegetation Science. DR. W. Junk Publishers, The Hague, pp. 111–125.

Stott, P., 1998. Biogeography and ecology in crisis, the urgent need for a new language. J. Biogeogr. 25, 1–2.

Svenning, J.-C., Fløjgaard, C., Baselga, A., 2011. Climate, history and neutrality as drivers of mammal beta diversity in Europe: insights from multiscale deconstruction. J. Anim. Ecol. 80, 393–402.

Tansley, A.G., 1935. The use and abuse of vegetational terms and concepts. Ecology 16, 284–307.

van der Merwe, M., Yap, J.-Y.S., Bragg, J.G., Cristofolini, C., Foster, C.S.P., Ho, S.Y. W., et al., 2019. Assemblage accumulation curves: a framework for resolving species accumulation in biological communities using DNA sequences. Methods Ecol. Evol. 10, 971–981.

Vellend, M., 2010. Conceptual synthesis in community ecology. Q. Rev. Biol. 85, 183–206.

Walker, L.R., del Moral, R., 2011. Primary succession. eLS. Wiley, Chichester. Available from: https://doi.org/10.1002/9780470015902.a0003181.pub2.

Walker, L.R., Wardle, D.A., Bardgett, R.D., Clarkson, B.D., 2010. The use of chronosequences in studies of ecological succession and soil development. J. Ecol. 98, 725–736.

Walter, G.H., Hengeveld, R., 2000. The structure of the two ecological paradigms. Acta Biotheoretica 48, 15–46.

Whittaker, R.H., 1951. A criticism of the plant association and climatic climax concepts. Northwest Sci. 25, 17–31.

Whittaker, R.J., Bush, M.B., Richards, K., 1989. Plant recolonization and vegetation succession on the Krakatau Islands, Indonesia. Ecol. Monogr. 59, 59–123.

Wright, H.E., 1977. Quaternary vegetation history – some comparisons between Europe and America. Annu. Rev. Earth Planet. Sci. 5, 123–158.

Wright, H.E., 1980. Surge moraines of the Klutlan glacier, Yukon Territory, Canada: origin, wastage, vegetation succession, lake development, and applications to the Late-Glacial of Minnesota. Quat. Res. 14, 2–18.

Zizka, G., 1991. Flowering Plants of Easter Island. Palmarum Hortus Francofurtensis, Frankfurt.

CHAPTER FIVE

Humans: occupation and humanization of the planet

Contents

Climatic change has been a decisive biogeographical, ecological, and evolutionary driver during the Quaternary, but human influence has also played a crucial role, especially during the Holocene. In many cases, human influence over the Earth System has become equally or more important for the dynamics of the biosphere than climate or other environmental factors. For example, our species has even been able to significantly modify climatic trends and global biogeochemical cycles over the last few centuries (Waters et al., 2016). Therefore humanity has become a new telluric force that may be decisive in the future evolution of the biosphere. Here, we use the term "anthropogenic" specifically for everything that has been generated by humans and the consequences of such effects. In this context the terms "natural" and "preanthropogenic" could be regarded as synonyms when dealing with ecosystems, landscapes, and

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biomes. Human-modified versions of these biological entities have also been called "cultural" (e.g., cultural landscapes). There is a clear difference between the two concepts (i.e., natural and anthropogenic), regardless of philosophical controversies; however, it is not so easy to draw a chronological boundary between the natural and anthropogenic worlds. This question is one of today's hot topics; it is fundamental to the definition of what many consider a new epoch of Earth's geological history, the "Anthropocene" (Crutzen and Stoermer, 2000; Waters et al., 2014). We will discuss this further in the next chapter.

In addition to having been an important ecological agent, humans have also had significant evolutionary and biogeographical influences on other living things. Some of the key processes in this regard are (1) the domestication of plants and animals, by which we modified the gene pool of many species and created a multitude of new varieties; (2) the active or passive dispersal of flora and fauna all over the world, by which we largely homogenized the biota and eliminated reproductive barriers; and (3) the extinction of several species, by which we contributed to the decrease in general biodiversity (Goudie, 2006; Roberts, 2014). Moreover, recent developments in genetic engineering will result in an even more powerful influence over other species, as well as ourselves, in currently unimaginable ways. Based on present-day trends, it seems clear that we are going to continue eliminating species as a direct or indirect result of our activities, in what is considered by many as the sixth mass extinction (Sections 2.1.2 and 2.2.3). At the same time, environmental changes have also affected human evolution, spatial and temporal migration patterns (and, thus, the colonization of the whole planet) and the possibility of performing (or not performing) certain activities. These effects determined synergies between natural and anthropogenic factors and had important ecological, biogeographical, and evolutionary consequences.

The topic of this chapter is human influence over the biosphere in the Quaternary. To place this analysis in a proper context, we include the *Homo* species existing before us, but we focus on *H. sapiens* as the main party responsible for the humanization of the planet. We start with a brief introduction to human evolution, which is mostly a Quaternary phenomenon. Afterward, we give *H. sapiens* our full attention, starting with the full colonization of Earth and moving on to the ecological relations of this species at all levels (local, regional, and global) and all time scales, but with a special emphasis on the Holocene, the epoch when our influence has transformed the planet. The most important process, in this aspect, is the so-called Neolithic Revolution, the transition from nomadic societies to more sedentary ones and the development of agriculture. Finally, we discuss the Industrial Revolution and the consequences it has had for the biosphere and the Earth System in general. The books by Goudie (2006) and Roberts (2014) are recommended for a thorough history of human disturbance on planet Earth, especially during the last glacial cycle.

5.1 Human evolution

5.1.1 Hominids and hominins

Before going into detail, we have to pause for a terminological clarification. The term hominid is often used to refer to our species (*H. sapiens*) and all of our extinct ancestors together. The reason for this is that we all belong to the same zoological family called Hominidae. But the development of molecular phylogenetics (Chapter 3) changed the definition of hominids. While our species' classification was based solely on morphological characteristics, the family Hominidae is composed exclusively of our own lineage, of which we are the only living representatives. However, genomic studies modified this classification, and the family Hominidae now also includes other primates, such as the orangutan (*Pongo*), the gorilla (*Gorilla*), and the chimpanzee (*Pan*) (Fig. 5.1) (Mann and Weiss, 1996). This does not mean that we are no longer hominids but that our family is more extensive than we used to think. The new classification also gave rise to a new term, hominin (tribe Hominini), which coincides with the former use of hominids according to some researchers, while others also include the chimpanzee. The first group believes that the genetic differences between humans and chimpanzees are large enough to create two tribes (i.e., Hominini and Panini), while the second one thinks that we are not that different and adds both humans and chimpanzees to the tribe Hominini (Fig. 5.1) (von Holstein and Foley, 2017). We could say that there are two versions of the concept hominin: the strict version that equals former hominids and the extended version that includes chimpanzees. Whichever the case, the molecular clock method (Section 3.3) revealed that the divergence between our lineage and the chimpanzees took place before the Quaternary, between 7 and 5 Ma (Kumar et al., 2005).

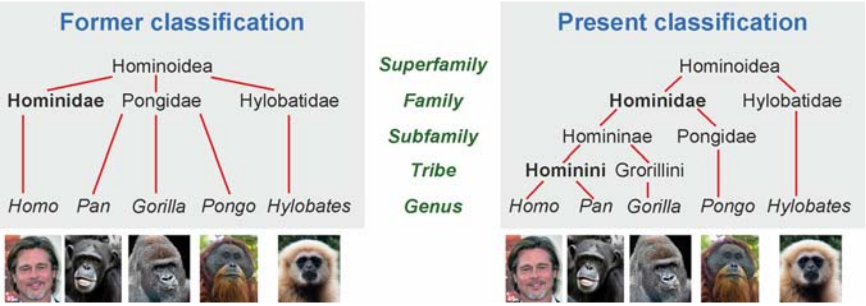

Figure 5.1 Comparison between different classifications of the hominoid superfamily (Hominoidea) based on morphology (former classification) and molecular (DNA) phylogenetics (current classification). Hominids (family Hominidae) and hominins (tribe Hominini) are in bold. Only one possible hominin classification is shown. The other alternative is that the chimpanzee forms a separate tribe (Panini) (see text). *Base image by K. Cantner, AGI (publicly available at earthmagazine.org).*

Therefore in this book, which is focused on the Quaternary segment of our lineage, the emphasis will be on the genus *Homo*.

5.1.2 The genus *Homo*

The following is only a brief summary on the evolution of the genus *Homo*, which is enough for the aims and scope of this book. The more specialized readers are referred to the synthesis by Galway-Witham et al. (2019)—which was published just after the writing of this book—for a thorough and updated review of the topic, including the latest paleontological, archeological, and phylogenetic findings. Two types of criteria are used to differentiate the human genus (*Homo*) from its ancestors and from coeval nonhumans: morphological and ethological criteria. On the one hand, paleontologists look for physical and genetic characteristics in fossils, based on which a human genus can be distinguished from earlier apes, taking into account conventional taxonomic criteria (e.g., Stringer, 2016). In addition, at sites with human fossils, archeologists seek evidence pointing to behaviors and cultural traits that are different from those of former genera and species and that could justify the human condition (e.g., Pinker, 2010). For Darwin (1871) a decisive evolutionary development with respect to other primates was to leave behind our tree-dwelling nature (the famous coming down from the tree) and to develop bipedalism, which introduced a fundamental difference by modifying locomotion patterns and leaving the hands free for tool use. This also required additional coordination tasks that shaped the evolution of intelligence and resulted in larger and more developed brains together with improved communication capabilities, which in turn led to the development of articulate language, one of the main vehicles of human evolutionary progress. From an ethological point of view, Darwin suggested that the most important distinguishing behavioral feature in the early phases of human evolution was the adoption of hunting as the chief means of subsistence. He also argued that this had a large influence on the division of work and was the main cause of sexual specialization. The manufacture of specialized hunting tools was also a distinguishing feature of humans, which was accompanied by a decrease in the size of canine teeth, which were no longer needed to directly attack prey.

These features (bipedalism, the use of hands, increased brain size, reduced canine teeth, articulate communication, making arms and tools), together with the mastery of fire, made up what we could call a singular evolutionary package that enabled the emergence of a new, distinct lineage of primates. Morphological and ethological modifications of humans seem to be so closely linked to each other, in what looks like a cause-and-effect relationship, that it might seem that they appeared simultaneously. However, the fossil record reveals that this batch of evolutionary advantages appeared in a gradual manner throughout most of the Quaternary (Rosas, 2016). From a biological point of view, we should not think about human evolution as a linear process where species followed each other by anagenesis, that is, by progressive evolutionary transformation (Section 3.1.2), with only one hominin species existing at any given time. This is an old view called the single-species hypothesis, according to which three human species (*Homo habilis*, *H. erectus*, and *H. sapiens*) existed during the Quaternary that followed each other in time without ever coinciding. But paleontological evidence demonstrated that there were more than three species of *Homo* and that several of them coexisted at certain times in their evolutionary history (Fig. 5.2).

With all this in mind, we now focus on the origin of our genus and its evolution throughout the Quaternary. The appearance of the genus *Homo* is also subject to controversy. Some think it happened close to the Pliocene–Pleistocene boundary, while others believe that the genus appeared only 2Ma, in the Early Pleistocene (Fig. 5.2). Between the two theories, there is a taxonomic difference, precisely, whether the oldest species, *H. rudolfensis* and *H. habilis* (which were already able to make and use tools, hence the specific epithet *habilis*), belong to the genus *Homo* or to the genus *Australopithecus*, which is our predecessor in the phylogenetic

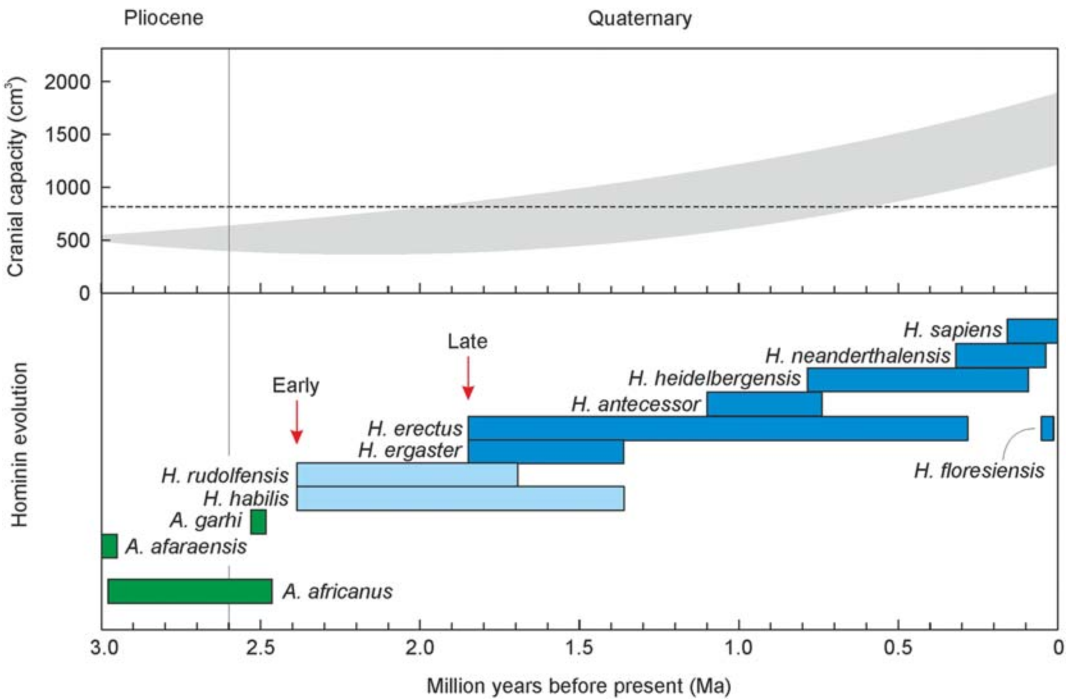

Figure 5.2 Chronological ranges add cranial capacity of the most important *Homo* species and their ancestors. Green bars correspond to *Australopithecus* species, light blue bars represent species that could correspond to either *Australopithecus* or *Homo*, and blue bars are *Homo* species. Red arrows mark the early and late hypotheses about the origin of the genus *Homo*. *Simplified from Maslin et al. (2015) and Shultz et al. (2012).*

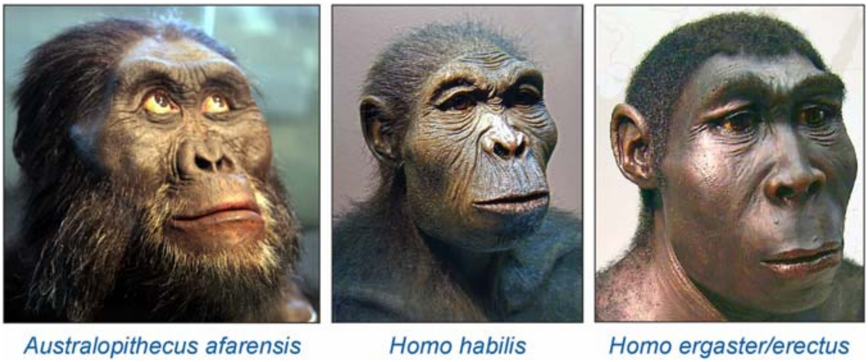

Figure 5.3 Reproductions of the first representatives of the genus *Homo* and its ancestor, *Australopithecus*. See Fig. 5.2 for their chronological ranges. From reproductions freely available at Wikipedia.org.

tree of hominins (Fig. 5.3) (Collard and Wood, 2014). According to the second view, we should be talking about *A. habilis* and *A. rudolfensis*. These species originated 2.4–2.1 Ma (Fig. 5.2), in the region of the African rift—which we already know to be home to one of the most spectacular Quaternary speciation events (see the case of the cichlid fishes in Section 3.5.3 and Fig. 3.16). If *habilis* and *rudolfensis* belong to the genus *Homo*, as morphological features of their fossils seem to suggest, this would be the date of the appearance of this genus. On the contrary, if they belong to the genus *Australopithecus*, in accordance with molecular phylogenetic criteria, the date of the origin of the human genus would coincide with the emergence of *H. ergaster* and *H. erectus*, ~2.0 Ma, also in East Africa (Fig. 5.2).

An argument in favor of the latter theory is that *H. ergaster* and *H. erectus* were the first species that truly lived on the ground and walked upright, while older species still lived in trees (Hunt, 1994). This adaption to living on the ground can be related to the expansion of East African savannas, which started around the Plio–Pleistocene boundary (3.0–2.5 Ma) as a consequence of drier climates, which would have favored the establishment of herbaceous vegetation instead of the typical rainforests of these equatorial latitudes (de Menocal, 1995, 2004; Reed, 1997). The upright position was the most appropriate option in this open vegetation type, with long-distance visibility being an advantage in finding prey and discovering possible enemies quickly. In this way, hominids that once "decided" to descend from the trees started to colonize the savanna ecosystem. This ecosystem was of relatively recent formation, and hominids had to evolve to become properly adapted to the new conditions. According to this hypothesis (known as the savanna hypothesis), our origin would be the result of a climatic change and its ecological consequences, that is, an unpredictable incident, a contingency. In addition, *H. ergaster* was the first to cross the 800 cm^3 cranial capacity limit (Fig. 5.2), which is considered by some to be a critical size for separating humans from australopithecines (Falk, 1980).

H. ergaster (literally "working man"), the first clearly ground-living hominin, had the same geographical origin as the earlier species, but it was also the first one to leave Africa in search of new worlds. Based on fossil evidence, the first human expansion was relatively fast. According to the current view, *H. ergaster* began its expansion by 1.9 Ma and reached northern Africa, the Middle East, China, and Indonesia in just 100−200 hundred years (Fig. 5.4). However, the recent discoveries of hominin fossils of ages between 2.5 and 2.1 Ma in Northern Africa, China, and the Middle East seems to demand a reconsideration of this hypothesis (Fig. 5.4) (Scardia et al., 2019). In the beginning, hominin fossils found

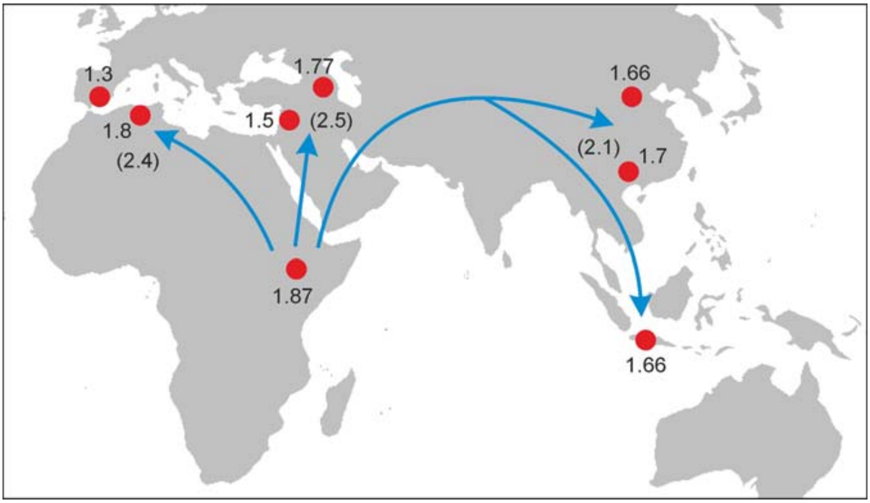

Figure 5.4 First great expansion of *Homo* out of Africa. Red circles show sites with fossils of *H. ergaster* and/or *H. erectus*. Numbers indicate the age of the fossils in millions of years before present (Ma), acording to Rosas (2016). Bracketed ages are from the more recent discoveries summarized by Scardia et al. (2019). The most likely migration paths from one continent to another and then to the islands were the continental shelves that were exposed during glaciations (Sections 1.2.2. and 1.2.4). *Raw data from Rosas (2016) and Scardia et al. (2019).*

in Asia were attributed to a new species, *H. erectus*. Today, whether these two species are the same or if *H. erectus* descended from *H. ergaster* remains undecided. The truth is that, morphologically, they are very similar. The African lineage (*H. ergaster*) went extinct approximately half a million years after its appearance, while the Asian counterpart (*H. erectus*) existed for more than 1.5 million years, which means that it went through many glacial–interglacial cycles. Leaving East Africa implied leaving the tropical climate and ecosystems behind, so that these travelers had to adapt or acclimate to new environmental conditions and to the use of new, different resources. Such a long existence (our species has lived for hardly a 10th of the time that *H. erectus* lived) without significant morphological changes is a good example of evolutionary stasis, as defined by the punctuated equilibrium hypothesis (Section 3.4.2). It is also an evidence of high phenotypic plasticity (undoubtedly enhanced by intelligence) and of evolutionary success. Evidence suggests that *H. erectus* already controlled fire around 800 ka BP (Goren-Inbar et al., 2004), much earlier than Neanderthals, which are usually considered the real masters of fire among hominins. *H. ergaster/H. erectus* also reached Europe (i.e., the Iberian Peninsula) by 1.3 Ma, probably originating from North African populations, which marks the first hominin occupation of this continent (Carbonell et al., 2008).

