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Mountains, Climate and Biodiversity: An Introduction

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Abstract

Mountains harbor about one-quarter of all terrestrial species in about a tenth of the world's continental surface outside Antarctica. This disproportionate diversity makes mountains a focal point for research on the generation and maintenance of biodiversity. Some of the key features that make mountains so biologically diverse are the elevational gradient, physiographic and climatic diversity, and prolonged isolation of their peaks and valleys. These features reflect the complex interactions between plate tectonics and mountain building, climate change and erosion over time scales extending to millions of years. It is now widely accepted that these large-scale processes play a fundamental role in biotic evolution across space and time. Together with ecological interactions among organisms, they form the basis for modern biogeography. But why, when and how the interactions between the geosphere, biosphere and atmosphere resulted in such high biodiversity in mountains is insufficiently understood. In this book, a multidisciplinary team of authors discusses the state of research at the interface between the geo- and biospheres and addresses these and other questions, while presenting examples from mountain systems around the world.

Keywords: *mountain building, biodiversity, plate tectonics, geo-biodiversity*

1.1 Introduction

Can you imagine a world without mountains? It would undoubtedly be a much less diverse place in terms of biomes, habitats and species. Mountains are the cradles of all major river systems, they are the central determinants of regional- and continental-scale climate and they comprise many unique biomes (Figure 1.1). They generate massive influxes of sediment that are divulged into adjacent territories (e.g., from the Andes across the Amazon basin, and from the Rockies into the Great Plains). For these reasons, the effects of mountains reach well beyond their immediate slopes (Gentry 1982; Finarelli & Badgley 2010; Hoorn et al. 2010).

Mountains also have a dual role in that they both generate and receive biodiversity (Hoorn et al. 2013). On

one hand, they can generate diversity through in situ adaptations and diversification, subsequently providing neighboring regions with new lineages (e.g. Antonelli et al. 2009; Santos et al. 2009). On the other, they are able to support pre-adapted lineages from other mountain regions that arrive via long-distance dispersal (Merckx et al. 2015). Nevertheless, teasing apart the relative contributions of in situ diversification versus dispersal (Antonelli 2015), and assessing how and when different climatic and geological conditions influenced different regions, is a matter of intense research. Likewise, we are just beginning to understand how and when climate and tectonism interact, and how they together affect biodiversity.

The effect mountain building has on climate, and how these processes together influence the speciation, extinction and migration of different taxa, is hotly debated.

