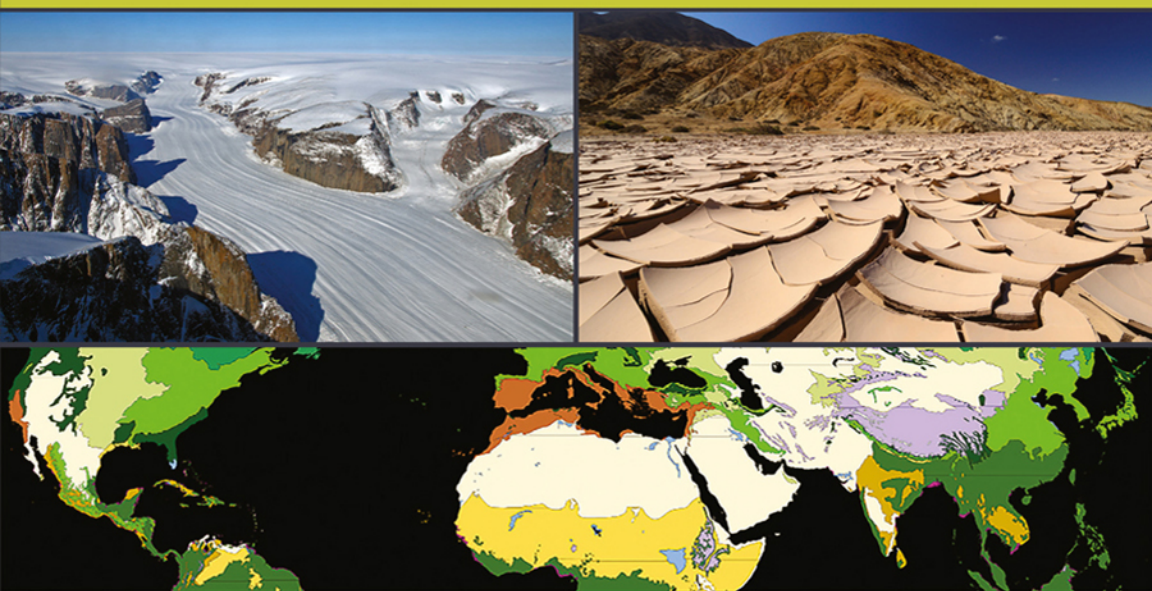


Valentí Rull

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 an 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.

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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.

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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 climatic 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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