Based on fossils known to date, the evolution of *H. ergaster* into modern humans seems to have happened through a combination of cladogenetic and anagenetic processes (Section 3.1.1). The first step would have been the evolution of *H. ergaster* into *H. antecessor*, which eventually stemmed into two species: *H. heidelbergensis* (the progenitor of *H. neanderthalensis*) and *H. rhodesiensis* (the predecessor of *H. sapiens*) (Fig. 5.5). Therefore *H. antecessor* would have been the last common ancestor of *H. sapiens* and *H. neanderthalensis*. However, the geographical context of these evolutionary steps remains unresolved since the Neanderthals were of European origin, while we are an African species. The currently most accepted hypothesis suggests that *H. antecessor* emerged in Africa, but some of its populations migrated to Europe. This resulted in two lineages: the African lineage culminating in *H. sapiens* and the European lineage ending with *H. neanderthalensis*. This hypothesis implies a second African-European crossing, after that of *H. ergaster*, by *H. antecessor*. Some paleoanthropologists think that there is not sufficient evidence to distinguish *H. antecessor* and *H. heidelbergensis* as separate species. In their opinion, it was *H. heidelbergensis* that divided into two lineages and reached Europe for the second time, where it evolved directly

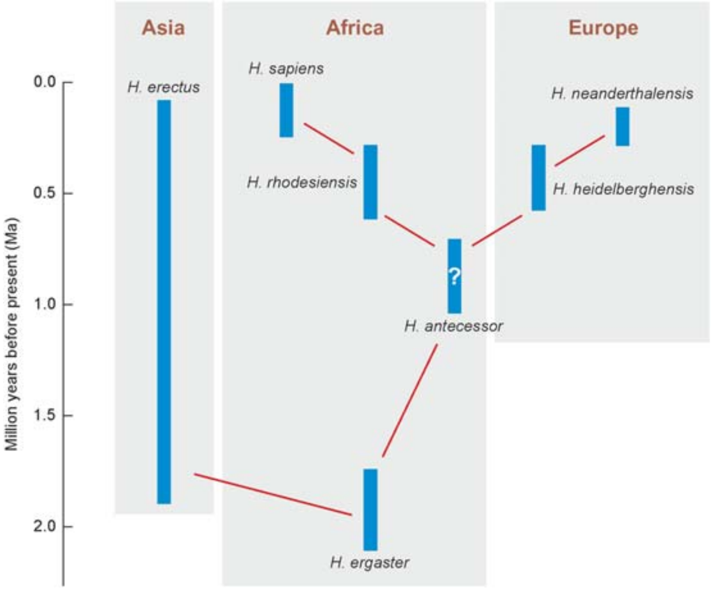

Figure 5.5 Evolutionary tree from *Homo ergaster* to modern humans based on the morphology of fossils found to date. The geographical location indicates the place of origin of each species, which does not exclude possible subsequent migration to other continents. Question marks next to *Homo antecessor* refer to the controversy regarding the existence of this species and its relationship with *Homo heidelbergensis* (see main text). *Modified and redrawn from Rosas (2016).*

into *H. neanderthalensis*. The African population thus gave rise to *H. rhodesiensis* and, afterward, to *H. sapiens*. Under this view, *H. heidelbergensis*, and not *H. antecessor*, would have been the last common ancestor of *H. sapiens* and *H. neanderthalensis*.

Altogether, human evolution from *H. ergaster* seems to be a typical case of long-range (nearly worldwide) adaptive radiation (Section 3.1.1) and a very spectacular one, given the remarkably high evolutionary rates. We can also find here examples of three extinction types mentioned previously (Section 3.1.2): the phyletic extinction of *H. neanderthalensis* that left no descendants; the cladogenetic extinction of *H. antecessor* (or *H. heidelbergensis*, according to the alternative theory), which was replaced by the lineages of *H. sapiens* and *H. neanderthalensis*; and the anagenetic extinction of *H. rhodesiensis*, which transformed into *H. sapiens* (Fig. 5.5). According to Maslin et al. (2015), climatic shifts, especially alternating phases of extreme humidity and aridity, may have driven hominin speciation and dispersal out of Africa (pulsed climate variability hypothesis) by mechanisms such as phyletic gradualism and punctuated equilibrium (Section 3.4.2). The same authors contend that during phases of climatic stability, the Red Queen (Section 3.4.3) could have been the dominant evolutionary process.

We must mention another, rather peculiar species of this saga, *H. floresiensis* (Fig. 5.2), the remains of which have been found only on the Island of Flores in Indonesia (Fig. 2.17). It is a species of small individuals, with heights of slightly more than 1 m, body masses of 20–30 kg, and rather small brains (less than half a liter). The oldest fossils of this species date back to 100 ka BP, and the date of the species' extinction was ~12 ka BP (Fig. 5.2) (Sutikna et al., 2016). It is debated whether *H. floresiensis* is a distinct species or a variety of *H. erectus* that colonized Indonesia during the first hominin expansion (Fig. 5.4) and was adapted to island conditions, which often leads to dwarfism in other animal species (Raia and Meiri, 2006). Other human species or subspecies have been described very recently, such as *H. naledi* or the Denisovans, which were more or less coeval with *H. sapiens* and the Neanderthals and, therefore, genetic interchange would have been possible among them (e.g., Slon et al., 2018). However, the study of these newly discovered species is still in progress (Galway-Witham et al., 2019).

From here, we will concentrate on our own species, which is the one that has changed the world. But first, we will dedicate a section to the coeval, albeit already extinct, species *H. neanderthalensis*, which played a significant role in the configuration of the modern world and intensively interacted with *H. sapiens* in both ecological and evolutionary terms.

5.1.3 The Neanderthals

A thorough and updated synthesis of Neanderthal ecology and evolution can be found in Carrión et al. (2019); here, only some hints are provided about this extinct species that coexisted and interacted with modern humans (*H. sapiens*) of the Late Pleistocene. *H. neanderthalensis*, a typical Eurasian species (Fig. 5.6), was morphologically similar to *H. sapiens*. Most likely, the largest difference was in cranial capacity, which was larger in Neanderthals (with an average of 1500 cm^3, but with values up to 1700 cm^3) than in *H. sapiens* (with an average of 1350 cm^3). Such differences, however, seem to be due to the larger size of the visual system of the Neanderthals, rather than to the size of their brain (Pearce et al., 2013). The first Neanderthals appeared 300,000–400,000 years ago; thus

Figure 5.6 Reconstruction of *Homo neanderthalensis* and its geographical range (in blue). This species originated in Europe and later expanded into parts of Asia. The red line separates the original area (left) from the Asian expansion (right). *Images from the Natural History Museum, London, publicly available at nhm.ac.uk.*

the species endured at least three glaciations (MIS 8, MIS 6, and MIS 3–4) and two interglacial periods (MIS 7 and MIS 5) (Section 1.2.2), but it reached its maximum development from approximately MIS 5b (80 ka BP) until the middle of MIS 3 (40 ka BP), when it went extinct. The prototype of the Neanderthal corresponds to the later phase (80–40 ka BP), a typical glacial phase during which ice sheets reached the southern parts of the British Isles (Section 1.2.4 and Fig. 1.10). Some researchers believe that the cold climate favored certain adaptive features, such as a robust constitution and elongated face, while others consider that the harsh conditions caused isolation and fragmentation of populations and thus boosted genetic drift (Section 3.1.1) and, as a consequence, nonadaptive evolution. Given the variety of glacial–interglacial climates that they endured, we cannot say that Neanderthals were a typical glacial species completely adapted to cold climates. The evolution of Neanderthal anatomy is still subject to debate. From a cultural point of view the Neanderthals were fairly similar to the *H. sapiens* of the same time. It has even been speculated that they were able to communicate verbally, as they possessed the same variant of the *H. sapiens* gene *FOXP2*, which is required for the proper development of human speech and language (Krause et al., 2007).

Neanderthals buried their dead and decorated themselves using paints, jewelry, and feathers. Neanderthal society was organized into metapopulations of small groups of 10–20 people of close genetic kinship. These groups were highly collaborative in many aspects, including hunting, food sharing, parenting, and healthcare, which reveals a relatively high degree of social organization and contradicts former speculations about cultural inferiority (Spikins et al., 2019). However, the small size of these groups led to high levels of inbreeding, which favored the accumulation of deleterious genetic combinations that had negative effects on life and reproduction. These groups were geographically isolated from each other, which produced low population densities and low genetic diversity, despite their wide distribution across Southern Europe and the Near East (Fig. 5.6). Evolutionary patterns of earlier hominin species were deduced from morphological and anatomical features of their fossils, but we already have genetic material (also extracted from fossils) of the Neanderthals, based on which it was possible to discover that the unknown common ancestor of *H. sapiens* and *H. neanderthalensis* lived between 550 and 700 ka BP. The Neanderthal genome is fairly well known, and hybridization with *H. sapiens* has been confirmed. Now we know that at least ~2% of the genome of non-African populations is Neanderthal and that modern East Asian individuals possess 12%–20% more Neanderthal ancestry than modern Europeans (Green et al., 2010; Prüfer et al., 2017). It is known that gene flow between *sapiens* and Neanderthals took place at least two times, ~100 and ~60 ka BP, but it is unclear whether this interbreeding occurred more frequently (Villanea and Schraiber, 2019). We will come back to this point in the next section when dealing with the dispersal of *H. sapiens* out of Africa.

As already mentioned, Neanderthals are considered to be the first real masters of fire. Evidence for the widespread, common use of fire in Europe has been dated to ~300–400 ka BP (Roebroeks and Villa, 2011), which coincides with the first records of *H. neanderthalensis*. Controlled use of fire, known as pyrotechnology, has profound biological, cultural, and social implications. Neanderthals were real specialists in this field; they had precise and sophisticated control over the element. Although we do not know exactly how they lit fire, they probably used flint and pyrite to produce sparks to ignite flammable plant tinder (Heyes et al., 2016; Sorensen et al., 2018). Among the several benefits of pyrotechnology, light and heat should be highlighted (which made life in caves much easier), together with food preservation (smoking) and cooking, defense against dangerous animals (including insects), and stone- or wood-working. Besides these practical uses, fire was also an essential element of socialization that boosted communication and strengthened group spirit. The first traditions and cultural identities most likely evolved around fire. In terms of ecology, however, fire was still not an element of importance. Before *H. sapiens* developed agriculture, most sedimentary records of ash and coal indicate that natural wildfires occurred in dry climates, while anthropogenic fires had only a local impact.

Extinction has always been in the spotlight of Neanderthal studies. The debate has focused on two main hypotheses involving either competition with *H. sapiens* or climate change (review in Roberts and Bricher, 2018). The most commonly accepted hypothesis is that Neanderthal extinction was due to their competitive inferiority with respect to *H. sapiens*, in particular in terms of technical skills, cognitive abilities, diet diversity, and social capabilities. This hypothesis is supported by the fact that Neanderthal extinction occurred shortly after the arrival of the first *H. sapiens* in Europe, ~40,000 years ago. Not only competence in holding a territory and natural resources but also violent conflicts and the introduction of new diseases for which Neanderthals' immune system was unprepared are considered relevant for Neanderthal extinction. A second hypothesis combines climate change and ecology. According to this hypothesis, one of the coldest episodes of the last glaciation occurred 40,000 years ago and favored the expansion of cold steppes at the expense of forests. Neanderthals were better adapted to forest habitats, so they used resources less efficiently under the new conditions, while *H. sapiens* were more efficient in open vegetation and won the ecological battle. In addition, the mentioned metapopulation fragmentation, low population density, low genetic diversity, and high level of inbreeding were factors that, in the case of extreme and unfavorable conditions, put Neanderthal survival at serious risk. In the words of Degioanni et al. (2019) the Neanderthals lived at the edge, in demographic terms.

5.1.4 *Homo sapiens* and the full occupation of the planet

One of the most typical characteristics of present-day humans is their morphological and genetic diversity, despite all belonging to the same species. This diversity is a result of acclimation to practically all types of environments on the planet. It is still not clear if this variety developed in a gradual manner over the course of human evolution as our species progressively settled on different continents and in different biomes or if it is of more recent origin. But let us start at the very beginning. The first clear fossil evidence of *H. sapiens*, also known as Anatomically Modern Humans (AMHs), was found in East Africa (how could it be otherwise?) and dates back to ~200 ka BP (Stringer, 2016). More recent findings seem to point toward an earlier appearance (~300 ka BP) and a pan-African origin, thus demanding a reconsideration of *H. sapiens* evolution (Hublin et al., 2017). As already mentioned (Section 5.1.2), this kind of evidence is not based only on paleontological findings of human body remains but also includes archeological observations regarding the presence of certain tools that reveal advanced technology and had been missing in the cases of earlier hominins. Such advancements included specialized stone working, bone tools, cave paintings, body decoration, rituals, and the development of exchange networks. Some of these activities were already present in Neanderthal populations in an initial form, but all of them together characterized only our species.

Previously, we talked about two phases of gene flow (hybridization) between early AMHs and the Neanderthals: one ~100 ka BP and another ~60 ka BP. In both cases, it was *H. sapiens* that left Africa because Neanderthals never set foot on that continent. On the first occasion, *sapiens* left Africa through the Near East, and all evidence suggests that they did not get any farther; thus it could be considered a failed migration. The second one, on the other hand, was largely successful, and the species spread through Europe and, eventually, all over the planet (Fig. 5.7). Once again, they entered Europe through the Near East, which seems to be an obvious choice as it is the closest exit route from the geographical origin of the species. The first AMH fossil recorded in Europe dates back to ~40 ka BP, but there is evidence of cultural complexes compatible with AMH presence (lithic assemblages, and bone implements and ornaments) dating back to several millennia before. Our species expanded throughout Europe from east to west, from Israel to the Iberian Peninsula. In Asia the oldest *H. sapiens* remains were found in Laos (46 ka BP) and North China (40 ka BP), which means that they lived at approximately the same time as the first modern Western Europeans. Australia and the surrounding areas probably saw hominins for the first time with the arrival of *H. sapiens* ~40 ka BP. The islands and archipelagos of the Pacific (Melanesia, Micronesia, and Polynesia) were the last to be colonized, much later, between 3 ka BP and the last millennia. The settlement of the Americas also happened quite late, although not as late as that of the Pacific. American settlement took place during the last glaciation, taking advantage of the route offered by Beringia, the continental shelf of today's Bering Strait, which was exposed at this time due to low sea levels (Section 1.2.4 and Fig. 1.11). The emigrants were a group of Siberian *H. sapiens* that lived in Beringia between ~30 and 15 ka BP and

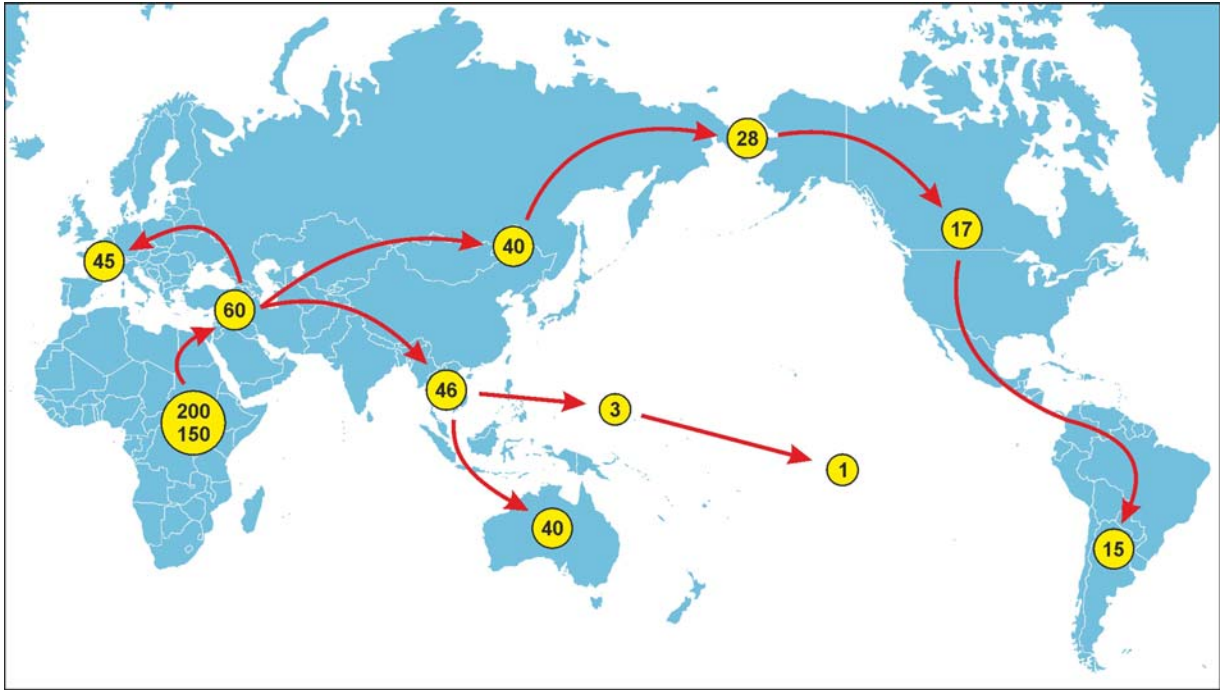

Figure 5.7 *Homo sapiens* expansion across the planet. Numbers are approximate ages in thousands of years before present (ka BP). *Based on data from Rosas (2016).*

started to move southwards approximately 17,000 years ago (review in Waters, 2019). Their expansion was relatively fast since *H. sapiens* sites were found in the southern part of South America (in present-day Chile), dating back 15,000 years.

With this evolutionary and biogeographical information in mind, we will now deal with cultural aspects that are necessary to comprehend the role that humans play in the functioning of the biosphere as global ecological agents. The geological epoch in which human activities became a basic component of the biosphere's metabolism is the Holocene. As discussed in Chapter 1, the Holocene is yet another interglacial, the last one to date. What makes it different from other interglacials is the presence of humans and the ecological consequences and, especially, the geological footprint of this presence (Walker et al., 2009).

5.2 The Holocene and the Neolithic Revolution

According to the British geographer Neil Roberts, what we used to call the virgin or pristine state of nature should be sought in the Early Holocene (Roberts, 2014). Before that time, biomes and ecosystems were very different from present-day ones due to glacial climates and the presence of large ice masses, while beginning in the Middle Holocene, human action had a profound effect on Earth's life cover. We saw in Chapter 2, and Chapter 4, how the beginning of the Holocene brought the reforestation of continents that had been under ice sheets or were occupied by tundra and cold steppes during the last glaciation. During this phase, human influence was not as substantial as from the mid-Holocene onwards, and we can picture the land covered by large extents of pristine forests and other still-untouched natural communities. However, as discussed in previous chapters, the postglacial recolonization of large continental masses in the Early Holocene was far from peaceful and calm in terms of ecology. Instead, it was an extremely dynamic random process when organisms and communities continuously and unsuccessfully tried to keep up with rapidly changing environmental conditions (Section 2.2.2). Therefore ecologically speaking, the Early Holocene seems to have been a highly stressful, rather than a bucolic, phase for life. It was under this condition that humans began to significantly affect ecosystems, thus adding more pressure by modifying or interrupting (depending on the case) the process of natural adaption to changing environments. Human activities introduced a new element that shifted ecological dynamics into a new, less random and more directional scenario headed toward benefiting only one species, ours.

The shift from natural to anthropogenic forcing of the biosphere was not sudden but occurred in a more or less gradual fashion between the Pleistocene—Early Holocene passage, known as the Mesolithic transition, and the striking mid-Holocene transformation, which has been called the Neolithic Revolution. The next sections briefly describe these cultural developments and their ecological relevance. The master reference here is the book by Roberts (2014).

5.2.1 The Mesolithic transition

The Pleistocene—Holocene transition, which included the Late Glacial and the Early Holocene, was transitional in every sense. Regarding climate, it was characterized by a warming trend (although interrupted by some cold interstadials, Fig. 1.12) that triggered the fast retreat of continental ice sheets toward the poles until they reached their current positions. The sea level was rising, and the sea started to cover the continental shelves that the glaciation had left exposed, which progressively reduced the living area of terrestrial organisms (including humans) and extended that of marine ones. In ecological terms, terrestrial species that suffered a glacial reduction and/or fragmentation of their distribution area progressively colonized areas left uncovered by the retreating ice, which eventually resulted in the organization of communities that we see today (Section 2.2.2). In Eurasia and North America, this phase witnessed great forest expansions, which replaced the cold meadows and steppes that characterized the last glaciation. In terms of culture a major change occurred in the eating habits of humans, which conditioned other aspects of life as well. During the Pleistocene, group hunting of large animals (e.g., buffalo, bear, mammoth, and rhinoceros) was the principal means of human subsistence, but at the beginning of the Holocene, a new model of environmental exploitation was introduced, which was based on the more complex hunting of smaller animals (e.g., deer, wild boar, lynx, fox, and rabbit), fishing, and gathering. This cultural shift from big-prey predators to hunter-gatherers brought about a more varied diet and the development of technology and hunting devices, which became smaller and more sophisticated (Crombé, 2019). We should keep in mind that the mass extinction of megafauna took place during the

Pleistocene–Holocene transition (Section 2.2.3); thus it was to be expected that—independently of the causes of their extinction—the hunting of large mammals would decline in importance and be supplemented and, eventually, replaced by more efficient activities. Hunter-gatherers already had a certain capacity to alter the environment for their own benefit and to process their food. They even developed methods to manage some natural resources and food production, but they did not domesticate plants and animals, nor did they depend on them for sustenance.

In cultural terms, this transitional phase is known as the Mesolithic (Trigger, 1989), as it represented the gradual change from the Paleolithic (or Old Stone Age), which was characterized by chipped stone tools, to the Neolithic (or new Stone Age), which was typified by polished stone tools and the development of agriculture. The term "Mesolithic" is not universal in use. As a transitional unit, several nomenclature systems avoid its usage and prefer to call this cultural phase the Epipaleolithic or early Neolithic. From a chronological point of view the boundaries of the Mesolithic vary according to the region under study because cultural phenomena that characterized this phase did not appear everywhere at the same time. The beginning of the Mesolithic is usually placed somewhere in the Late Glacial or the Early Holocene, depending on the region, while the end has even more variable dates because the shift from hunter-gatherer to agricultural societies took place at very different times in different corners of the planet, ranging between ~12 ka BP in the Near East and ~5 ka BP in Northern Europe (Pinhasi et al., 2005).