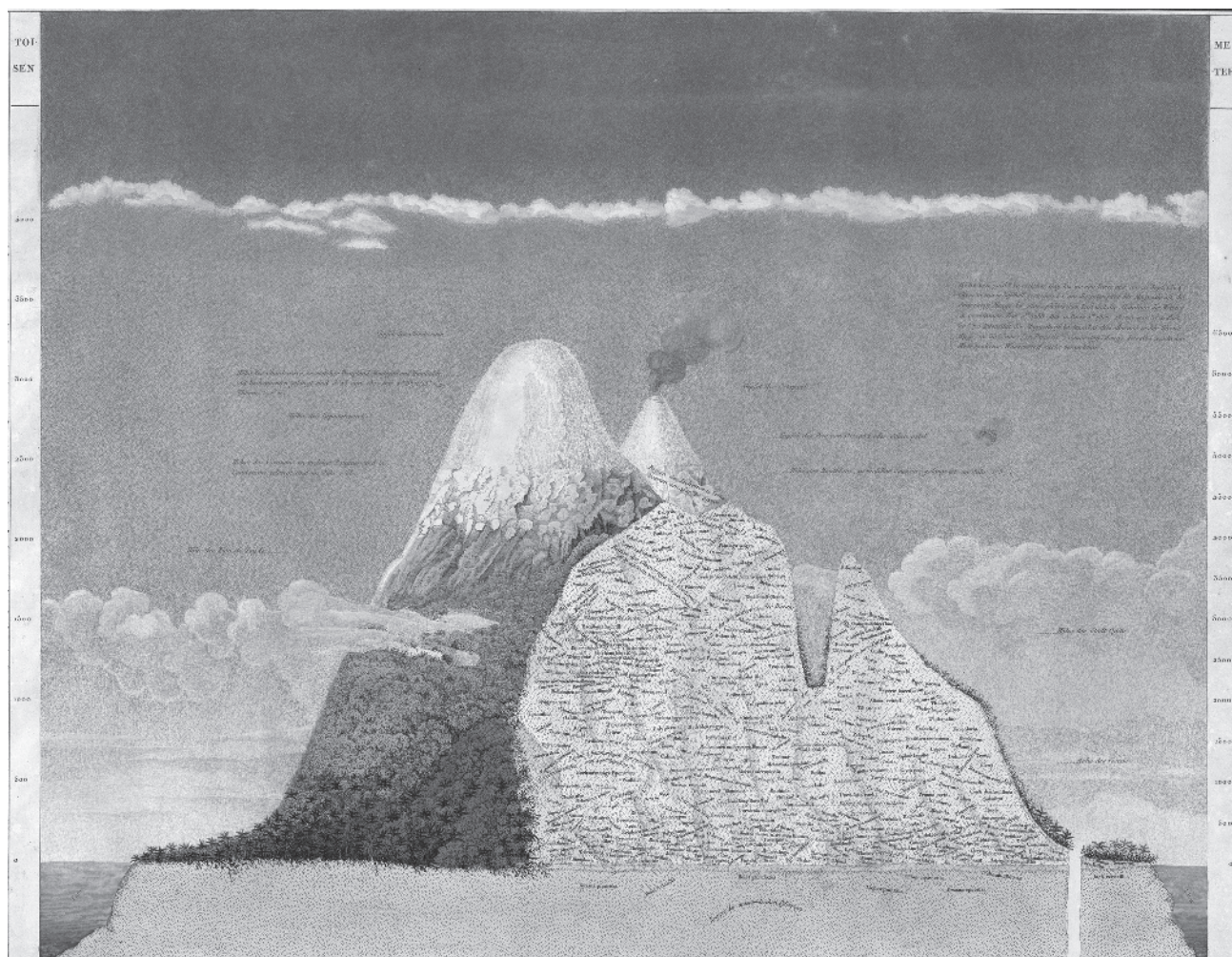


Figure 1.1 The center section of Humboldt’s classical tableau, illustrating a cross-section of the Chimborazo volcano in Ecuador, the highest mountain peak as measured from the center of the globe. This detailed drawing depicts one of the earliest studies of how the mountain biota is structured along an elevation gradient. Humboldt recognized the existence of distinct vegetation zones at different elevations with largely unique sets of species, constrained by climatic and physiological adaptations. This pioneering work is often considered a landmark in biogeography. *Source:* Humboldt & Bonpland (1807). See also Plate 1 in color plate section.

A number of studies have touched on some or many aspects of this set of interactions (Hughes & Atchison 2015; Hughes 2016; Lagomarsino et al. 2016), yet none has fully addressed the complexity of the field in a single work. We have therefore commissioned 31 peer-reviewed chapters that, when taken as a whole, address this need.

One of the fundamental questions to address is: *How can we untangle mountain building and climate change, and what influence did each of these processes have on biological diversification?* It has been known for some time that Plio–Pleistocene climate change is responsible for pronounced changes in relief and a vast increase in global erosion rates (Molnar & England 1990). However, in recent years, mountain uplift, rates of erosion and paleoaltitude have begun to be measured more accu-

rately, thanks to advances in analytical methods in geosciences (e.g., in the fields of isotope and fission-track analysis) (Gosse & Stone 2001; McElwain 2004; Reiners & Brandon 2006; Forest 2007; Polissar et al. 2009; Lomax et al. 2012; Mulch 2016). These developments have enabled a global assessment of the timing and geographic extent of mountain building, erosion and relief (Herman et al. 2013; Herman & Champagnac 2015). Together, the data thus obtained provide a geohistorical guideline that helps to improve models of biotic evolution. Accurate mountain uplift ages have already been successfully applied in the context of molecular phylogenetic studies that test for the influence of surface uplift on species diversification (Lagomarsino et al. 2016).