5.2.2 The Neolithic Revolution

Conceptually, the passage from the Paleolithic to the Neolithic is known as neolithization and refers not only to the changing style of stone work (from simply chipped to polished) but also to a series of radical changes in human life and its influence on the biosphere, which resulted in a real cultural and ecological revolution, the so-called Neolithic Revolution. One of the most decisive of these changes was the domestication of plants and animals, since it entailed the shift from a nomadic lifestyle based on small hunter-gatherer groups to sedentary societies organized in larger communities dedicated to agriculture and animal husbandry. The oldest farming practice is the so-called slash-and-burn agriculture, which represents an intermediate phase between nomadic and sedentary societies. This type of exploitation involves partial deforestation, usually with

Figure 5.8 Present-day examples of slash-and-burn agriculture in the Orinoco rainforests between Venezuela and Brazil. Left: recently opened clearing in the forest with cut and burned tree trunks. Bottom right: similar situation as in the left image. Top right: cultivated clearing. *Photos by V. Rull.*

the aid of fire, to create agricultural fields, taking advantage of the humidity and nutrients of the soil until their depletion, after which the field is abandoned and the process is repeated in another area. Slash-and-burn practices are a form of subsistence agriculture that provides sufficient resources for the temporary survival of a group of people without any accumulation of surplus production. The method is still in use today by several indigenous groups, especially in tropical areas that are covered with dense rainforests (Fig. 5.8). The evolution of agricultural practices led to more extensive and more permanent crops as well as the use of irrigation techniques and fertilizers from livestock to improve soil fertility. This enabled the formation of more stable human settlements.

Once again, the Near East played a crucial role; it was the first center of domestication of species that are still important in our lives, such as wheat (*Triticum* spp.), barley (*Hordeum vulgare*), rye (*Secale cereale*), pea (*Pisum sativum*), lentil (*Lens culinaris*), dog *(Canis lupus*), goat (*Capra aegagrus*), sheep (*Ovis orientalis*), and pig (*Sus scrofa*) (Roberts, 2014). This happened between 11.5 and 10 ka BP, very soon after the Pleistocene—Holocene boundary, in Mesopotamia and South Anatolia, a region that today would include some parts of Iraq, Syria, and Turkey (Fig. 5.9). This region is known as the Fertile Crescent. From this cradle, agriculture expanded all over Europe and reached its maximum development between 7 and 5 ka BP. It is still an open question whether the Fertile Crescent was the center of diffusion of agriculture at a global level (Fuller et al., 2011). Obviously, we are referring to the diffusion of the invention of agriculture and not the exportation of

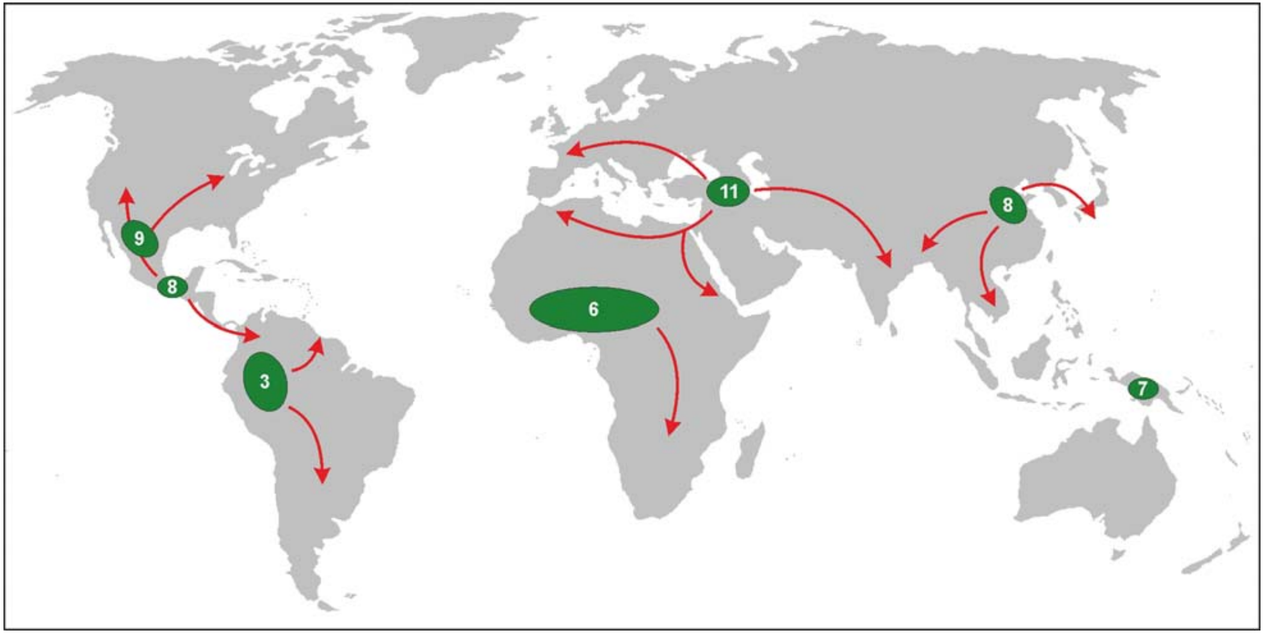

Figure 5.9 Main areas of domestication (*green ellipses*) during the Neolithic Revolution and possible expansion routes from each of them (*red arrows*). Numbers give ages when animal and plant domestication started at each site, in thousands of years before present (ka BP). *Based on raw data from Roberts (2014)*.

products from the Near East. Actually, every continent, even every biome, had its own center of dispersal of autochthonous domesticated animals and plants. Let us see which of these other centers were the most important.

In the eastern part of present-day China, we find another important hub of agricultural development where millet (*Panicum miliaceum*) and rice (*Oryza sativa*) were domesticated between 8 and 7 ka BP. Central America was another important agricultural center, where the domestication of corn (*Zea mays*) took place ~8–7.5 ka ago. Also in the Americas, in today's Mexico, pepper (*Capsicum* spp.), avocado (*Persea americana*), and bean (*Phaseolus vulgaris*) were domesticated, ~9 ka BP. Other domestication centers are more recent; for example, sorghum (*Sorghum bicolor*) was domesticated in an unknown spot in sub-Saharan Africa ~5.7 ka BP, while yucca (*Manihot esculenta*) and potato (*Solanum tuberosum*) originated in South America ~3 ka BP (Roberts, 2014). Newly domesticated species expanded from these centers, spreading agriculture and farming practices all over the world. New Guinea is an exceptional case as the Neolithic Revolution started very early (~7 ka BP) with the cultivation of sugarcane (*Saccharum officinarum*) and banana (*Musa* spp.), but these products did not expand, not even to nearby areas, such as Australia, until the arrival of Europeans. Larson et al. (2014) identified approximately 10 independent centers of plant and animal domestication worldwide. The geographical and biological diversities of these domestication centers are among the main arguments of those who defend the multiple-origin theory of agricultural practices. In all of these centers, local species were chosen for domestication, which would not be logical if all of them had the same origin.

Regarding climate, the Neolithic Revolution started at the beginning of the Early Holocene Warming (EHW; 11.7–9 ka BP) and finished with the Holocene Thermal Taximum (HTM; 9–5 ka BP), when the maximum temperatures of this epoch were recorded (Section 1.2.5). A relevant point that should be highlighted is that during the EHW and the HTM, the present-day Sahara Desert was completely covered with vegetation and plenty of lakes in what is called the African Humid Period (AHP), which lasted between ~11and 5 ka BP (de Menocal et al., 2000). Most civilizations of the planet are thought to have engaged in agriculture between 8 and 6 ka BP, which was the peak of the HTM. Therefore besides intrinsic cultural development, climatic conditions would also have favored the emergence and expansion of agriculture worldwide. This also led to an increased concentration of human societies, the formation of the first urban centers, and, eventually, the first cities (also in the Near East, of course).

Farming products were preserved and processed, which boosted labor specialization and industry. The accumulation of surplus products required management and distribution, and thus, new sociopolitical roles emerged. The exchange of goods and the trade between different regions enhanced the development of communication networks and contributed to the homogenization of civilizations. All this advanced the progressive development of societies and, ultimately, the growth of the human population. Undoubtedly, this authentic social revolution had consequences for the biosphere, as will be discussed in the next section.

5.2.3 Ecological consequences of the Neolithic Revolution

The Neolithic Revolution affected the biosphere in two principal ways: the direct effect was the remarkable modification of organisms and ecosystems, while the indirect one was on atmospheric composition and, as a consequence, global biogeochemical cycles and even the climate. The first species to suffer these effects were the domesticated species. Humans selected them (in what we could regard as the first steps of genetic engineering) to obtain more productive varieties, which progressively differentiated from the original species. Besides undergoing morphological modifications mostly intended to increase the size of the more valued parts for human consumption, many species lost their reproductive and dispersal autonomies, which made them completely dependent on agricultural practices for their continuity. But wild species also experienced diverse side effects. For example, domestic breeding of sheep required protecting them from natural predators, which provoked the extinction of the wolf in most parts of Europe. On the other hand, successful agriculture requires arable land, which has been obtained by reducing or eliminating natural communities so that crops and pastures can take their place. The most obvious case is the reduction in forests, in which fire has played a crucial part since the Neolithic Revolution. In Europe, for example, the expansion of agriculture started approximately 8000 years ago and finished ~5 ka BP. From that date on, deforestation progressed at a high speed, decreasing the forest cover by ~1% per century (Fig. 5.10) (Roberts et al., 2017). The replacement of natural communities by crops and pastures, together with forest exploitation to obtain fuel and building materials, also enhanced the extinction of autochthonous species due to habitat loss (Section 2.1.2) and the disappearance of migration and dispersal paths among metacommunities and metapopulations (Chapter 4).

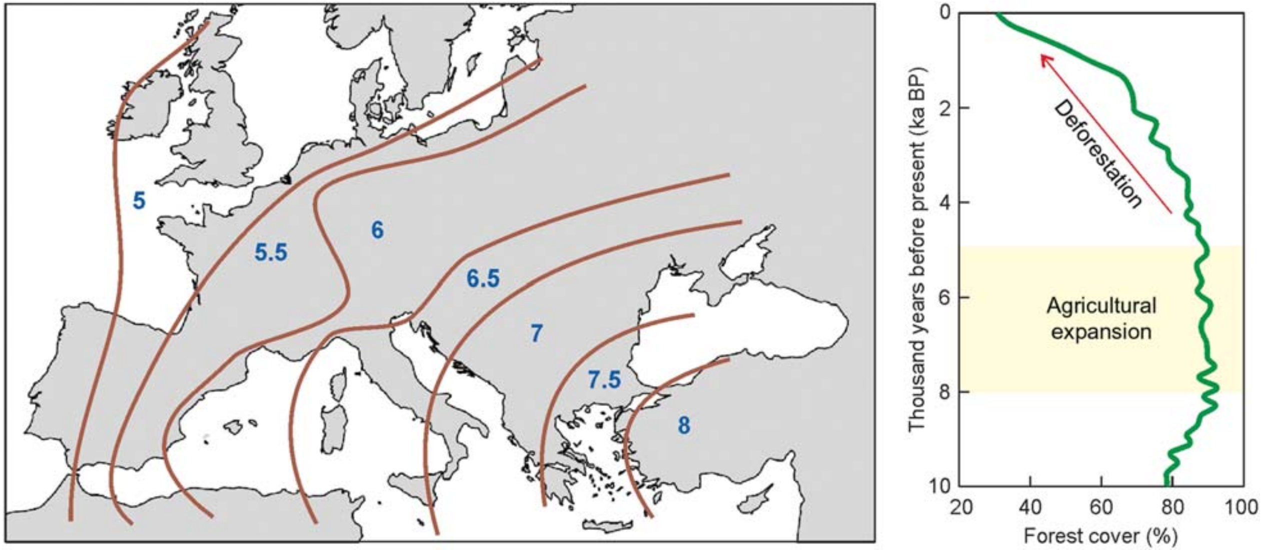

Figure 5.10 Expansion of agriculture and subsequent deforestation in Europe. Left: progress of expansion of agriculture in Europe. Numbers are ages in thousands of years before present (ka BP). Right: changes in temperate forest cover. Expansion of agriculture (*yellow band*) happened without causing a serious decrease in forest cover (*green line*), but once agriculture was widespread all over the continent, forest cover decreased from 90% to less than 40% in 5000 years, at a speed of 1% per century. *Based on data from Burroughs (2005) and Roberts et al. (2017).*

Some years ago, the North American paleoclimatologist William Ruddiman discovered that the atmospheric carbon dioxide (CO_2) and methane (CH_4) trends of the Holocene differed from those in records of earlier interglacial periods in polar ice cores (Section 1.2.2). Given that the main difference between the Holocene and earlier interglacials was human cultural development, Ruddiman deduced that these atmospheric anomalies could be related to human activity. Moreover, differences really started to become obvious in the Middle Holocene, coinciding with the Neolithic Revolution, which further reinforced the idea of a possible anthropogenic effect (Fig. 5.11). Ruddiman (2003, 2013) interpreted the

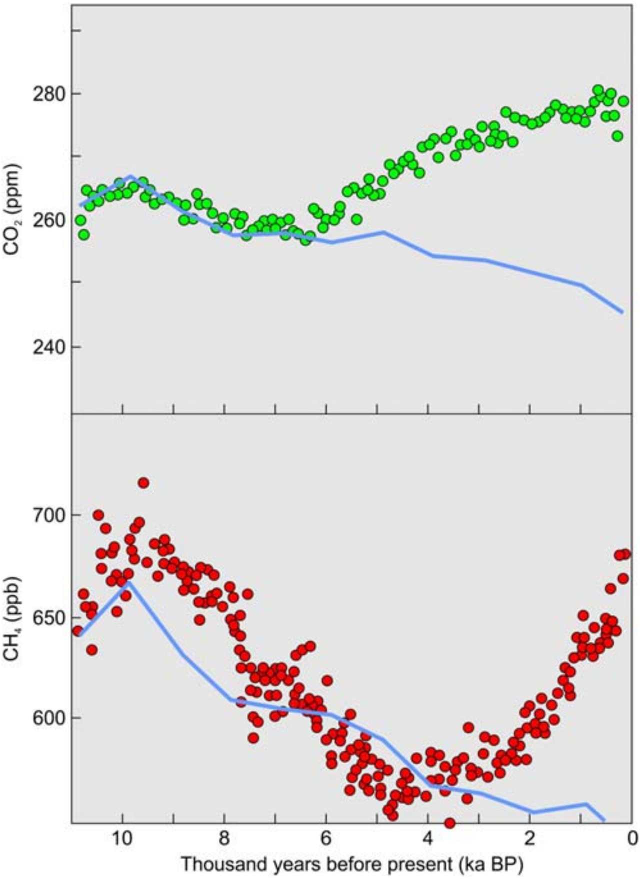

Figure 5.11 Holocene trends of atmospheric CO_2 (above; *green dots*) and CH_4 (below; *red dots*) concentrations compared to the averages of the same parameters in the last three interglacial periods (*blue lines*). Units are in parts per million (ppm) and parts per billion (ppb), respectively. *Modified and redrawn from Ruddiman (2013).*

increase in CO_2 after 7−6 ka BP as a result of large-scale deforestation by fire, since during this process, large quantities of CO_2 are emitted into the atmosphere. He attributed the increase in CH_4 around 5−4 ka BP to the expanding rice cultivation in Asia; rice requires permanent flooding, which creates an anoxic environment that emits significant amounts of CH_4 into the atmosphere. As both CO_2 and CH_4 are greenhouse gases, their increase may have provoked global warming, which is consistent with the occurrence of the HTM. Later, when talking about the "Anthropocene" (Section 6.3), we will reexamine Ruddiman's ideas. What is important for this section is the potential link between the mentioned atmospheric changes and the Neolithic Revolution, on the basis of their chronological coincidence; the mechanisms of the possible cause-and-effect relationship, however, are still subject to debate.

5.3 From one revolution to another; the last 5000 years

In this section, we cover a phase that could be considered an intermediate step between the Neolithic Revolution and the Industrial Revolution that started in the middle of the 18th century and that we will examine later on. As already discussed, climate was the principal agent of the Quaternary ecological and evolutionary transformation, until the Neolithic Revolution. Afterward, humans became more protagonistic, and their activities, together with the synergies between those activities and climate changes, started to affect biogeographical patterns and ecological and evolutionary processes. Therefore the interval between the mid-Holocene Neolithic Revolution and the Industrial Revolution, which started a couple of centuries ago, was a phase of continuous interaction between humans, the climate, and ecosystems at different spatial and temporal scales. During this phase, humans became agents of global transformation similar in magnitude to that of some natural agents, impacting even global climatic trends. The biosphere configuration and functioning processes in which natural and anthropogenic factors together participate can be considered from different perspectives and may have a subjective component depending on the scientific background of the researcher. For example, a number of climatologists and paleoclimatologists take it for granted that climate is the most powerful component of the system; it not only determines the ecological changes in natural communities but also has a decisive influence on cultural changes in human societies and heavily influences their rise or fall. This position, known as environmental determinism, irritates many archeologists and anthropologists who are convinced of the leading role of sociocultural relations and believe that environmental changes simply modulate autogenous cultural processes. This line of thought is called human determinism (no to be confused with the cultural determinism of the social sciences) (Rull, 2018). Finally, a number of (neo)ecologists and geographers take a more descriptive approach by adopting the concept of the landscape as a basic unit and differentiating between natural landscapes and anthropogenic landscapes (also cultural landscapes), with the latter having different grades of anthropization.

In the preceding chapters, we have adopted a biological perspective, and the subjects of study have changed from species and populations to communities and ecosystems, in accordance with the objectives, which could be biogeographical, ecological, or evolutionary. From now on, as we also take humans into account, we will use a new, holistic approach. Instead of referring to the landscape as a unit of description, we refer to it as a functional complex formed by the combination of minor functional units, ecosystems, in which humans are actors and agents of change at the same time. Before the Neolithic Revolution the ecological system that we study in this book was composed of two main elements, climate and landscape, and their interactions, or feedbacks. This relatively simple system is called a Climatic-Landscape/Feedback (CLF) system (Fig. 5.12). Once humanity enters as an important agent of change, a new component (i.e., humans) and a new type of interaction (i.e., synergies) are introduced into the system. The new system is a Climatic-Landscape-Anthropogenic/Feedback-Synergy (CLAFS) system (Rull et al., 2018). In Sections 5.3.1−5.3.3 the CLAFS framework will be used to discuss environmental and human determinism and the descriptive landscape approach.

From a climatic perspective the phase of intensifying environment−landscape−human interactions occurring between the Neolithic Revolution and the Industrial Revolution started at the end of the HTM, when global temperatures exhibited a slight decrease until they reached present-day average values. This happened at the same time that sea level rise stabilized (Fig. 1.12), which means that continental shelves were already inundated and present-day coastlines became fixed. At a

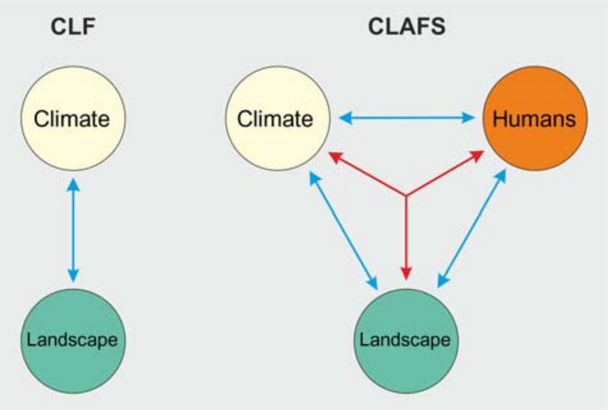

Figure 5.12 Schematic representation of processes involved in the ecological changes in a simple system that includes only the landscape and climate (CLF) and of a more complex system that also includes the human component (CLAFS). In the first case, climate affects the landscape and vice versa in a simple feedback system (*blue arrow*). In the second case the climate, the landscape, and humans form a more complex network that still includes simple but multiple feedbacks (*blue arrows*) and synergies between two elements (*red arrows*) that affect the third element of the system.

regional scale, important climatic changes took place, such as the establishment of dry conditions that caused the desertification of the Sahara between 6.5 and 4.5 ka BP, right after the AHP (Wright, 2017). In essence, the climatic and physical conditions of Earth looked more and more like those today, except for some changes that were yet to come, such as the Medieval Climatic Anomaly (MCA) and the Little Ice Age (LIA) (Section 1.2.6). The climatic events that most affected the development of agricultural societies throughout history were long droughts, usually of a local or regional scale, although some of them had quasiglobal effects (Chapter 1). With this in mind, it could seem surprising that the Near East, a region characterized by low and irregular rainfall and frequent droughts, was the cradle of agriculture. The answer may be linked to the presence of two big rivers, the Tigris and the Euphrates, which would have provided sufficient water for agriculture. This is where the technologies of irrigation and canalization were born, as the river water was used for agriculture and for human consumption in the cities. Nevertheless, in such a dry land, even large rivers undergo significant flow changes, which in turn affect human activities. Indeed, one of the first cases known in the history of climatic influence on agricultural societies based on irrigation—or hydraulic civilizations, as Roberts (2014) dubbed them—is precisely the case of Mesopotamia, the region situated between the Tigris and the Euphrates. This example will be useful to illustrate what environmental determinism is.

5.3.1 Environmental determinism

The Akkadian Empire was the first great empire in Mesopotamia and dominated the valleys of the Tigris and the Euphrates, from north to south, approximately 4300 years BP. After approximately a century of prosperity, the empire collapsed abruptly, and the entire population migrated to the south, leaving fertile Mesopotamia deserted. It was only approximately 400 years later (~3.9 ka BP) that permanent settlements were reestablished in the area, although they did not even come close to their former glory. The possible cause of this sudden collapse was debated for years. It was mostly attributed to gradual water and soil salinization provoked by intense evaporation. But studies of a core of marine sediments from the Gulf of Oman documented an especially dry climatic event that happened at the same time as the fall of the Akkadian Empire (de Menocal, 2001). The sediments of the Gulf of Oman contain eolic particles of dolomite and calcium carbonate transported from Mesopotamia. The drier the Mesopotamian climate was, the larger the extent of deserts there and, thus, the higher the proportion of these particles sedimented in the Gulf of Oman. Therefore the quantity of these particles deposited in the sediments of the gulf is a proxy for arid conditions in Mesopotamia. The fall of the Akkadian Empire occurred simultaneously with a very sharp peak in dolomite and calcium carbonate particles ~4 ka BP, which allowed the Akkadian demise to be related to an extended period of drought (Fig. 5.13).

Another well-known example, among the many similar situations in history, is the collapse of the Maya civilization in Central America ~1.2 ka BP. Here, overpopulation, deforestation, soil erosion, wars, and epidemics had been proposed as potential causes, until several paleoecological studies, based on both physicochemical and biological proxies from lake sediments, revealed that a very dry period took place between 1.3 and 1.1 ka BP. These and other similar examples demonstrate the most extreme facet of environmental determinism regarding the effects that climatic changes may have on human civilizations. Although we cannot rule out the possible existence of internal cultural mechanisms in these

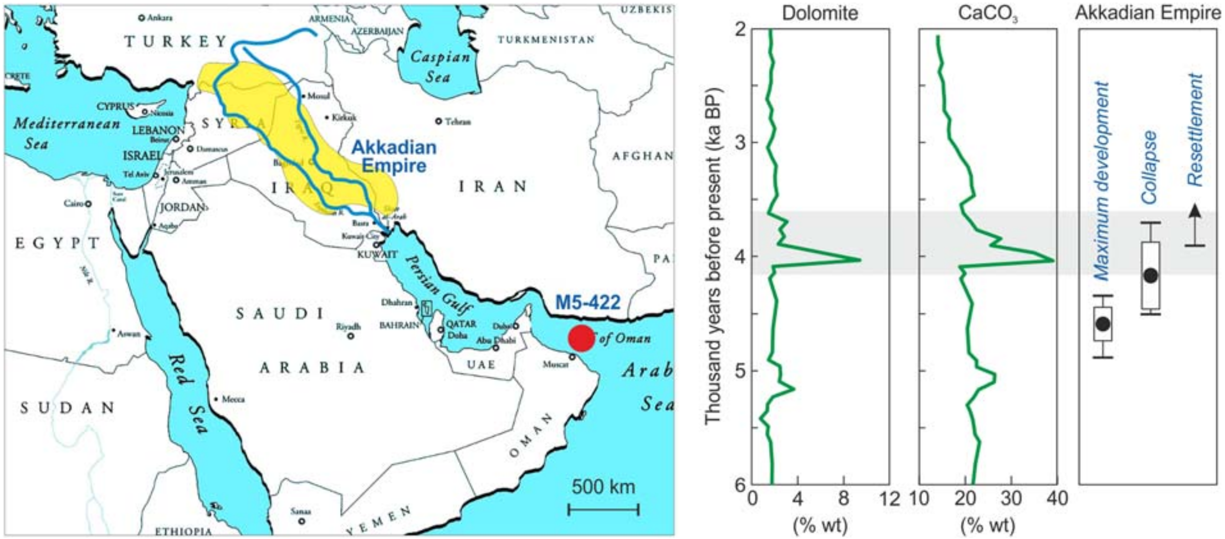

Figure 5.13 Map of the Near East (left) showing the Tigris and the Euphrates in blue and the extent of the Akkadian Empire in yellow. The red circle marks the position of sea sediment core M5-422, taken in the Gulf of Oman. Right: curves of dolomite and calcium carbonate composition in core M5-422, revealing a peak ∼4 ka BP, the time of the fall of the Akkadian Empire. Radiocarbon dates are given as average values (black circles) with confidence intervals 1σ (box) and 2σ (segment). *Modified and redrawn from de Menocal (2001).*

cases, for example, poor water resource management during droughts, it seems clear that climate was the decisive factor (de Menocal, 2001). Another example could be the origin of the Mediterranean biome in Southern Europe. The formation of typical Mediterranean evergreen sclerophyll forests has been attributed to progressive adaption to a climate that became gradually drier beginning in the mid-Holocene (Jalut et al., 2009). We will analyze this case in more detail in the section on the holistic approach (Section 5.3.4) because other interpretations have also been offered to explain this phenomenon. For obvious reasons, paleoclimatologists are the most ardent supporters of hypotheses of environmental determinism, which are usually based on chronological coincidence and, thus, do not guarantee a cause—effect relationship. It would be interesting to check if a more holistic analysis including cultural factors would still conclude that the climate was the main factor responsible for the cultural crisis of the Akkadians, the Maya or other similar civilizations.

5.3.2 Human determinism

There are also a number of examples on the other end of the spectrum, which is the absolute control of human activities over the landscape together with every environmental and cultural consequence. Most of these examples are from the last millennia. Oceanic islands, for example, have been especially sensitive to human action. A rather extreme but not unique example is the case of some islands in the archipelago of the Azores, in the middle of the Atlantic Ocean, where natural ecosystems have been almost completely replaced by crops and plantations of exotic tree species with a great variety of geographical origins (Dias, 2007). Many of these species have been naturalized and have formed completely anthropogenic, albeit unintentional, functional ecosystems, the appearance of which would have been impossible without human intervention. It is like a vast ecological experiment that calls into question the Clementsian vision of the formation of ecological communities and demonstrates that species are able to construct functional ecosystems in a spontaneous manner despite belonging to completely different biomes.

For example, the natural (preanthropogenic) vegetation on the Island of São Miguel, which suffered the highest degree of alteration by humans, was characterized by dense and luxuriant laurisilvae (evergreen forests of warm and humid temperate regions) dominated by *Laurus azorica* (Azorean laurel), *Juniperus brevifolia* (Azorean juniper), *Prunus azorica*

(Azorean cherry tree), and *Morella faya* (faya), among others. Only small patches or scattered remnants of these species remain today among communities of exotic plants (Moreira, 1987). When Europeans arrived at the islands in the 15th century (there is no trace of aboriginal peoples, so the Europeans were probably the first humans to colonize the islands), these laurel forests were gradually replaced, first by extended cereal crops and, later, by various forest and ornamental species. Today, the forests of São Miguel are dominated by *Pittosporum undulatum* (sweet pittosporum), *Acacia melanoxylon* (blackwood acacia), and *Eucalyptus globulus* (Tasmanian blue gum) from Australia; *Cryptomeria japonica* (Japanese cedar) from Japan; and *Pinus pinaster* (maritime pine) from the Mediterranean. Hortensia (*Hydrangea macrophylla*) from Japan, *Hedychium gardnerianum* (ginger lily) from the Himalayas, and other naturalized ornamental plants grow everywhere on the island (Fig. 5.14). The progressive replacement of preanthropogenic landscapes by present-day landscapes has been documented by palynological studies of lake sediments from São Miguel and other Azorean islands (Connor et al., 2012; Rull et al., 2017).

In this case, there is no doubt that the decisive element was human intervention. Paleoclimatic records have shown that Azorean climates have not remained constant throughout the Holocene, especially in terms of moisture, which has exhibited centennial- to millennial-scale oscillations (Björk et al., 2006). However, these long-term environmental shifts did not lead to significant changes in the former laurisilvae, which remained more or less constant during the Holocene. The intensive and extensive disturbances that led to the present-day landscapes and vegetation configuration were exclusively anthropogenic. Of course, cultural trends also followed the same law and depended mainly on political and economic criteria, so climate change seems to have played a minor role in human life since the colonization of the island. However, combined high-resolution paleoclimatic and paleovegetational records are still lacking, and potential climatic and ecological changes at decadal and interannual scales cannot be ruled out. The case of the Azores is similar to that of many oceanic islands, where the vegetation and landscape have remained more or less constant for millennia and have suffered deep transformations leading to present-day situations only after human settlement (Gillespie and Clague, 2009).

5.3.3 The descriptive approach

In the last chapter, we used the Neotropical region of Guiana to illustrate the concepts of resilience and stability (Section 4.4.5). Now, we come

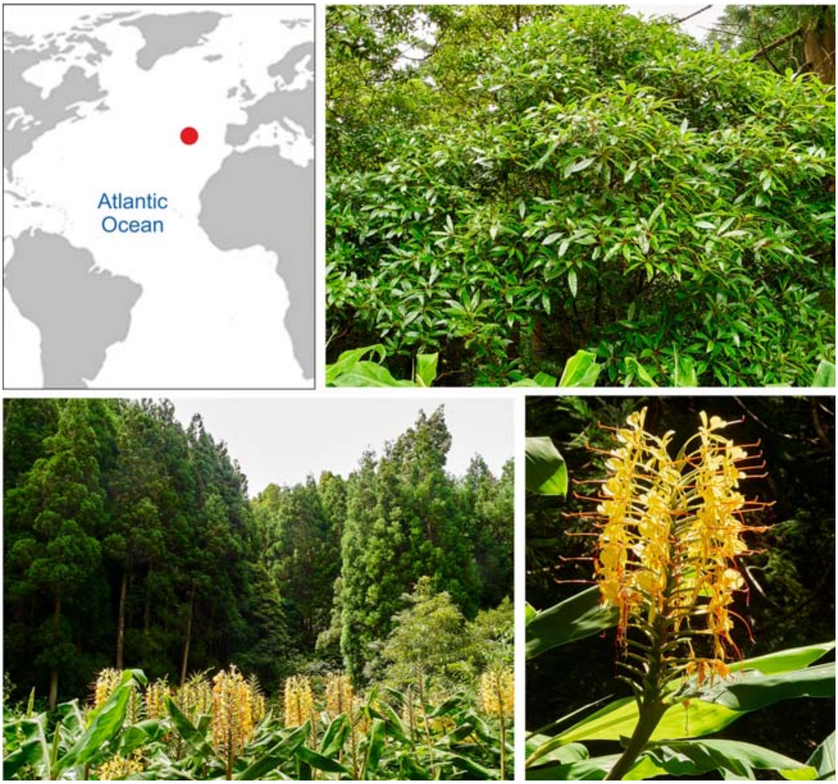

Figure 5.14 Vegetation of the Island of São Miguel, in the archipelago of the Azores (*red circle*). Top right: isolated specimen of *Laurus azorica* (Azores laurel) that dominated the forests of the island before human colonization. Bottom: *Cryptomeria japonica* (Japanese cedar) forest with *Hedychium gardnerianum* (of Himalayan origin) in the undergrowth, a very common combination on the island today. *Photo by V. Rull.*

back to this region because it encompasses both pristine and completely anthropogenic (or cultural) landscapes in the same area. The tops of tepuis, independent of having suffered the consequences of Quaternary climatic changes, have never been colonized or even temporally occupied by any human culture—at least during the last glacial cycle—which is a rather exceptional situation these days. There seems to be nothing of interest for humans on these densely vegetated flat summits attaining an $\sim 6000\ \text{km}^2$ total extent. First of all, they are in a particularly remote location; many of them can be reached only by air, so the construction of any kind of infrastructure would be extremely difficult and hardly profitable. The tepui summits do not have any economic resources to offer either, at least not at a large scale. The soils are organic, mainly consisting of peat (histosols);

they are acidic and depleted in nutrients, which makes agriculture impracticable. The climate is extremely rainy, with no marked seasonality; it always rains and always a lot (values can reach up to 4000 mm/year). There is no vegetation suitable for pastures, nor can pastures be developed in this type of soil. The existing forests are not apt for extensive exploitation and are made up of very slow-growing trees that would not yield much profit. There are no oil, coal, or other mineral resources, such as gold and diamonds, as in the surrounding uplands of the Gran Sabana. Although tepuis have a great touristic interest for those who like exploring, extreme sports, or singular landscapes, the infrastructure to carry out activities of this type is missing due to strict visit restrictions. Of course, there are always exceptions, for example, the illegal touristic visits organized for high-standing tourists, but they have not been significant so far. There have also been scientific or pseudoscientific expeditions (both legal and illegal), but they are becoming less frequent due to the increased difficulty in obtaining permits to collect samples, specimens or simply access the tepui summits. Finally, the indigenous people of the area view these mountains as sacred and believe that they are home to their gods, so they do not even visit the mountains, let alone settle there. In summary, despite short, sporadic incursions, the tepuis can be considered among the very few pristine environments still remaining on the planet (Rull et al., 2019).

Nevertheless, if we descend from the tepuis to the surrounding Gran Sabana uplands, we find the exact opposite situation. The landscape of the Gran Sabana region is almost completely anthropogenic, in large part because of the human use of fire, mostly by the Pemón indigenous group. At present, the savanna is undergoing expansion to the detriment of montane and gallery forests. This has generated a debate between those who defend fire practices and those who think that burning should be stopped immediately. According to the latter, the Gran Sabana was formerly covered with large forests, and anthropogenic fires are responsible for present-day savannization. This kind of controversy based on landscape description criteria and focused on the possible degree of anthropization is a dead-end street from which the only exit is offered by studying the ecological history of the region.

Palynological studies revealed that the savannization of the Gran Sabana started during the Young Dryas (YD), long before the arrival of the Pemón to the region (Rull et al., 2015). Before the YD the Gran Sabana was covered by a mosaic landscape of forests, shrublands, and savannas, the last being of minor importance. Fires started ~13–12 ka BP, and savannas soon extended (Fig. 5.15). It has been suggested that these first fires could

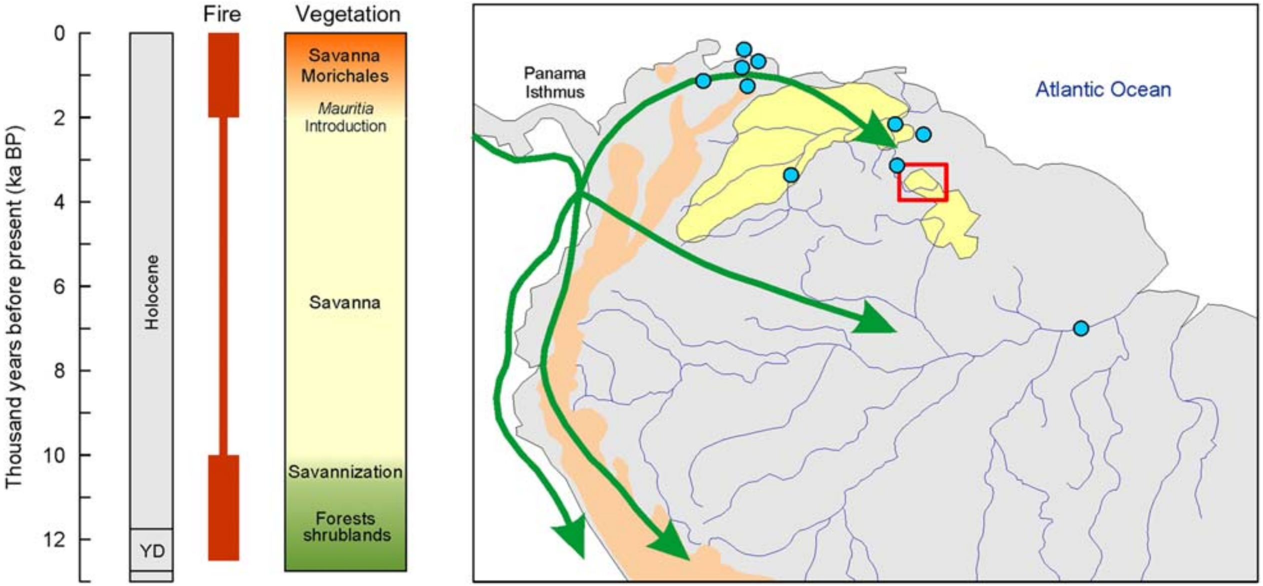

Figure 5.15 Changes in the vegetation of the Gran Sabana (left) based on pollen analysis. Savannization took place after the YD within a phase of intensive fires. Savannas prevailed throughout the Holocene despite the decrease in fire events. Approximately 2 ka BP, morichales (dominated by the palm *Mauritia flexuosa*) appeared, and fire events intensified again (probably due to the arrival of the Pemón people that still live in the area today). Right: migration routes of the first colonizers (*green arrows*) on their way from Central America, after crossing the Isthmus of Panamá. The Gran Sabana (*red rectangle*) was probably colonized via the Caribbean coast, where several sites of YD age have been found (red circles) with remains of megafauna and hunting devices. Yellow patches show the present-day distribution of savannas. *Modified and redrawn from* Rull et al. (2015).

have been provoked by the first colonizers of South America on their way from Central America, as remains of weapons used to hunt large mammals (that still existed in South America in that period) have been found at sites in nearby areas. These archeological findings have been dated to approximately the same age as the fires, which could support this idea. Either way, the forests never recovered, and savannas dominated the landscape throughout the Holocene despite the significant decrease in fire frequency and intensity. The next change came ~2 ka BP, when fire events became more frequent once again and were followed by the appearance of a new type of vegetation that did not exist before but that began to form part of the landscape, the already mentioned morichal, dominated by the palm-tree *Mauritia flexuosa* or moriche (Section 4.4.5). The increase in fire and the arrival of the moriche palm (which is widely used by the Pemón and other Amazonian cultures) suggest that the Pemón culture was established in the Gran Sabana by that time. The conclusion that we can draw from these examples is that speculation based on the narrative description of the landscape and the assumed degree of anthropization does not offer a realistic explanation for the observed phenomena and should be complemented with empirical evidence of the historical and socioecological processes involved.

5.3.4 The holistic approach

We use the example of yet another island, this time in the Pacific Ocean, to illustrate the holistic approach. The remote Easter Island, or Rapa Nui, was already mentioned in relation to the origin of island communities (Section 4.4.1). The case of this island is very interesting because its study has shifted historically from human to environmental determinism to finally culminate in a holistic approach. As occurred with the Akkadian and Maya civilizations, Easter Island also witnessed a cultural collapse that terminated the ancient Rapanui culture, which is known for the megalithic cult statues known as moai that constitute the cultural symbol of the island (Fig. 5.16). The first hypotheses envisioned what was to be known as an "ecocide". Pollen analyses revealed that the island originally was covered with endemic palm tree forests, which disappeared all of a sudden and were replaced by extensive grass meadows (Flenley and King, 1984). This would have happened between the years 1400 and 1600 of the Common Era (CE). We do not know which species the palm tree belonged to; it went extinct. The abrupt ecological change seems to have

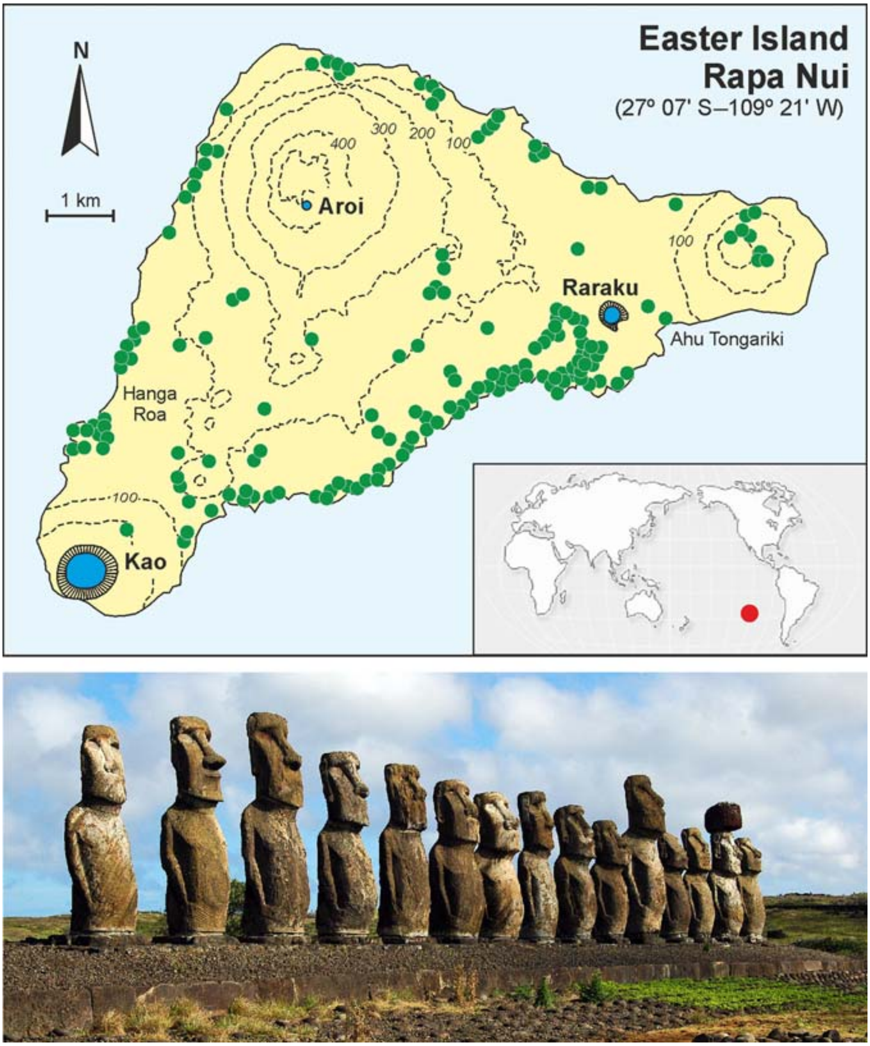

Figure 5.16 Schematic map of Easter Island (top) showing the distribution of moai (*green circles*) and Raraku and Kao Lakes. The red circle shows the location of the island on the world map. Below: the moai of Ahu Tongariki (see map), one of the most emblematic groups of statues on the island. The largest moai of this group is 9 m high and weighs ~80 t. *Modified and redrawn from Rull (2016).*

taken place at the same time as the Rapanui cultural breakdown, which led to the conclusion that the Rapanui people deforested the whole island and used up all its resources, in turn causing their own extinction (Flenley and Bahn, 2003). This is a classic example of human determinism, so much so that Easter Island has been used to illustrate what might happen at a global scale if humans continue to exploit the planet in the same way that they do today (Diamond, 2005). Another explanation for the Rapanui collapse that is also human deterministic is the genocidal hypothesis, according to which the cultural demise occurred after European contact (1722 CE) and was caused by slavery practices and the introduction of epidemic diseases (Hunt and Lipo, 2011). Some researchers, however, pointed out that the sociocultural disaster occurred during the LIA when, in addition to dropping temperatures, there were frequent, long droughts (McCall, 1993). This means that the deforestation and subsequent cultural breakdown could have been the consequences of a dry-climate phase (environmental determinism). But the lack of direct evidence for climatic changes on the island has remained a weak point of this hypothesis and has maintained the advantage of the ecocidal theory, until recently.