Other major questions include: *When did taxa evolve, how did they respond to the ecological opportunities*

that followed from mountain building and what were their geographic distributions through time? The generation of novel, carefully sampled biological data from extant species, together with improved databases on the fossil record – including enhanced geochronology from the Neotoma Paleocology database, the Paleobiology database and Neclime, to name but a few – offers new perspectives on biotic evolution in mountain regions (e.g., Favre et al. 2015; Flantua et al. 2015). This, combined with new methods for predicting diversification and range evolution based on fossil records (e.g. Silvestro et al. 2016) and molecular sequences (e.g. Antonelli et al. 2016; Morlon et al. 2016) and methods for cleaning and processing vast amounts of extant species-occurrence data (Töpel et al. 2016), provides researchers with valuable tools and data for testing specific hypotheses on the evolution of mountain biodiversity.

Finally, determining the relative roles of abiotic and biotic processes in the assembly, generation and maintenance of biodiversity is a central task in understanding

biological distributions, and it forms the core of this book. Here, specialists from different disciplines have joined forces to synthesize the current knowledge on mountain building, climate and biodiversity. To help the reader through this cross-disciplinary volume, the text is accompanied by a glossary of terms and a geological time scale (see back-cover inset).

1.2 What are Mountains?

Mountains are defined as “landforms that rise prominently above their surroundings, generally exhibiting steep slopes, a relatively confined summit area, and considerable local relief” (Molnar 2015). They cover over a tenth of the continental surface of the Earth (Figure 1.2), based on a recent evaluation by Körner et al. (2016), who used the ruggedness of Earth’s terrestrial surface, excluding Antarctica, as the constraining feature for identifying “mountains” (Figure 1.3). Based on this estimate, they calculated that mountains cover