Over the last decade, new paleoecological evidence has been discovered that has forced the scientific community to reconsider this question while adopting a less dogmatic and exclusive (either environmental or human deterministic) perspective. On the one hand, periods of extremely dry climate were recorded during the last millennia that caused the complete desiccation of some lakes. The last one took place during the LIA, approximately between 1570 and 1720 (Cañellas-Boltà et al., 2013). On the other hand, it was realized that deforestation was not an instantaneous process and did not happen at the same time everywhere on the island (Rull, 2019). By combining these and other findings, another explanation emerged that includes both climatic and cultural factors together with their corresponding synergies and feedbacks. Briefly, the quarry of volcanic tuff where the moai were carved, and the cultural center of the ancient Rapanui civilization, was the Raraku crater, which contained Lake Raraku (Fig. 5.16). The basin of this lake was under cultivation until approximately 1400 CE, and some 50 years later, it had already suffered complete deforestation. The drought that started approximately 1570 CE and lasted approximately for a century and a half caused the total dry-out of the lake. The synergy between human deforestation and aridity—which, due to a positive feedback effect, would have made the recovery of the palm forest impossible (Section 4.3)—would have transformed the Raraku crater into a barren, hostile area unsuitable for human life. Under these conditions the Rapanui would have been forced to move on in search of freshwater and forests, which they eventually found in the basin of Lake Kao, which was not desiccated during the LIA drought

(Rull et al., 2018). But the volcanic crater of Kao is made up of hard basalt, so the basalt tools (the ancient Rapanui did not know metals) used to carve the moai in the soft Raraku tuff were of no use in Kao, and the moai industry ceased. The Moai Cult was replaced by the Birdman Cult, which marked a radical cultural, political and religious transition (Robinson and Stevenson, 2017). The island was already totally deforested by 1600 CE, roughly a century before European arrival. However, the end of the Moai Cult and the total deforestation of the island did not represent the end of the ancient Rapanui civilization, which remained healthy until European arrival, thanks to the return of wetter climates and the development of very specialized and efficient cultivation practices. What is beyond all doubt, as it is documented historically, is that the Rapanui were almost eradicated by slavery practices and epidemic diseases shortly before European contact. The story, in reality, is longer and more complex (Rull, 2018), but this much should be enough to illustrate the holistic nature of the social–ecological change that was the consequence of environmental and human processes and their respective synergies and feedbacks. This kind of phenomenon is too complex to be reduced to simple explanations based on the causal relationships of a few factors.

We cannot leave the Mediterranean biome out when talking about the interaction of natural and anthropogenic factors in ecosystems and landscapes. The Mediterranean region was the cradle and arena of the cultural development of Western civilizations throughout the Holocene, but especially for the last 5000 years, when the Neolithic Revolution reached even the most remote corners of the continent (Section 5.2.3 and Fig. 5.10). The establishment and development of the Mediterranean biome in Southern Europe is still a controversial issue. Based on paleoecological, archeological, and historical evidence, we know that Mediterranean vegetation has suffered continuous anthropogenic disturbances, such as deforestation, frequent fires, overgrazing, and soil erosion, especially during the second half of the Holocene. This would suggest that the Mediterranean vegetation has been extremely abused and that the Mediterranean landscape is highly degraded. Nevertheless, the vegetation in this region is remarkably diverse compared to that in biomes at the same latitude on other continents; in certain places, it is even comparable to that in tropical biomes (Fig. 3.6). So, we could also think that human activity has been a factor of diversification and stabilization. Human determinists would stop here, satisfied with one of these answers. There exists, however, another hypothesis that claims that the progressive colonization of Southern Europe by the Mediterranean biome was not the result of human activities but of the gradual regional aridification that started in the Mid-Holocene, ~5.5 ka BP (Jalut et al., 2009). This drier climate, characterized by very dry and warm summers, would have provided ideal conditions for the development of Mediterranean vegetation. This argument is clearly in line with environmental determinism and fuels the descriptive approach focused on which factor (i.e., climate or human activities) has been more important in the configuration of the Mediterranean biome. A more holistic approach emerges when we consider fire, which can be either natural or anthropogenic in origin. Natural fires would be considered an additional environmental factor besides climate. Anthropogenic fires, on the other hand, are part of human activities. Either way, fire and climate feedback into each other and thus mutually enhance each other, which might lead to nonlinear responses (Section 4.3). Recent studies revealed that at a regional scale, Mediterranean fires of anthropogenic origin significantly increased starting 4−3 ka BP, while before that, fire regime was controlled by orbital variations and by phenomena such as the North Atlantic Oscillation (Sections 1.2.1 and 1.2.7), which affected summer insolation and rainy seasons, respectively (Vannière et al., 2011). Once again, we can see that the problem is more complex than a simple debate about climate versus humans and should thus be analyzed with the most appropriate tools to reflect this complexity.

5.4 The Industrial Revolution and the Great Acceleration

If, with the Neolithic Revolution and its consequences, it took humans millennia to transform ecosystems, landscape, and biomes, with the Industrial Revolution and its aftermath, it took only a couple of centuries to alter all the elements of the Earth System (lithosphere, hydrosphere, atmosphere, biosphere, and cryosphere) and their interplay. The Industrial Revolution began in Great Britain around 1760 and spread over all of the continents, and although several nonindustrialized regions remain on the planet (Fig. 5.17), the effects were of a global extent (Waters et al., 2014). Industrialization put an end to the dominance of agriculture as a human activity, profoundly changed the human way of life and even created a new global economic order, capitalism. Before this

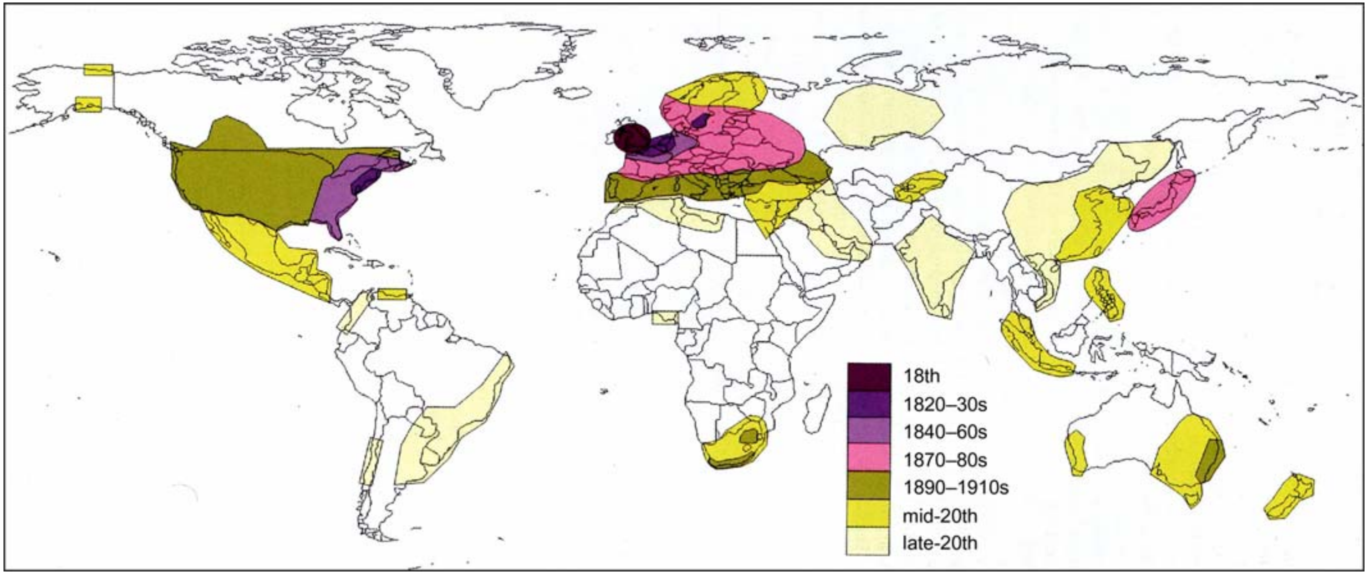

Figure 5.17 Origin and expansion of the Industrial Revolution over the planet. Colors show time intervals (in centuries or decades) of the industrialization of each area shown on the map. *Modified from Waters et al. (2014)*.

change, air and water movements and the metabolism of living beings were the main sources of energy. All these energy types derive from solar energy, which controls both atmospheric circulation and the water cycle and provides the base energy for photosynthesis, which in turn is the origin of every kind of biological metabolism. The low efficiency of this energy use (i.e., plants use only 1% of the solar energy, and animals utilize only 10% of the energy provided by the plants they consume) placed a limit on the growth of human populations. But the discovery of fossil fuels (especially coal and oil) triggered a radical change. Thanks to the exploitation of fossil fuels, the global human population grew from 1 to 6 billion people between 1800 and 2000, while energy was multiplied by a factor of 40 and economic production by a factor of 50. CO_2 is one of the main products of the combustion of fossil fuels; burning these fuels emits CO_2 and produces an increasing concentration of this gas in the atmosphere (Lewis and Maslin, 2015).

Within the industrial era the most drastic change took place after the Second World War (WWII), in the 1950s, with what we call the Great Acceleration. From that moment on, all indicators of human activity accelerated, and many new activities appeared. The global population grew from 3000 to 6000 million in only 50 years, and economic production was multiplied by a factor of 15 in the same period of time. The population distribution also saw significant changes, since the Great Acceleration brought about rural depopulation and a decrease in farming activities on a massive scale as people moved to the cities, where all industrial activities and associated services were developing. Today, almost half of the human population lives in cities, which implies a drastic increase in consumption, another important indicator of acceleration (Ellis, 2015; Ellis et al., 2010). The number of motor vehicles rose from 40 at the end of the WWII to 700 million in 1996. Fuel consumption has grown by a factor of 3.5 since 1960, causing a dramatic increase in the amount of atmospheric CO_2 and, as a consequence of the provoked greenhouse effect, a rise in global temperatures known today as Global Warming (GW) (Fig. 5.18). The concentration of other greenhouse gases (CH_4, fluorocarbons, etc.) increased in a similar manner and contributed to the warming. But the climate was not the only thing to change. All subsystems of the Earth System and their general functioning have undergone alterations; this is why we talk about Global Change (GC), which includes changes in climate, the extent of polar ice caps, sea level, the population, the economy, energy consumption, transport, communication,

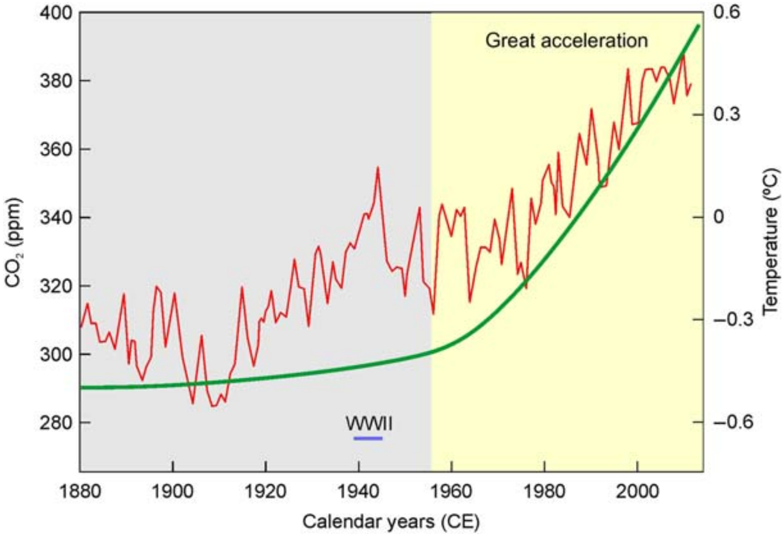

Figure 5.18 Increases in atmospheric CO_2 concentration (*green line*) in parts per million (ppm) and in temperature (*red line*) since the Industrial Revolution. The Great Acceleration is highlighted in yellow. The blue line represents the WWII. *Modified and redrawn from Lewis and Maslin (2015).*

globalization, land use, the exploitation of natural resources, urbanization, atmospheric circulation, the water cycle and other biogeochemical cycles (notably those of carbon and nitrogen), biodiversity, contamination, waste accumulation, and human health. In other words, humans have been able to alter the global dynamics of the planet (Waters et al., 2014; Lewis and Maslin, 2015).

Evidence of the Industrial Revolution and the Great Acceleration is starting to accumulate not only in paleoecological records but also in historical processes at the human scale. By way of example, we return to what was discussed in Chapter 2 (Section 2.1.2) about the migration of several species toward the poles or high mountain areas in response to GW. This is a general phenomenon that can be observed all over the planet, even in tropical regions. As in the past, these changes are taking place in an idiosyncratic manner, which is leading to changes in the composition of communities and in biodiversity patterns. For example, a study of more than 300 European mountains revealed that for the last 145 years, there has been a significant increase in plant species richness on the summits in accordance with the temperature increase observed in the same areas (Steinbauer et al., 2018). This circumstance that becomes obvious by comparing past and present floristic inventories is due to the upward migration of plants provoked by GW. Moreover, this increase in biodiversity significantly accelerated between 1957 and 1966, coinciding with the onset of the Great Acceleration (Fig. 5.18). A synthetic review of the effects of global change on 94 ecological processes of land, sea, and freshwater ecosystems found significant changes in 77 of these processes (84%) at the levels of organisms, species, populations, and communities (Scheffers et al., 2016). Regarding organisms, the most important changes occurred in genetic diversity, morphology (i.e., body size and shape), and physiology (i.e., activity). For species, major alterations were found in biogeography, especially the location and extent of their distribution areas, and habitat quality. Concerning populations, significant changes were documented in phenology (e.g., the timing of sprouting, blooming, and egg laying) and population dynamics (abundance, age distribution, and seasonal migrations). The most significant changes at the community level were found in productivity (biomass and primary production), composition, and interspecific relationships. All of these ecological changes had and are having serious effects on humans with regard to natural resource availability (e.g., less fishing, fewer pollinators, and more invasive species and pests) and health (new disease vectors, more social conflicts, etc.).

Many people believe that this transformation is a change in state or a regime shift (Section 4.3) at a global scale since it has reached a point of no return. This apparent irreversibility suggests that the Holocene is over and a new geological epoch, the "Anthropocene", has begun, which is characterized by complete human "control" over the planet. This opinion will be further discussed in the next chapter (Section 6.3).

5.5 Synthesis: a humble origin but limitless ambition

In this chapter, we dealt with one of the elements that (together with climate) had the greatest influence on Quaternary local, regional, and global ecologies: the genus *Homo*, particularly *H. sapiens*, whose influence has been decisive since the Holocene and highly transformative during the last few centuries. The complexity already present in climatic changes (Chapter 1) and magnified by ecological and evolutionary responses (Chapters 2 and 4) reaches its maximum when also considering human activities and their consequences. With this new element, complexity has approached levels that did not exist even in former, human-free geological times. Human influence on the planet has proceeded in crescendo since the origin of humans. The first hominins were too few and their technology too primitive to have a significant effect on the communities and biomes they lived in. Apparently, it was precisely an ecological event (i.e., the appearance of vast African savannas) that provoked a change in the evolutionary direction of our ancestral species. Following their African origin, hominins embarked on two great expansions; the first one was led by *H. ergaster/H. erectus* and was limited to Eurasia, while *H. sapiens*, the protagonist of the second expansion, reached every corner of the planet.

Fire, which *H. erectus* already used on a daily basis, could have been the first environmental disturbance agent, but there is no evidence of significant changes that can be attributed to fire, not even in the times of *H. neanderthalensis*, the grand master of this element. The first global ecological change in which *H. sapiens* might have played a part was the extinction of megafauna at the end of the last glaciation. But the role of humans in these extinctions is still unclear in relation to other possible causes, especially the climate. There can be no doubt, however, about the complete responsibility of *H. sapiens* in the Neolithic Revolution (Early to Mid-Holocene), which marked the beginning and expansion of agriculture and farming on every continent and the consequent transformation of communities, landscapes, and even biomes. Since the Neolithic Revolution, the world has not been the same, and ecological and biogeographical changes have depended not only on climate but also on the interaction between climate and human activities. Human influence significantly increased over time and reached its maximum after the Industrial Revolution, which meant a shift from agriculture to industry as the principal mode of economic activity. But this was not all because right after the WWII, industrialization underwent a spectacular acceleration, which placed humanity at the top of the hierarchy in terms of global ecological alteration capacity, similar to other telluric forces. The result was what we know today as Global Change, of which Global Warming is only one of the components. It also resulted in the idea that a new geological epoch, the "Anthropocene", began (Section 6.3) following the already finished Holocene.

References

Björk, S., Rittenour, T., Rosén, P., França, Z., Möller, Z., Snowball, I., et al., 2006. A Holocene lacustrine record in the Central North Atlantic: proxies for volcanic activity, short-term NAO mode variability, and long-term precipitation changes. Quat. Sci. Rev. 25, 9–32.

Burroughs, W., 2005. Climate change in the prehistory. The End of the Reign of Chaos. Cambridge University Press, Cambridge.

Cañellas-Boltà, N., Rull, V., Sáez, A., Margalef, O., Bao, R., Pla-Rabes, S., et al., 2013. Vegetation changes and human settlement of Easter Island during the last millennia: a multiproxy study of the Lake Raraku sediments. Quat. Sci. Rev. 72, 36–48.

Carbonell, E., Bermúdez de Castro, J.M., Parés, J.M., Pérez-González, A., Cuenca-Bescós, G., Ollé, A., et al., 2008. The first hominin of Europe. Nature 452, 465–469.

Neanderthals: ecology and evolution. In: Carrión, J.S., Lalueza-Fox, C., Stewart, J. (Eds.), Quat. Sci. Rev., 217. pp. 1–340.

Collard, M., Wood, B., 2014. Defining the genus *Homo*. In: Henke, W., Tattersall, I. (Eds.), Handbook of Paleoanthropology. Springer, Berlin, pp. 2107–2144.

Connor, S.E., van Leeuwen, J.F.N., Rittenour, T.M., van der Knapp, W.O., Amman, B., Björk, S., 2012. The ecological impact of oceanic island colonization – a palaeoecological perspective from the Azores. J. Biogeogr. 39, 1007–1023.

Crombé, P., 2019. Mesolithic projectile variability along the southern North Sea basin (NW Europe): hunter-gatherer responses to repeated climate change at the beginning of the Holocene. PLoS One 14, e0219094.

Crutzen, P.J., Stoermer, E.F., 2000. The "Anthropocene". Glob. Change Newsl. 41, 17–18.

Darwin, C., 1871. The Descent of Man. John Murray, London.

Degioanni, A., Bonenfant, C., Cabut, S., Condemi, S., 2019. Living on the edge: was demographic weakness the cause of Neanderthal demise? PLoS One 14, e0216742.

de Menocal, P.B., 1995. Plio-Pleistocene African climate. Science 270, 53–59.

de Menocal, P.B., 2001. Cultural responses to climate change during the late Holocene. Science 292, 66–73.

de Menocal, P.B., 2004. African climate change and faunal evolution during the Pliocene-Pleistocene. Earth Planet. Sci. Lett. 220, 3–24.

de Menocal, P.B., Ortiz, J., Guilderson, T., Adkins, J., Sarnthein, J., Baker, L., et al., 2000. Abrupt onset and termination of the African Humid Period: rapid climate responses to gradual insolation forcing. Quat. Sci. Rev. 19, 347–361.

Diamond, J.M., 2005. Collapse: How Societies Choose to Fail or to Succeed. Viking, New York.

Dias, E., 2007. A chegada dos portugueses às ilhas – o antes e o depois. In: Silva, J.S. (Ed.), Açores e Madeira: a Floresta das Ilhas. Fundação Luso Americana, Lisboa, pp. 137–295.

Ellis, E.C., 2015. Ecology in an anthropogenic biosphere. Ecol. Monogr. 85, 287–331.

Ellis, E.C., Goldewijk, K.K., Siebert, S., Lightman, D., Ramankutty, N., 2010. Anthropogenic transformation of the biomes, 1700 to 2000. Glob. Ecol. Biogeogr. 19, 589–606.

Falk, D., 1980. Hominid brain evolution: the approach from paleoneurology, Yearbook of Physicical Anthropology, 23. pp. 93–107.

Flenley, J.R., Bahn, P., 2003. The Enigmas of Easter Island. Oxford University Press, Oxford.

Flenley, J.R., King, S.M., 1984. Late Quaternary pollen records from Easter Island. Nature 307, 47–50.

Fuller, D.Q., Wilcox, G., Allaby, R.G., 2011. Cultivation and domestication had multiple origins: arguments against the core area hypothesis for the origins of agriculture in the Near East. World Archaeol. 43, 628–652.

Galway-Witham, J., Cole, J., Stringer, C., 2019. Aspects of human physical and behavioural evolution during the last 1 million years. J. Quat. Sci. Available from: https://doi.org/10.1002/jps.3137.

Gillespie, R.G., Clague, D.A. (Eds.), 2009. Encyclopedia of Islands. University of California Press, Berkeley, CA.