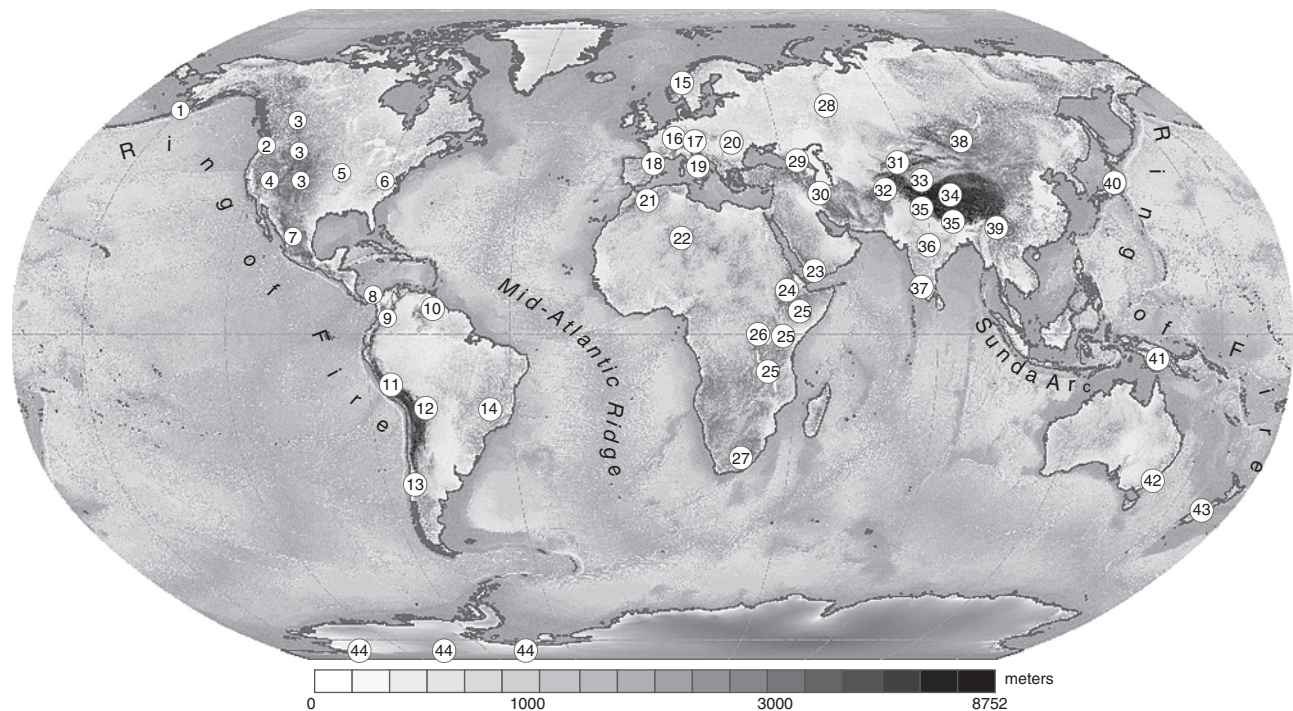


Figure 1.2 A selection of the most prominent mountain systems on Earth, as well as several other major geologic features and systems discussed throughout this book (image courtesy Suzette Flantua). Americas: 1, Aleutian Arc; 2, Cascades; 3, Rocky Mountains (Rockies); 4, Basin and Range Province; 5, Great Plains; 6, Appalachians; 7, Sierra Madre; 8, Panama Isthmus; 9, Northern Andes; 10, Guiana Highlands; 11, Central Andes; 12, Bolivian Altiplano; 13, Southern Andes; 14, Brazilian Highlands. Europe: 15, Scandinavian Mountains; 16, Jura Mountains; 17, Alps; 18, Pyrenees; 19, Apennines; 20, Carpathians. Africa-Arabia: 21, Atlas Mountains; 22, Ahaggar (Hoggar) Mountains; 23, Yemen Highlands; 24, Ethiopian Highlands; 25, East African Rift System (EARS); 26, Rwenzori Mountains; 27, Drakensberg. Asia: 28, Ural Mountains; 29, Caucasus Mountains; 30, Zagros Mountains; 31, Tien Shan; 32, Hindu Kush; 33, Kunlun Shan; 34, Tibetan Plateau; 35, Himalaya; 36, Deccan Plateau; 37, Western and Eastern Ghats; 38, Altai Mountains; 39, Hengduan Mountains; 40, Japanese Alps. Oceania: 41, New Guinea Highlands; 42, Eastern Highlands (Australia); 43, Southern Alps. Antarctica: 44, Transantarctic Mountains. See also Plate 2 in color plate section.