Goren-Inbar, N., Alperson, N., Kislev, M.E., Simchoni, O., Melamed, Y., Ben-Nun, A., et al., 2004. Evidence of hominin control of fire at Gesher Benot Ya'aqov, Israel. Science 304, 725−727.

Goudie, A., 2006. The Human Impact on the Natural Environment. Past, Present and Future. Blackwell, Malden, MA.

Green, R.E., Krause, J., Briggs, A.W., Maricic, T., Stenzel, U., Kircher, M., et al., 2010. A draft sequence of the Neanderthal genome. Science 328, 710−722.

Heyes, P.J., Anastasakis, K., de Jong, W., van Hoesel, A., Roebroeks, W., Soressi, M., 2016. Selection and use of manganese dioxide by Neanderthals. Sci. Rep. 6, 22159.

Hublin, J.-J., Ben-Ncer, A., Bailey, S.B., Freidline, S.E., Neubauer, S., Skinner, M.M., et al., 2017. New fossils from Jebel Irhoud, Morocco and the pan-African origin of *Homo sapiens*. Nature 546, 289−292.

Hunt, K.D., 1994. The evolution of human bipedality: ecology and functional morphology. J. Hum. Evol. 26, 183−202.

Hunt, T.L., Lipo, C., 2011. The Statues that Walked. Free Press, New York.

Jalut, G., Dedoubat, J.-J., Fontugne, M., Otto, T., 2009. Holocene circum-Mediterranean vegetation changes: climate forcing and human impact. Quat. Int. 200, 4−18.

Krause, J., Lalueza-Fox, C., Orlando, L., Enard, W., Green, R.E., Burbano, H.A., et al., 2007. The derived *FOXP2* variant of modern humans was shared with Neanderthals. Curr. Biol. 17, 1908−1912.

Kumar, S., Filipski, A., Swarna, V., Walker, A., Hedges, S.B., 2005. Placing confidence limits on the molecular age of the human-chimpanzee divergence. Proc. Natl Acad. Sci. U.S.A. 102, 18842−18847.

Larson, G., Piperno, D.R., Allaby, L.G., Purugganan, M.D., Andersson, L., Arroyo-Kalin, M., et al., 2014. Current perspectives and the future of domestication studies. Proc. Natl Acad. Sci. U.S.A. 111, 6139−6146.

Lewis, S.L., Maslin, M.A., 2015. Defining the Anthropocene. Nature 519, 171−180.

Mann, A., Weiss, M., 1996. Hominoid phylogeny and taxonomy: a consideration of the molecular and fossil evidence in an historical perspective. Mol. Phylogenet. Evol. 5, 169−181.

Maslin, M.A., Shultz, S., Trauth, M.H., 2015. A synthesis of the theories and concepts of early human evolution. Philos. Trans. R. Soc. B 370, 20140064.

McCall, G., 1993. Little Ice Age, some speculations for Rapa Nui. Rapa Nui J. 7, 65−70.

Moreira, J.M., 1987. Alguns Aspetos de Intervencão Humana na Evolução da Paisagem da Ilha de São Miguel (Açores). Serviço Nacional de Parques, Reservas e Conservaçao da Naturaleza, Lisboa.

Pearce, E., Stringer, C., Dunbar, R.I.M., 2013. New insights into differences in brain organization between Neanderthals and anatomically modern humans. Proc. R. Soc. B 280, 20130168.

Pinhasi, R., Fort, J., Ammerman, A.J., 2005. Tracing the origin and spread of agriculture in Europe. PLoS Biol. 3, 2220−2228.

Pinker, S., 2010. The cognitive niche: coevolution of intelligence, sociality and language. roc. Natl. Acad. Sci. U.S.A. 107, 8993−8999.

Prüfer, K., de Cesare, F., Grote, S., Mafessoni, F., Korlević, P., Hajdinjack, M., 2017. A high-coverage Neanderthal genome from Vindija Cave in Croatia. Science 358, 655−658.

Raia, P., Meiri, S., 2006. The island rule in large mammals: paleontology meets ecology. Evolution 60, 1731–1742.

Reed, K.E., 1997. Early hominid evolution and ecological change through the African Plio-Pleistocene. J. Hum. Evol. 32, 289–322.

Roberts, N., 2014. The Holocene. An Environmental History. Wiley-Blackwell, Chichester.

Roberts, M.F., Bricher, S.E., 2018. Modeling the disappearance of the Neanderthals using principles of population dynamics and ecology. J. Archaeological Sci. 100, 16–31.

Roberts, N., Fyfe, R.M., Woodbridge, J., Gaillard, M.-J., Davis, B.A.S., Kaplan, J.O., et al., 2017. Europe's lost forests: a pollen-based synthesis for the last 11,000 years, Sci. Rep., 8. p. 176.

Robinson, T., Stevenson, C.M., 2017. The cult of the Birdman: religious change at Orongo, Rapa Nui. J. Pac. Archaeology 8, 88–102.

Roebroeks, W., Villa, P., 2011. On the earliest evidence for habitual use of fire in Europe. Proc. Natl. Acad. Sci. U.S.A. 108, 5209–5214.

Rosas, A. (Ed.), 2016. *La Evolución del Género Homo*. CSIC-La Catarata, Madrid.

Ruddiman, W.F., 2003. The anthropogenic greenhouse era began thousands of years ago. Clim. Change 61, 261–293.

Ruddiman, W.F., 2013. The Anthropocene. Annu. Rev. Earth Planet. Sci. 41, 45–68.

Rull, V., 2016. Natural and anthropogenic drivers of cultural change on Easter Island: review and new insights. Quat. Sci. Rev. 150, 31–41.

Rull, V., 2018. Strong fuzzy EHLFS: a general conceptual framework to address past records of environmental, ecological and cultural change. Quaternary 1, 10.

Rull, V., 2019. The deforestation of Easter Island. Biol. Rev. Available from: https://doi.10.1111/brv.12556.

Rull, V., Montoya, E., Vegas-Vilarrúbia, T., Ballesteros, T., 2015. New insights on palaeofires and savannisation in northern South America. Quat. Sci. Rev. 122, 158–165.

Rull, V., Lara, A., Rubio-Inglés, M.J., Giralt, S., Gonçalves, V., Raposeiro, P., et al., 2017. Vegetation and landscape dynamics under natural and anthropogenic forcing of the Azores Islands: a 700-year pollen record from the São Miguel Island. Quat. Sci. Rev. 159, 155–168.

Rull, V., Montoya, E., Seco, I., Cañellas-Boltà, N., Giralt, S., Margalef, O., et al., 2018. CLAFS, a holistic climatic-ecological-anthropogenic hypothesis on Easter Island's deforestation: proposals and testing prospects. Front. Ecol. Evol. 6, 32.

Rull, V., Vegas-Vilarrúbia, T., Huber, O., Señaris, C. (Eds.), 2019. Biodiversity of Pantepui, the Pristine "Lost World" of the Neotropical Guiana Highlands. Elsevier-Academic Press, London.

Scardia, G., Parenti, F., Miggins, D.P., Gerdes, A., Araujo, A.G.M., Neves, W.A., 2019. Chronologic constraints on hominin dispersal outside Africa since 2.48 Ma from the Zarqa Valley, Jordan. Quat. Sci. Rev. 219, 1–19.

Scheffers, B.R., De Meester, L., Bridge, T.C.L., Hoffman, A.A., Pandolfi, J.M., Corlett, R.T., et al., 2016. The broad footprint of climate change from genes to biomes to people. Science 354, aff7671.

Shultz, S., Nelson, E., Dunbar, R.I.M., 2012. Hominin cognitive evolution: identifying patterns and processes in the fossil and archaeological record. Philos. Trans. R. Soc. B 367, 2130–2140.

Slon, V., Mafessoni, F., Vernot, B., de Filippo, C., Grotte, S., Viola, B., et al., 2018. The genome of the spring of a Neanderthal mother and a Denisovan father. Nature 561, 113–116.

Sorensen, A.C., Claud, E., Soressi, M., 2018. Neanderthal fire making technology inferred from microwear analysis. Sci. Rep. 8, 10065.

Spikins, P., Needham, A., Wright, B., Gatta, M., Hitchens, G., 2019. Living to fight another day: the ecological and evolutionary significance of Neanderthal healthcare. Quat. Sci. Rev. 217, 98−118.

Steinbauer, M., Grytnes, J.A., Jurasinski, G., Kulonen, A., Lenoir, J., Pauli, H., et al., 2018. Accelerated increase in plant species richness on mountain summits is linked to warming. Nature 556, 231−234.

Stringer, C., 2016. The origin and evolution of *Homo sapiens*. Philos. Trans. R. Soc. B 371, 20150237.

Sutikna, T., Tocheri, M.W., Morwood, M.J., Saptomo, E.W., Jatmiko, Awe, R.D., et al., 2016. Revised stratigraphy and chronology for *Homo floresiensis* at Liang Bua in Indonesia. Nature 532, 366−369.

Trigger, B.G., 1989. A History of Archaeological Thought. Cambridge University Press, Cambridge.

Vannière, B., Power, M.J., Roberts, N., Tinner, W., Carrión, J., Magny, M., 2011. Circum-Mediterranean fire activity and climate changes during the mid-Holocene environmental transition (8500-2500 cal. BP). Holocene 21, 53−73.

Villanea, F.A., Schraiber, J.G., 2019. Multiple episodes of interbreeding between Neanderthals and modern humans. Nat. Ecol. Evol. 3, 39−44.

von Holstein, L., Foley, R.A., 2017. Hominin evolution. In: Shackelford, T.K., Weekes-Shackelford, V.A. (Eds.), Encyclopedia of Evolutionary Psychological Science. Springer, Berlin, pp. 1−22.

Walker, M., Johnsen, S., Rasmussen, S.O., Popp, T., Steffensen, J.-P., Gibbard, P., et al., 2009. Formal definition and dating of the GSSP (Global Stratotype Section and Point) for the base of the Holocene using the Greenland NGRIP ice core, and selected auxiliary records. J. Quat. Sci. 24, 3−17.

Waters, M.R., 2019. Late Pleistocene exploration and settlement of the Americas by modern humans. Science 365, eaat5447.

Waters, C.N., Zalasiewicz, J.A., Williams, M., Ellis, M.A., Snelling, A.M. (Eds.), 2014. A Stratigraphical Basis for the Anthropocene. Ceological Society, London.

Waters, C.N., Zalasiewicz, J.A., Summerhayes, C.P., Barnosky, A.D., Poirier, C., Gałuszka, A., et al., 2016. The Anthropocene is functionally and stratigraphically distinct from the Holocene. Science 351, aad2622.

Wright, D.K., 2017. Humans as agents in the termination of the African Humid Period. Front. Earth Sci. 5, 4.

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CHAPTER SIX

The future: natural cycles and human interference

Contents

In this chapter, which is slightly more speculative than the former chapters, we analyze what can be expected under the global change initiated with the Great Acceleration, but without addressing specific topics such as conservation, restoration, and the use and abuse of natural resources. As already explained in the introduction of the book we are not going to deal with possible practical applications of immediate use because they have been widely covered in specific books and articles by experts in the field (review in Vegas-Vilarrúbia et al., 2011). Still, everything discussed in this book is of genuine interest for the conservation of biodiversity, for the rational exploitation of natural resources, and for the development of the best ecosystem and landscape restoration strategies, among other activities. For example, the Quaternary offers ideal past analogs to study biotic responses to climatic changes, which is of real use in forecasting possible reactions that species and communities might have to Global Warming (e.g., Fig. 2.16) and, thus, in predicting possible consequences for biodiversity, landscapes, and biomes in the immediate future. This will also help us prepare appropriate conservation action plans. In addition, we can learn useful lessons about human societies, which in one way or another

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have also been affected by past environmental variability (Section 5.3). Regarding restoration, Quaternary studies offer first-hand information about the preanthropogenic state of ecosystems; therefore we can always have the so-called baseline of any area or region, based on which we can decide on the best specific restoration strategies (Willis et al., 2010). In this case, we must keep in mind that environmental conditions—especially the climate—might have changed and that the restoration of preanthropogenic landscape characteristics might not be possible. For example, it would not make much sense to restore the megafauna that went extinct during the Late Pleistocene (Section 2.2.3)—which is an idea that was widely considered several years ago (Donlan et al., 2006)—because it would be impossible (or largely unnatural) to reestablish the glacial climatic conditions and ecosystems inhabited by those large mammals. The Quaternary can help us out again with possible alternatives for restoration, as there we can find examples of different states that a given ecosystem can adopt within its domain of attraction (Sections 4.3 and 4.4) without losing its ecological character.

We leave these topics to the experts but not without a word of warning: the best way to preserve the world is by not destroying it, and this is possible only by radically changing the current model of global economic development based on the utopia of unlimited growth (Rull, 2011, 2014). This is the real global change that we need. Stop-gap solutions of conservation and restoration measures serve only to perpetuate the system, following the well-known conservative paradox "to change everything so that nothing changes". But for now, we are going to deal with speculations about the future based on all we have learned about the Quaternary and about evolution in general.

6.1 Will we disrupt natural variability?

In the present context the main question is whether glacial–interglacial cycles will follow their natural course or human-generated global warming will be able to modify or even stop that course. The second option implies control over astronomical cycles, which is an idea belonging more to magic or mythology. But we are so anthropocentric that some researchers have already been developing predictive models of the possibility of postponing or blocking the next glacial (remember, we are living in an interglacial period) with our actions. In defense of this apparently atrocious possibility, we must point out that these models do not consider the possibility of changing astronomical cycles (which would be an impossibility, even for the most anthropocentric minds) but of changing the effects these astronomical cycles exert on the Earth and, more precisely, on the climate. In this sense, it is opportunity to remember that astronomical cycles set the pace of Pleistocene climate cycles but seem unable to provoke sufficient variation in incident solar energy to trigger glaciations on their own. They need signal amplification mechanisms, such as changes in greenhouse gases, thermohaline circulation patterns, or albedo, among others (Section 1.2.2). Obviously, the alteration or interruption of glacial cycles means the alteration of the principal natural environmental mechanism that controlled ecology and evolution throughout the Quaternary. This would entail radical changes in organisms, populations, species, communities, and biomes. At the end of the fifth chapter, we mentioned that the biotic modifications caused by the first decades of global warming are becoming significant. It is easy to imagine that larger changes in climatic cycles would lead to more drastic biotic changes.

6.1.1 Our interglacial: the Holocene

To conduct an empirically based analysis, we will examine if the current interglacial period, the Holocene, follows the pattern of earlier interglacials or if it is already anomalous as a consequence of the great human development that characterized this geological epoch. Exhaustive and detailed studies of earlier glacial cycles found that the transition from the MIS18 glacial to the MIS19 interglacial (Fig. 1.4) was the most similar past analog to the LGM—Holocene transition. The MIS18-MIS19 transition took place between 800 and 770 ka BP, exactly when the glacial—interglacial periodicity changed from 41 to 100 ka (Section 1.2.1). This is why the MIS18—MIS19—MIS20 cycle is used as an analog to estimate the duration of the Holocene and the possible beginning of the next glaciation (Tzedakis et al., 2012). Fig. 6.1 shows that temperature and CO_2 concentration trends are practically the same up to the maximum point of each period, which is 787—786 ka BP for MIS19 and 9—6 ka BP (i.e., the HTM) for the Holocene. Afterward, however, differences become obvious. In MIS19, both temperature and atmospheric CO_2

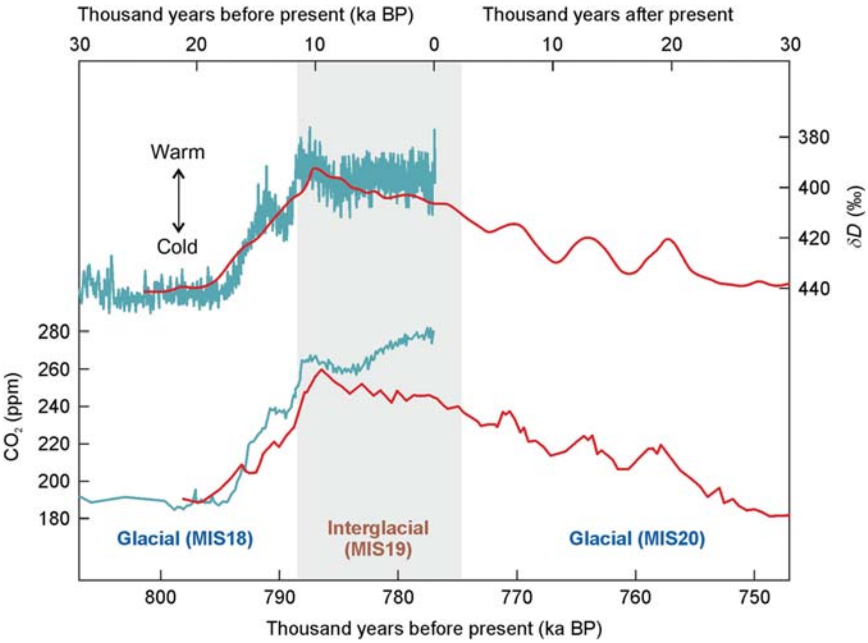

Figure 6.1 Comparison between the MIS18–MIS19–MIS20 glacial cycle (*red lines*) and the last glacial cycle (i.e., the LGM and the Holocene to date) (*blue lines*), using deuterium concentration (*δD*) as a proxy of paleotemperature and atmospheric CO_2 concentration to express the greenhouse effect (both parameters were obtained from polar ice cores). The time scale at the bottom belongs to the MIS18–MIS19–MIS20 cycle, and the time scale at the top belongs to the last glacial cycle and future millennia. *Simplified and redrawn from Tzedakis et al. (2012).*

concentration show a decreasing trend after the maximum, but in the Holocene, CO_2 undergoes a significant increase, and temperatures become stable. All this supports the observations of Ruddiman (2003, 2013), who attributed increasing CO_2 levels and consequently increasing temperatures to the boost of the Neolithic Revolution (Section 5.2.3 and Fig. 5.11).

Here, we have two situations that are very similar in terms of astronomical control of climatic cycles, but one is completely natural, and the other is under anthropogenic influence that alters the climatic trend by increasing greenhouse gases, especially CO_2. The start and end dates of the interglacial MIS19 period were established to be 788 ka BP, the end of the last glaciation (MIS18), and 775 ka BP, the beginning of the next glacial (MIS20), respectively (Fig. 6.1). The Holocene equivalents are

11.5 ka BP for the beginning of this geological epoch and approximately 1500 years from now for its end (Tzedakis et al., 2012). In other words, under natural conditions, that is, without human influence, the next glaciation should start in approximately 1500 years, a little bit after the year 3500 BCE, which leaves us 1500 years of "good weather". But this theory would hold true only if atmospheric concentrations of greenhouse gases remained below 260 ppm, as in MIS19, which appears rather improbable, as they are currently over 411 ppm and rising (www.co2.earth), approximately 36% higher than they should be. These facts point to a possible delay of the next glaciation, just as Ruddiman (2003, 2013) predicted, although the only way to know how long that delay might be is through modeling.

6.1.2 The next glaciation

There is great variation in the results of different models that seek the start date of the next glaciation, but they all agree that the current interglacial will be anomalous, compared to former interglacial periods, due to the anthropogenic increase in greenhouse gases. Some of these models forecast the prolongation of the Holocene and the consequent delay of the next glaciation, while others herald the end of glacial—interglacial cycles. Let us see an example of each case, without going into the mathematical details.

Our first example is a model called 3τ that uses Milankovitch cycles to calculate incident solar radiation (or insolation) and combines it with atmospheric CO_2 concentration to estimate the continental ice volume, which serves as a basis for the definition of glaciations and interglacials (Herrero et al., 2014). This model was used to simulate the next 300,000 years in two different situations: a natural one (which is hypothetical) and an anthropogenic one (which is more realistic). The natural model assumes that atmospheric CO_2 concentration follows the trends of the last glacial cycles (Fig. 1.6) and is used as a reference case of what would happen without anthropogenic CO_2 emissions. The other, more realistic model is based on forecasts of CO_2 emissions from fossil fuel combustion that follow the current trend, increase until 2040s, reach a maximum at that point, and then start to descend until reaching preindustrial levels around the first quarter of the 24th century (2320s). We must point out that this estimation is based not on hypothetical human awakening and abandonment of fossil fuel use but on the depletion of exploitable fossil fuels. Regarding atmospheric CO_2, the simulation predicts a 520 ppm maximum concentration in the year 2300, followed by a long exponential decrease, which will take place with an almost 50,000 year lag compared to natural cycles and will need three glacial cycles to catch up (Fig. 6.2). Simulation results also show that, in the natural case, the next glaciation

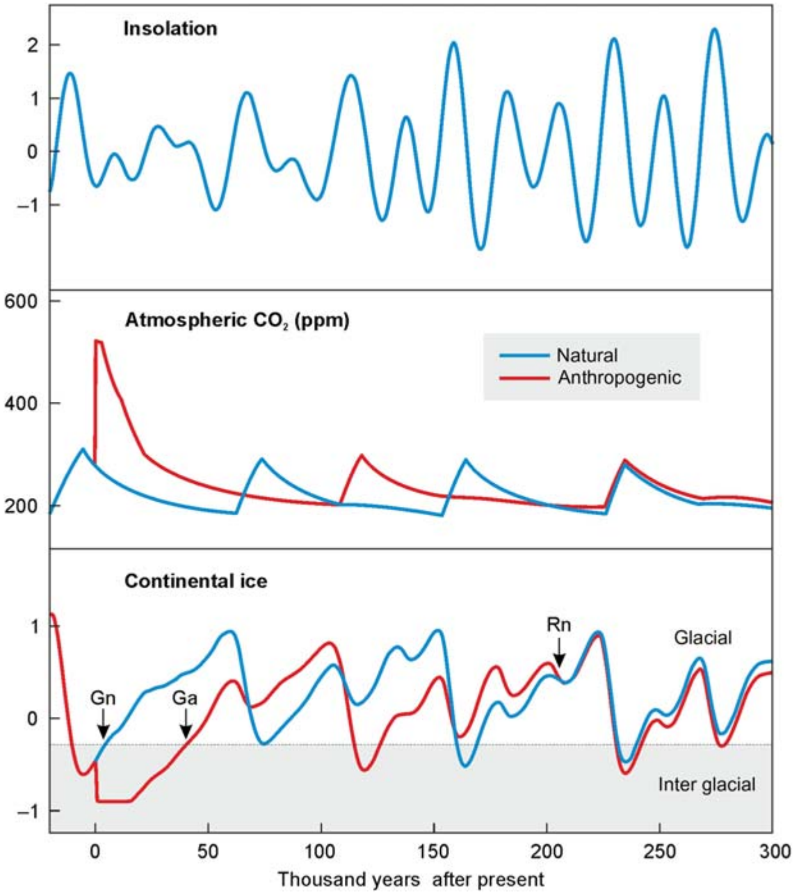

Figure 6.2 Simulation results of the 3τ model, which uses insolation and atmospheric CO_2 concentration to estimate continental ice volume, comparing a natural situation (blue) to an anthropogenic situation (red) for the next 300,000 years. In the graph of continental ice, the gray band represents interglacial ice volumes (glacials are in white). Insolation and ice volume are shown on normalized scales, and CO_2 concentration, in parts per million (ppm). *Gn*, Beginning of the next glaciation under natural conditions; *Ga*, beginning of the next glaciation under anthropogenic conditions; *Rn*, recovery of natural periodicity. *Modified and redrawn from Herrero et al. (2014)*.

should start within approximately two millennia, while in the anthropogenic situation, it would not start until within 40,000 years (Herrero et al., 2014). This means that the Holocene would last approximately 38,000 years longer than expected, which is approximately 50,000 years altogether (as a reminder, the average duration of interglacial periods during the last eight cycles was 20,000 years; Section 1.2.2). It is also worth noting that, according to this model, the effects of the anthropologically increased CO_2 concentrations would not disappear until more than 200,000 years in the future, when the natural glacial–interglacial cycles would recover and harmonize with the cycles of CO_2.

Another type of model uses the global energy balance of the Earth to estimate temperature changes at a global scale. These models are called Energy Balance Models (EBMs). With the aid of an EBM, the climate effect of increasing CO_2 concentration was simulated in two scenarios: a moderate and an extreme case (Haqq-Misra, 2014). The moderate scenario assumes that CO_2 concentration will increase twofold in the next 100–200 years, which is a common assumption in many forecasts, including that of the Intergovernmental Panel on Climate Change (IPCC). The extreme scenario assumes that all the exploitable fossil fuel will be consumed, in which case the atmospheric CO_2 concentration would be multiplied by eight. After running the model, two results were evident. The first one was an expected temperature increase, the value of which depended on the magnitude of the greenhouse effect, which was different between the two scenarios. The second, much less expected, result was the disappearance (in both the scenarios) of the climatic cycle that has a periodicity of 100 ka and is controlled by eccentricity, which was the dominant factor of the last eight glaciations (Section 1.2.1). This means that, although the astronomical cycles would follow their natural course, a CO_2 increase (even in the moderate case, without using up all fossil fuel) could suppress their effect on global temperatures, and glacial–interglacial cycles would be interrupted for at least a million years (Haqq-Misra, 2014). The simulation does not go any farther than this, but it indicates that this situation could be maintained indefinitely (whatever that means).

A group of scientists has formulated similar ideas about how close we might be to reaching the point-of-no-return threshold, which would mean an end to glacial–interglacial cyclicity and the beginning of a new state similar to what we called the greenhouse state (Fig. 1.1) or even the hothouse state, characterized by high atmospheric CO_2 concentrations, high temperatures, little difference between the poles (which would not have an ice cover) and the equator, and a sea level way above present-day levels. During geological history, there have been at least 15 hothouse phases that lasted between one and several million years and corresponded to biological extinction events (Kidder and Worsley, 2014). With the leadership of an American chemist Will Steffen, who is one of the most active defenders of the "Anthropocene" as a new geological epoch (Section 6.3), some of these researchers claim that a global temperature increase of only 2°C would be enough to provoke a cascade effect based on positive feedback mechanisms (Section 4.3) that would eventually result in a hothouse Earth (Fig. 6.3) (Steffen et al., 2018). For now, this option is completely speculative as it lacks any empirical basis and has not been modeled, but it will be a hot topic in the coming years.

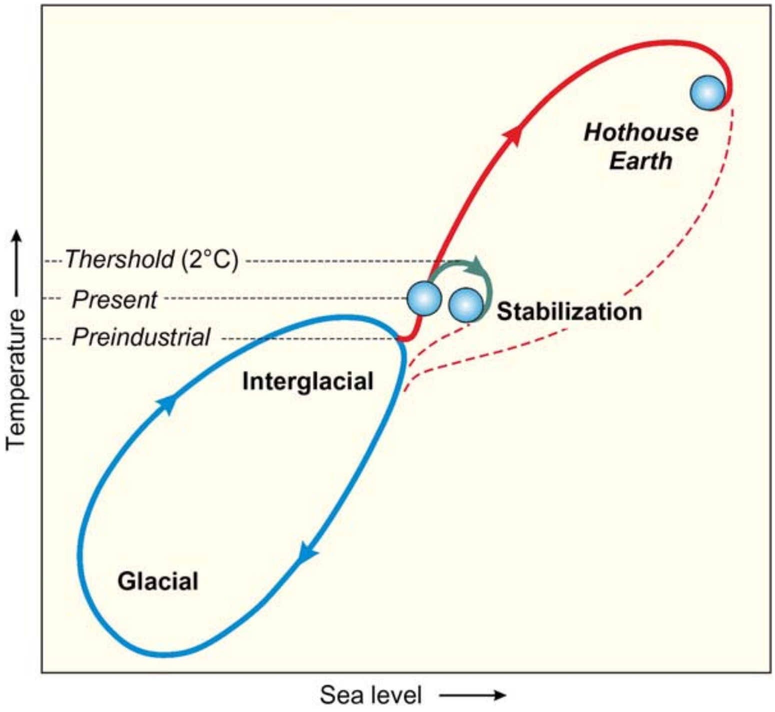

Figure 6.3 Graphic representation of the hypothetical interruption of glacial–interglacial cycles by a 2°C increase in the average global temperature. Glacial–interglacial cycles are represented by the blue trend. The red line shows what has happened since the Industrial Revolution and what might happen in the future if we go over the 2°C limit. The Earth System (*blue spheres*) would still be able to stabilize in the present state (*green line*) if we were to stay below this limit. *Redrawn from Steffen et al. (2018).*

6.2 A natural end to the planet's destruction

Right now, it seems improbable that we will be able to change our habits, so if it is up to us, global warming, pollution and contamination of the planet, and waste accumulation will probably go on as before. Therefore we might ask ourselves the question of whether it is possible for things to change in a natural manner, without us having to do anything about it, even if it is over the long term. In theory, there are three possibilities for the natural recovery of the planet: (1) that our species will go extinct; (2) that our civilization will be practically, but not totally, destroyed by some kind of natural catastrophe; or (3) that our cultural evolution will result in superior consciousness and living in harmony with nature. The last option is not the same as the mentality change that we practically ruled out at the beginning; we are referring to an evolutionary phenomenon that would change human nature. Some people believe (or rather hope) that this possibility will really come true, sooner or later, as an evolutionary survival mechanism in accordance with the Red Queen hypothesis (Section 3.4.3) (Nekola et al., 2013). Large amounts of teleology and finalism are involved in this wish for an evolutionarily more advanced consciousness, together with the belief that biological evolution is over and it is the turn of cultural evolution, which will take us to an almost alchemical level of perfection. As we saw in Chapter 3, predictability is not one of biological evolution's qualities; it works in a totally random, contingent manner. Therefore this type of evolutionary ambition is more a question of faith than of science (Rull, 2013). However, we can analyze, at least partially, the other two options based on what we have learned throughout this book and what we know about biological evolution before the Quaternary.

6.2.1 Our extinction

The fossil record, the principal empirical basis of evolution, proves that there are no eternal species; all go extinct in the end, and there is no scientific reason to believe that we will be the exception. Nobody is really interested in this truth because our anthropocentric perspective makes us scorn a possible biosphere without humans or even think that our extinction would mean the end of life on the Earth. This is far from the case. The biosphere does not need us, at all, given that it existed without us for almost 4000 million years since life appeared on the Earth. We, as a species, have been present for hardly 200,000 years, and only 20,000 years ago we expanded all over the planet (Chapter 5). After our extinction, life would go on as always; we would be yet another failed evolutionary attempt that damaged the planet more or less seriously for a while, nothing else. It is probably due to science fiction books and movies that we always picture our extinction as a catastrophic, relatively fast event, like a nuclear war or similar cataclysm, which is usually a result of our own actions (Rull, 2009). This is what we call an endogenous catastrophe, which would erase our complete gene pool from the face of the Earth in a phyletic extinction (Section 3.1.2). But, as we have seen before, there are three other types of extinction, so-called pseudoextinctions, in which our genome would not disappear completely (Section 3.1.2; Fig. 3.5).

In the event of anagenetic extinction, we would turn into a new species via fundamental genetic modification, and this new species would replace us either gradually or all of a sudden. This is not only an abstract idea; this type of extinction brought an end to our predecessor, *Homo rhodesiensis* (Section 5.1.2). As for our species, our growing capacity for genetic manipulation and our expected skills in creating hybrid forms between humans and robots (cyborgs) could play an important role in this process without having to wait for biological evolution to act. When all this becomes a technological reality, we will be able to meddle with our own evolution, which will pose a real threat not only to us but also to the whole biosphere, considering the current degree of our consciousness as a species. If biological evolution is already unpredictable in itself, it is hard to imagine what could happen if humans started to play god, but one thing is for sure that we can hardly expect anything good. Cladogenetic extinction of our species would mean that two or more descending species would appear and that one of them would occupy our niche or the niche would disappear. This is what happened to *H. antecessor* (Section 5.1.2). As already discussed (Section 3.1.1), this process depends on the formation of reproductive barriers, which is rather improbable considering the current globalization level. In the future, however, cladogenetic extinction stands a chance, in a scenario of overexploitation and destruction of the planet, when humans migrate to colonize other habitable planets (supposing that there are any) and the colonizing human civilizations become so isolated from each other that new species evolve. Genetic drift (Section 3.1.1), especially the founder effect, and punctuated equilibrium (Section 3.4.2) could both play a part in this process. Lastly, extinction by hybridization would take place if we could reproduce with another species and the resulting hybrids occupied the niches of both parent species. We cannot find any present-day example of this case on the Earth, but there used to be hybridization between *H. sapiens* and *H. neanderthalensis*, as discussed in the fifth chapter. In the future, the eventual new species formed during the colonization of other planets could be reunited and reproduce. We can imagine a romantic story of the descending species returning to the home of their forefathers (after it recovered from the disaster provoked by us) and starting a new life, a second chance, on the original planet of the species. But this would be possible only if the returning species learned how to live in harmony with nature; otherwise, history could only repeat itself, following another of Gould's time cycles.

Of the analyzed types of pseudoextinction, cladogenetic extinction would probably be the most favorable to the Earth in the long term if we really abandoned the planet to colonize others. As we said before, the biosphere does not need us, and our absence would make it possible for life to regenerate from whatever we left behind. This idea is not pure science fiction, as similar cases occurred during the history of the Earth when mass extinctions drastically reduced the diversity of life but it always managed to recover and bloom once again. Unfortunately, this theory is based on the assumption that we are forced to flee the planet because we already made it unserviceable, at least for ourselves. Therefore it is still the phyletic and catastrophic type of human extinction that would be best for the planet, supposing that it does not imply the disappearance of life altogether (e.g., by radioactive contamination).

From the anthropocentric perspective, of course, nothing could outweigh the continuity of our species, be it on this planet or on any other. Ironically, this option could imply returning to ancient practices, reversing our cultural evolution. During the Neolithic Revolution (Section 5.2.2), the most primitive type of land use was shifting cultivation (often by slash-and-burn techniques), when seminomadic groups moved on to a new location after depleting local resources, and so on. Leaving the Earth for the same reason could be the start of a similar shifting exploitation at an interplanetary level. We have no reason to believe that humanity would act any differently on other planets. Our objectives would still be anthropocentric, focused on what we consider the greater good, that is, the continuity of our species, no matter at what price, even if that price is destroying one planet after the other. It is easy to see why for some people the only hope is an evolutionary change, be it biological or cultural, that changes human nature. For others, "... human nature does not change. We continue to carry the enormous potentials for both good and evil that have been implanted into our genome long ago in the savannah" (Kováč, 2019).

6.2.2 Alive but not decisive

Besides extinction, our destructive leading role could be stopped by an exogenous or endogenous process that drastically diminished the human population of the planet and/or our technological possibilities. Possible causes include an immense volcanic eruption, a global epidemic, a nuclear war, a meteorite impact, a glaciation, and the depletion of natural resources, among others (Crutzen and Stoermer, 2000). The only one that is relatively predictable among these options is glaciation, given that it is a cyclic phenomenon; all the others are completely unpredictable.

If the next glaciation were to be similar to the last one, we could rely on the LGM as a model. Large parts of the continents of the Northern Hemisphere would be covered by ice sheets with a thickness of kilometers or would be uninhabitable due to frozen soils (Section 1.2.4). During the LGM, the human population of the planet was relatively small, but today, this situation would be a serious obstacle to human development. Human habitat and natural resources would be substantially decreased, which would primarily affect the most industrialized countries and hinder global technological capacity, not to mention the conflicts arising from the race for resources and space. In Europe, for example, the Mediterranean would be the only area suitable for human occupation both climatologically and ecologically. We have seen that if the rhythm of glaciations follows its natural course (i.e., astronomical Milankovitch cycles), the next glaciation should begin within a couple of millennia and reach its maximum in 60,000 years (Fig. 6.1). We also discussed that this is highly unlikely to take place because of the increase in the greenhouse effect provoked by anthropogenic emissions. This increase affects the global climate in such a way that the next glacial cycle could suffer a delay of 40,000 years or glacial—interglacial cycles could even be stopped and the present interglacial, the Holocene, could go on "indefinitely." This means that we would have to wait either 60,000 (in the natural case) or 100,000 years (in the anthropogenic case) for the next glacial maximum (Fig. 6.1), if it is actually ever going to happen. This is good news for our species, but for the planet, it means that exploitation could go on for a long time, as long as the planet could stand it.

6.3 The "Anthropocene"

According to what we have learned so far, the only thing that can put an end to the anthropogenic destruction of the planet in time is an unpredictable, relatively fast, exogenous or endogenous catastrophe that either exterminates our species or diminishes it so much that we lose the influence over the Earth System that we have been exerting since the beginning of the Industrial Revolution. In the meantime, we have no other choice but to face the consequences of our deeds. At the beginning of this century the Danish chemist Paul Crutzen and the American ecologist Eugene Stoermer proposed that as the situation brought about by the Industrial Revolution could last for millennia or even millions of years, it might be reasonable to define a new geological epoch, the "Anthropocene", which may become a new, official stratigraphic unit that follows the Holocene (Crutzen and Stoermer, 2000). The topic is surrounded by a heated controversy that we cover here very briefly.

6.3.1 State of the art

The idea of a new stratigraphic unit based on human action and its traces in the geological record was born in the third quarter of the 19th century when an Italian geologist, Antonio Stoppani, proposed the creation of a new era called the "Anthropozoic" (Stoppani, 1873). Other terms have been suggested for the same use ever since, but "Anthropocene" is the only one that is going to be considered (to be named an epoch and not an era as Stoppani suggested) by the International Commission on Stratigraphy (ICS) and the International Union of Geological Sciences (IUGS), which are the organizations in charge of the formalization (i.e., approval and ratification) of units in the International Chronostratigraphic Chart (ICC), the system used to decipher Earth's geological history. The proposition of the "Anthropocene" as a new geological epoch is still in its infancy, hence the quotation marks, which are used to denote informal stratigraphic terms. The Anthropocene Working Group (AWG), composed of the most ardent defenders of this initiative, including Crutzen, is working on an official proposal and hopes to have it ready in 2020 or later (Rull, 2018). Then, the proposal will be submitted to the ICS for its eventual approval and ratification (Fig. 6.4). According to the rules of the ICS (www.stratigraphy.org), the standard procedure for proposing a stratigraphic unit for

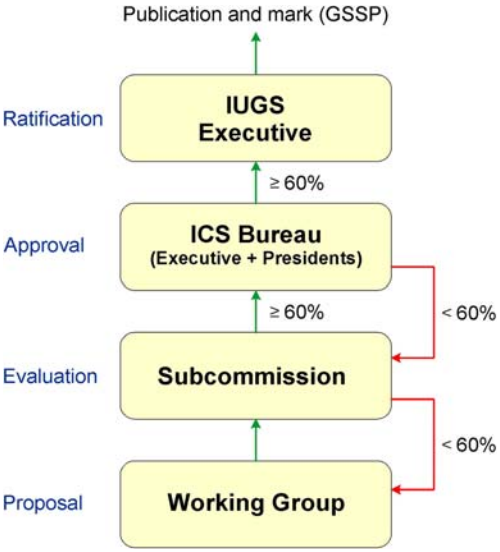

Figure 6.4 Procedure of approval and ratification of new stratigraphic units in the ICC. In the present case the Anthropocene Working Group and the Subcommission on Quaternary Stratigraphy are the affected parties. A proposal moves to the next, higher level (*green arrows*) if more than 60% of the members at the given level vote favorably. Otherwise (*red arrows*), the proposal is sent back to the lower level. *GSSP*, Global Boundary Stratotype Section and Point; *ICC*, International Chronostratigraphic Chart; *ICS*, International Commission on Stratigraphy; *IUGS*, International Union of Geological Sciences.

ratification consists of the following steps: (1) identification of the stratotype, which is a physical location or outcrop identified by a stratigraphic marker that defines the unit and differentiates it from the former unit, in this case, the Holocene; (2) determination of the age of the limit between the two units; and (3) definition of the so-called Global Boundary Stratotype Section and Point (GSSP) based on the previous criteria. To be approved, a GSSP must be recognizable and synchronous at a global scale.

The AWG seems to have started to work in a reverse order as, so far, they have been focused on defining the possible age of the limit, which is normally the second step. The original proposal of Crutzen and Stoermer of using the Industrial Revolution as the starting date of the "Anthropocene" is not feasible because it was neither global nor synchronous (Fig. 5.17). The Neolithic Revolution has also been considered a possible Holocene—"Anthropocene" limit since, according to Ruddiman (2003, 2013), it was the first serious human impact on the

Earth System (Section 5.2.3). This idea had to be dismissed for the same reason (i.e., it was not globally synchronous) (Section 5.2.2). However, a very recent compilation of archeological evidence suggests that the planet was already globally transformed by hunter-gatherers, farmers, and pastoralists by 3000 years ago (Stephens et al., 2019) and this date should seriously be considered in the near future for the definition of the "Anthropocene." Upon considering all the possibilities existing a couple of years ago, the AWG decided that the best candidate was the Great Acceleration, which began in approximately the mid-20th century, and the best stratigraphic marker is the presence of radioisotopes (i.e., radioactive isotopes) generated by the first nuclear explosions in 1945, at the end of the Second World War (Zalasiewicz et al., 2017a). The AWG is now busy with trying to find the most appropriate stratigraphic section to define the corresponding GSSP and thus complete their proposal for its presentation to the ICS. A great variety of possible candidates are currently under consideration, including lake sediments, marine sediments, polar ice, coral skeletons, and speleothems (stalactites and stalagmites) of karst caves (Waters et al., 2018).

6.3.2 The controversy

The AWG prospect has been widely criticized. First, the AWG has been accused of following historical criteria instead of geological criteria because of the mentioned reverse order of the procedure, which is deemed inappropriate for the proposal of a new stratigraphic unit. First deciding on the date of the limit and then subsequently looking for suitable rocks to define the GSSP do not comply with the evidence-based scientific procedure, which should be based on a rock body considering a new unit of the ICC. Another criticism centers on the selection of a limit so close to the present (only some 70 years ago), which means that the sedimentary records of the "Anthropocene" are extremely scarce (a few centimeters in lake sediments and a millimetric layer in sea sediments) or even nonexistent in some areas. This might make finding a proper stratotype and a globally synchronous GSSP fairly difficult. The "Anthropocene" seems to be more a speculation about the future than evidence of the past, and stratigraphy is concerned only with the latter. Therefore a new stratigraphic unit cannot be defined using this meager and likely ephemeral evidence. An even more fundamental criticism is that human influence, which would be the basis of the definition of the "Anthropocene", was already used in the definition of the Holocene and cannot be utilized again in the "Anthropocene." Besides these scientific arguments, the AWG and the defenders of the "Anthropocene" are accused of using political criteria to lobby for their cause through mass media. The formalization of the "Anthropocene" is regarded by many as an official acknowledgment of human influence over the planet that could be used as a social and political tool to raise awareness. Critics claim that there is no need to raise further awareness since society is well aware of the situation and that it is not a valid reason to create a new stratigraphic unit. Many of these critical voices come from the higher circles of the ICS and IUGS (e.g., Finney, 2014; Gibbard and Walker, 2014; Edwards, 2015; Finney and Edwards, 2016), so in the present atmosphere, the proposal of the "Anthropocene" as a new ICC unit is unlikely to be approved. The AWG has responded to these critiques, but its criteria for defining the "Anthropocene" remain unaddressed (Zalasiewicz et al., 2017b).

However, the idea of the "Anthropocene" is so extended at all levels, including the scientific, that in all probability, it is going to be used independently of being ratified as a geological epoch. In the words of Ruddiman et al. (2015), "the Anthropocene is here to stay." The term is widely used in a broad range of disciplines as if it were already an approved term, without quotation marks, and with meanings that vary according to the discipline; everybody adapts it to his or her needs. The "Anthropocene" has become a kind of wild card used to refer to highly diverse ideas, such as a new historical phase of humanity, an expression of modernity, an attack against the Earth System, a biological condition inherent to human nature, an assault on human rights, a logical consequence of global capitalism and consumerism, or a definite breach between human and environmental well-being (Autin, 2016). In this situation, any criticism of the "Anthropocene", even if it is purely scientific and aims only to clarify things, comes across as a denial of human influence over the planet and puts the critics in the same category as those who deny anthropogenic climate change under the leadership of ultraconservative defenders of wild capitalism and nature's indiscriminate exploitation. The "Anthropocene", if used incorrectly, could become a dogmatic, even fundamentalist ideological orthodoxy (Monasterski, 2015). High circles of the ICS and IUGS are perfectly aware of this danger and know that if the proposal of the AWG is rejected, even on the basis of failing to fulfill the criteria of official ICC units, they will be regarded as part of a largely unpopular, reactionary group. Although there is still some time until the AWG presents its proposal, Stanley Finney, the former president of the ICS, member of the Executive Committee of the IUGS, and the one entrusted with the task of making the final decision (Fig. 6.4), said that he feels like "... a lighthouse with a huge tsunami wave coming at it ..." (Voosen, 2016). To avoid these kinds of misunderstandings, it becomes crucial to state clearly what the "Anthropocene" is and what it is not.

6.3.3 What is and what is not the "Anthropocene"?

Let us clear up some concepts. What is the "Anthropocene"? It is an unofficial geological term that the AWG is trying to define, to be proposed to the ICS–IUGS for its formalization as a new geological epoch following the Holocene. What is not the "Anthropocene"? All the rest. Anyone referring to anything else must look for a new term. In stratigraphy, the suffix "-cene" is reserved exclusively for the geologic epochs of the Cenozoic Era (Paleocene, Eocene, Oligocene, Miocene, Pliocene, Pleistocene, and Holocene), and it cannot be used for other terms or concepts. If we wanted to talk about an epoch of human history that chronologically coincided with the "Anthropocene", as provisionally defined by the AWG, we could use terms such as "Great Acceleration" or "Atomic Era", which are free from geological connotations. If this new epoch is ultimately formalized, we will be able to use the term at our pleasure and without quotation marks, but always as a geological epoch, nothing else. Any other use, however popular it might be, would be incorrect. But if we want to forecast the future, and that is what we are doing in this chapter, we can boldly predict that, knowing human nature, very few will pay attention to scientific rigor, and people will use the term at whim in the same way that they follow traffic rules and do many other things in everyday life. It is an easy prediction, first, because it is already happening, and second, because most people comply with the law because they fear the consequences and not because they believe in it, and the incorrect use of scientific terms is not punishable (if we do not consider failing some exams).

6.4 Synthesis: between science fiction and the "Anthropocene"

In this chapter, we analyzed possible future consequences of human activities for the Earth System, more precisely for the natural variability of the climate represented by glacial cycles. We used the results of recent modeling studies and a bit of science fiction (which is also a kind of modeling), always within the limits of empirically based knowledge discussed throughout this book. Models confirm the opinions that foresee a significant delay (approximately 40,000 years) of the next glaciation or even its "indefinite delay." As our ability to purposefully redirect this situation is fairly questionable, we examined the possibility that our influence over the climate and the planet will be avoided or reduced in a natural manner. The most efficient option seems to be the relatively fast extinction of our species by an exogenous catastrophe, which is unpredictable. Another productive alternative could be a drastic reduction in the human population and its technological capacity. The only relatively predictable option here is the arrival of the next glaciation, but the mentioned models estimate a very long time before that can take place, if ever; so, we are likely to continue overexploiting and damaging the planet until its carrying capacity. The possibility of an evolutionary change in our species to reach a higher degree of conscience and a type of humanity that respects nature is too teleological and more becoming to moral or religious convictions. Everything points in the direction that the planet will have to suffer our presence for a long time. This notion has led some to believe that we are living in a new geological epoch, the "Anthropocene", characterized by a completely humanized Earth System. The proposal for the formalization of the new epoch is currently under development by the AWG. Once finished, it will be submitted to the ICS and the IUGS, which will decide whether or not the "Anthropocene" is formalized as the epoch following the Holocene, according to exclusively scientific (stratigraphic) criteria. There is a lot of controversy around this possibility, but the term "Anthropocene" is already widely used in many disciplines, both scientific and nonscientific, despite being an unofficial term, which is not likely to change independently of its formalization.

References

Autin, W.J., 2016. Multiple dichotomies of the Anthropocene. Anthropocene Rev. 3, 218−230.
Crutzen, P.J., Stoermer, E.F., 2000. The "Anthropocene". IGBP Newsl. 41, 17−18.
Donlan, C.J., Berger, J., Bock, C.E., Bock, J.H., Burney, D.A., Estes, J.A., et al., 2006. Pleistocene rewilding: an optimistic agenda for twenty-first century conservation. Am. Naturalist 168, 660−681.
Edwards, L.E., 2015. What is the Anthropocene? EOS 96, 6−7.

Finney, S.C., 2014. The "Anthropocene" as a ratified unit of the ICS International Stratigraphic Chart: fundamental issues that must be addressed by the Task Group. In: Waters, C.N., Zalasiewicz, J., Williams, M., Ellis, M.A., Snelling, A.M. (Eds.), A Stratigraphical Basis for the Anthropocene. Geological Society, London, pp. 23−28.

Finney, S.C., Edwards, L.E., 2016. The "Anthropocene" epoch: scientific decision or political statement. GSA Today 26, 4−10.

Gibbard, P.L., Walker, M.J.C., 2014. The term "Anthropocene" in the context of formal geological classification. In: Waters, C.N., Zalasiewicz, J., Williams, M., Ellis, M.A., Snelling, A.M. (Eds.), A Stratigraphical Basis for the Anthropocene. Geological Society, London, pp. 29−37.

Haqq-Misra, J., 2014. Damping of glacial-interglacial cycles from anthropogenic forcing. J. Adv. Model. Earth Syst. 6, 950−955.

Herrero, C., García-Olivares, A., Pelegrí, J.-L., 2014. Impact of anthropogenic CO_2 on the next glacial cycle. Clim. Change 122, 283−298.

Kidder, D.L., Worsley, T.R., 2014. A human-induced hothouse climate? GSA Today 22, 4−11.

Kováč, L., 2019. The biology of dying democracies. EMBO Rep. 20, e48934.

Monasterski, R., 2015. Anthropocene: the human age. Nature 519, 144−147.

Nekola, J.C., Allen, C.D., Brown, J.H., Burger, J.R., Davidson, A.D., Fristoe, T.S., et al., 2013. The Malthusian-Darwinian dynamic and the trajectory of civilization. Trends Ecol. Evol. 28, 127−130.

Ruddiman, W.F., 2003. The anthropogenic greenhouse era began thousands of years ago. Clim. Change 61, 261−293.

Ruddiman, W.F., 2013. The Anthropocene. Annu. Rev. Earth Planet. Sci. 41, 45−68.

Ruddiman, W.F., Ellis, E.C., Kaplan, J.O., Fuller, D.Q., 2015. Defining the epoch we live in. Is a formally designated Anthropocene a good idea? Science, 348. pp. 38−39.

Rull, V., 2009. Beyond us. EMBO Rep. 11, 1191−1195.

Rull, V., 2011. Sustainability, capitalism and evolution. EMBO Rep. 12, 103−106.

Rull, V., 2013. Are we willing to build a better future? Trends Ecol. Evol. 28, 443−444.

Rull, V., 2014. Conservation, human values and democracy. EMBO Rep. 15, 17−20.

Rull, V., 2018. What if the "Anthropocene" is not formalized as a new geological series/epoch? Quaternary 1, 24.

Steffen, W., Rockström, J., Richardson, K., Lenton, T.M., Folke, C., Liverman, D., et al., 2018. Trajectories of the earth system in the Anthropocene. Proc. Natl. Acad. Sci. U.S.A. 115, 8252−8259.

Stephens, L., Fuller, D., Boivin, N., Rick, T., Gauthier, N., Kay, A., 2019. Archaeological Assessment reveals Earth's early transformation through land use. Science 365, 897−902.

Stoppani, A., 1873. Corso di Geologia. Vol. II, Geologia Stratigrafica. G. Bernardoni eG. Brigola Ed., Milano.

Tzedakis, P.C., Channell, J.E.T., Hoddell, D.A., Kleiven, H.F., Skinner, L.C., 2012. Determining the natural length of the current interglacial. Nat. Geosci. 5, 138−141.

Vegas-Vilarrúbia, T., Rull, V., Montoya, E., Safont, E., 2011. Quaternary palaeoecology and nature conservation: a general review with example from the Neotropics. Quat. Sci. Rev. 30, 2361−2388.

Voosen, P., 2016. Atomic bombs and oil addiction herald earth's new epoch: the Anthropocene. Science. Available from: https://doi.org/10.1126/science.aah7220.

Waters, C.N., Zalasiewicz, J., Summerhayes, C., Fairchild, I.J., Rose, N.L., Loader, N.J., et al., 2018. Global Boundary Stratotype Section and Point (GSSP) for the Anthropocene series: where and how to look for potential candidates. Earth-Sci. Rev. 178, 379−429.

Willis, K.J., Bailey, R.M., Bhagwat, S.A., Birks, H.J.B., 2010. Biodiversity baselines, thresholds and resilience: testing predictions and assumptions using palaeoecological data. Trends Ecol. Evol. 25, 583−591.

Zalasiewicz, J., Waters, C., Summerhayes, C.P., Wolfe, A.P., Barnosky, A.D., Cearreta, A., et al., 2017a. The Working Group on the Anthropocene: summary of evidence and interim recommendations. Anthropocene 19, 55−60.

Zalasiewicz, J., Waters, C.N., Wolfe, A.P., Barnosky, A.D., Cearreta, A., Edgeworth, M., et al., 2017b. Making the case for a formal Anthropocene Epoch: an analysis of the ongoing critiques. Newsl. Stratigr. 50, 205−226.

Epilogue

The missing link between ecology and evolution

There is a latent aspect to everything discussed in this book that might not have been highlighted enough but underlies any comparative analysis of ecology and evolution. Traditionally, these two disciplines were differentiated on the basis of a temporal criterion that separates ecological time (also called real time) and evolutionary time (also known as deep time). There seems to be a huge gap between these two timeframes, similar to the above-discussed breach among past, present, and future. Ecological or real time covers time periods considered in ecology, which reach the level of microevolutionary events at most (Section 3.1.1). Deep time, on the other hand, starts at the level of speciation (i.e., macroevolution). Once again, it is a scientific specialization and not a biological reality that determines our perception of time and its division. However, in reality, there is not a time when species evolve and another when they do not, in the same way that there is not a time in which species interact and another when they do not. Everything happens at the same time, and everything is in constant, and sometimes causal, interaction at all space-timescales. We must get used to complexity because this is how things work in our biological world. The separation of macro- and microevolutionary phenomena is hardly useful in understanding biological reality; it is actually confusing and leads to unnecessary controversy (Jablonski, 2000). Ecology and evolution have acted hand in hand throughout the history of the biosphere. Their separation for purely practical (i.e., academic) reasons does not make any sense; it just distorts reality.

At the beginning of this century, Jackson (2000) introduced a third temporal category, Quaternary time or Q-time, to describe events that fit neither ecological time (for it was too short-scaled) nor deep time (for it was too long-scaled). In fact, Q-time is not a time interval but a time dimension, the dimension of Quaternary paleoecology (or long-term ecology, as used in this book) that encompasses a range between a few and 10^6 years (Fig. 1). If our objective is to understand the biosphere in its current state, this temporal dimension will be represented (mostly but not exclusively) by the Quaternary. But the same temporal dimension and

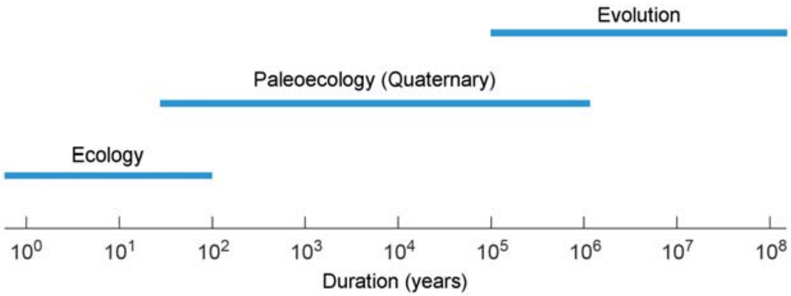

Figure 1 Time frames of ecology, evolution (both taken in the classical sense), and Quaternary paleoecology. *Modified and redrawn from Jackson and Blois (2016).*

the same ecological and evolutionary processes have been present throughout biological history. Therefore we can generalize Q-time as the particular expression of what we could call the intermediate time frame or the time interphase between ecology and evolution. Birks et al. (2010) called this temporal dimension the "lost dimension" of ecology. Rull (2014) considered Q-time as the "missing link" between ecology and evolution based on its much neglected capability to provide direct empirical evidence of processes that take place in the ecology—evolution interphase. Further, Jackson and Blois (2016) refer to this intermediate time frame as the "missing middle."

Ideally, the ecology—evolution interphase must be studied from a multidisciplinary perspective where the synergy between paleoecology and genomics might play a fundamental role in supplying empirical evidence (Rull, 2012). One way is the study of populations, where natural selection operates in the Darwinian sense (Section 3.1.1). Microevolutionary processes that take place during speciation cannot be detected by paleoecology either because the paleoecological record is too fragmented or because the quantitative genetic variations do not have phenotypic expression that could be discovered in the fossil record. In this situation, genomics can offer both modern analogs that can be applied to the study of past events and molecular evidence of the genetic structure of the population within a given species that may cause the segregation of lineages and represent incipient speciation processes. A good example of this kind of application can be found in the microevolutionary (population-level) processes documented during the postglacial colonization of continents after the last glaciation (Section 3.5.1). On the other hand, phylogeography can provide the evidence necessary to verify paleoecological hypotheses, such as the existence of glacial microrefugia that could explain the apparently unrealistic dispersal rates of the postglacial colonization of Europe and North America after the Last Glacial Maximum (Section 2.2.2). The unknown distribution and small size of these microrefugia make it practically impossible for a paleoecological study to find them, except by chance. However, a phylogeographical study of the affected species and their populations can detect areas of maximum genetic diversity that can be expected to be dispersal centers for subsequent colonization. In addition, the so-called ancient DNA (Section 3.6) extracted from some fossils (the number of which is increasing rapidly) can provide evidence of populations or species that do not leave other types of fossils behind, and this can bring us closer to the understanding of population paleoecology. For example, hybridization between *Homo sapiens* and *Homo neanderthalensis* (Section 5.3) was proven by the DNA extracted from their fossils together with studies of present-day DNA that demonstrated our Neanderthal legacy.

On the other hand, paleoecology establishes the appropriate context regarding environmental instability to understand biogeographical and phylogeographical patterns observed at the metacommunity level and considered static by many (neo)ecologists. Without this context, we could not fully understand the mechanisms and possible causes of community assembly and disassembly that took place under conditions of continual change, maintained disequilibrium and are the result of individual idiosyncratic dynamics at the species or population level. This is fundamental for the comprehension of possible ecological and evolutionary responses to climatic changes and their consequences for the composition of current and future communities in the context of Global Change. Succession is yet another process in which ecological and evolutionary mechanisms constantly interact with each other and relies on both paleoecology and genomics to be fully understood. Communities are in a continuous process of succession controlled by natural and/or anthropogenic processes. Evolution takes place in a successional context that, at the same time, is shaped by evolutionary changes. We can hardly hope to understand anything about the genesis of the present-day biological world without combining ecology and evolution, taking into account their permanent interaction. But, to date, neither ecology nor evolution, as a scientific discipline, has provided us with the appropriate time frame with which to decipher the interactive relationship between these two fundamental processes of the biosphere. We need an extra time dimension, the missing link between ecology and evolution, between real time and deep time.

To properly understand the current world in which we live, this intermediate time frame is the Quaternary.

Some (neo)ecologists and phylogeographers have already realized the importance of historical biogeography for the understanding of present ecological patterns and have also emphasized the need for interdisciplinary synergies. However, as already mentioned in the fourth chapter (Section 4.5.2), these scholars used to ignore the Quaternary timescale, paleoecological evidence, or both. Therefore in addition to a missing time dimension (i.e., the Quaternary), there is a missing discipline (i.e., paleoecology). Continued neglect of Quaternary paleoecology could result in a major loss of empirical evidence that would have been an invaluable and irreplaceable source of ecological and evolutionary information (Rull, 2014). Moreover, as has been seen throughout the book, Quaternary paleoecology goes far beyond supplying straightforward empirical data and provides new analytical approaches and ecological and evolutionary hypotheses, which would be impossible to envisage with only short-term observations and measurements. Therefore for interdisciplinary collaboration to be true, Quaternary paleoecology should be part of the game, both in empirical and conceptual terms. Otherwise, our view of the current biosphere and its possible future developments runs the risk of being quite myopic (Silvertown et al., 2010; Gillson and Marchant, 2014) and, therefore, highly distorted.

The Finnish ecologist Ilkka Hanski, well known for advancing and developing metapopulation research, attributed this type of human myopia to evolutionary causes and relied on education to fix the issue. Speaking about environmental threats, Hanski (2008) wrote

> *As humans, we are only able to perceive a small region of space and a short length of time. These limits to our sensual and cognitive capacities are the result of our biological evolution. Both our senses and our cognitive apparatus evolved in response to challenges in our immediate neighborhood — such as a predator hiding in tall grass or an upcoming thunderstorm — and they have served us well throughout most of our history. Today, we have vastly improved our knowledge in terms of both time and space: an educated human knows about scales as different as the age of the universe, the size of our solar system and the size of a cell. Yet, humans are not capable of coping with the global environmental deterioration that we are inflicting upon ourselves. I therefore argue that the most prevalent threats to our societies and our environment are caused by the mismatch between the vastly expanded range of human influence and our limited perception of the world, which is still no more advanced than that of our African ancestors living more than 100,000 years ago.*

In ecology, we should also be capable of overcoming our inherent temporal myopia by introducing Quaternary paleoecology into our lives. It is hoped that this book provides a sample of what Quaternary study may provide in this sense that it could be useful for incorporating a truly long-term ecological approach and for bridging the gap been ecology and evolution.

References

Birks, H.J.B., Heiri, O., Seppä, H., Bjunne, A.E., 2010. Strengths and weaknesses of quantitative climate reconstructions based on Late-Quaternary biological proxies. Open. Ecol. J. 3, 68–110.

Gillson, L., Marchant, R., 2014. From myopia to clarity: sharpening the focus of ecosystem management through the lens of palaeoecology. Trends Ecol. Evol. 29, 317–325.

Jablonski, D., 2000. Micro- and macroevolution: scale and hierarchy in evolutionary biology and paleobiology. Paleobiology 26, 15–52.

Jackson, S.T., 2000. Integrating ecological dynamics across timescales: real-time, Q-time, and deep-time. Palaios 16, 1–2.

Jackson, S.T., Blois, J.L., 2016. Community ecology in a changing environment: perspectives from the Quaternary. Proc. Natl. Acad. Sci. U.S.A. 112, 4015–4021.

Hanski, I., 2008. The world that became ruined. EMBO Rep. 9, S34–S36.

Rull, V., 2012. Community ecology: diversity and dynamics over time. Commun. Ecol. 13, 102–116.

Rull, V., 2014. Ecological palaeoecology: a missing link between ecology and evolution. Collectanea Bot. 33, 65–73.

Silvertown, J., Tallowin, J., Stevens, C., Power, S.A., Morgan, V., Emmett, B., et al., 2010. Environmental myopia: a diagnosis and a remedy. Trends Ecol. Evol. 25, 556–561.

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QUATERNARY ECOLOGY, EVOLUTION, AND BIOGEOGRAPHY

Valentí Rull

A comprehensive assessment of ecological–evolutionary interplay under the influence of Quaternary climate changes

- Includes the latest developments in genomics and their relevance within Quaternary evolution
- Offers a holistic view of the origin of biodiversity patterns and community assembly
- Discusses the role of climate on human evolution and the ecological consequences for natural systems

Quaternary Ecology, Evolution, and Biogeography offers an introduction to the study of the ecological and evolutionary processes that have shaped our present biosphere under the influence of glacial–interglacial cycles. Written by an ecologist with paleoecological expertise, this book reviews the climactic changes that have occurred during the last 2.6 million years, along with the responses of organisms and ecosystems. It offers an understanding of the evolutionary origin of extant biodiversity, its biogeographical patterns, and the composition of modern ecological communities. In addition, it explores human evolution and the influence of our activities on the biosphere, especially in the last millennia.

This book offers the latest information on how studying the past can contribute to our understanding of present climate issues for a better future, and is an ideal resource for researchers and students in the natural sciences.

About the author

Valentí Rull is a biologist with a PhD in paleoecology. He is a senior researcher of the Spanish Council for Scientific Research (CSIC) at the Institute of Earth Sciences Jaume Almera, Barcelona. He uses paleoecological evidence to study the type and characteristics of biotic responses to environmental shifts, the natural and anthropogenic drivers of ecological change, and the role of tectonics and environmental change on the origin of biodiversity. He also works on the contribution of paleoecology to biodiversity conservation. Dr. Rull has conducted his research on several temperate (Pyrenees, Azores Islands), tropical (Andes, Orinoco delta, Maracaibo basin, Gran Sabana, Pantepui), and subtropical (Easter Island) regions.

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