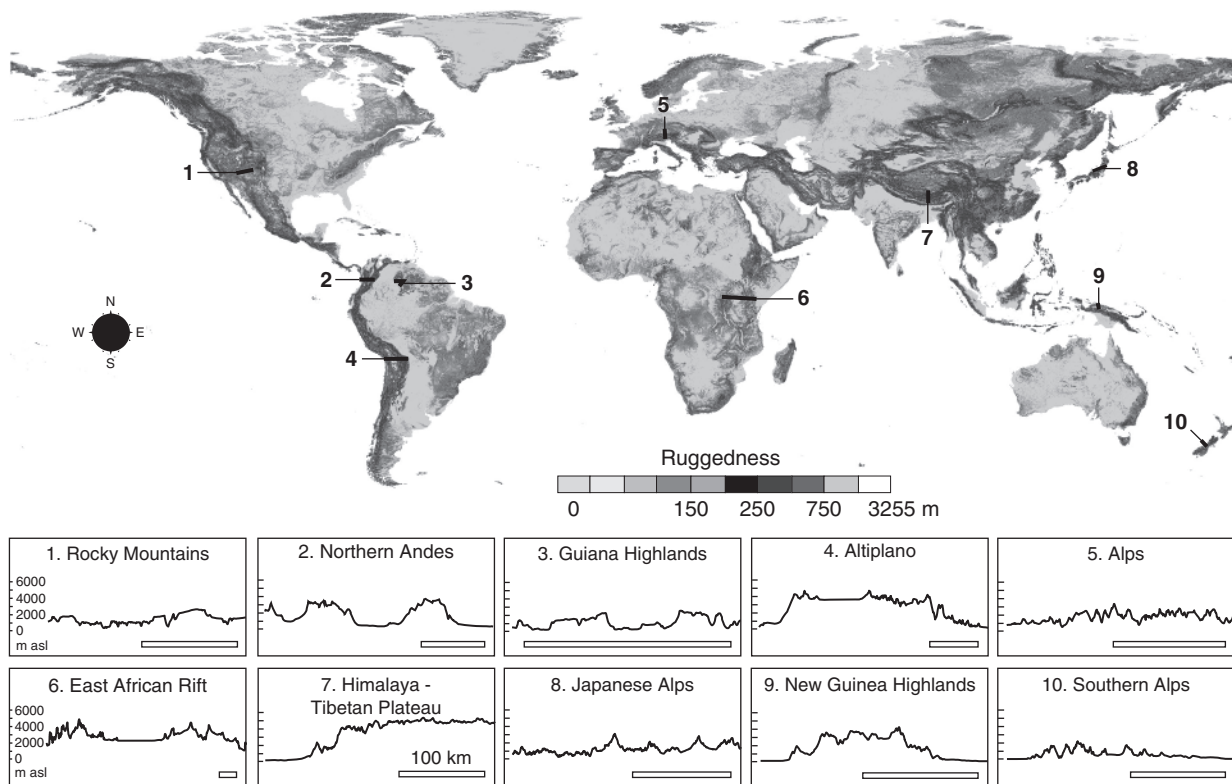


Figure 1.3 Mountain areas based on ruggedness, as defined by Körner et al. (2011) (maximal elevational distance between nine grid points of 30" in 2.5' pixel; for a 2.5' pixel to be defined as "rugged" (i.e., mountainous), the difference between the lowest and highest of the nine points must exceed 200 m). Numbers indicate topographic profiles of selected mountain ranges around the world. The characteristic topography of a mountain directly relates to the potential impact and frequency of connectivity breaks caused by Pleistocene glacial cycles, and thus the expression of the flickering connectivity system. Bars below profiles indicate a 100 km distance proportional to the profile shown. *Source:* Adapted from Körner et al. (2011). Figure from Chapter 12. See also Plate 3 in color plate section.

13.8 million km² of Earth's land surface (12.5%), of which 3.3 million km² comprises alpine and nival belts.

Mountains are topographically complex, and are often rich in biodiversity. Barthlott et al. (1996, 2005) related this topographic complexity – or geodiversity (see also Gray 2004) – directly to biodiversity. Based on 100 × 100 km species-richness data, Barthlott et al. (1996, 2005) identified five global centres of vascular plant diversity, all of which are situated in or adjacent to mountainous regions (Figure 1.4a). Körner & Ohsawa (2006) and Körner et al. (2016) further estimated that half of all biodiversity hotspots (as defined by Myers et al. 2000) and a quarter of all terrestrial biodiversity is situated in mountains. Moreover, mountains host some of the most diverse ("hottest") biodiversity hotspots on the planet, including the tropical Andes and the Hengduan Mountains (Barthlott et al. 1996, 2005; Hughes & Eastwood 2006; Spehn et al. 2010, 2011; Madriñán et al. 2013; Hughes & Atchinson 2015). Recently, Badgley et al. (2017) presented a four-part framework under which

the processes that lead to this relationship between topographic complexity and high levels of biodiversity can be robustly assessed.

The connection between mountains and biodiversity is also seen in several taxa with well-understood species-richness patterns. These include mammals, birds and amphibians (extensive data on species ranges are accessible from www.iucnredlist.org and www.birdlife.org). However, as with hotspots, in making such connections it is important to consider that humans have influenced the distribution of many species (Faurby & Svenning 2015). The European brown bear *Ursus arctos*, for instance, once had a much wider distribution in Europe, but is presently mainly confined to mountainous regions due to anthropogenic pressure. However, when the anthropogenic modifications to species ranges are excluded, the correlation between mountainous regions and mammal diversity is evident (Figure 1.4b). While humans may have exaggerated the pattern of montane diversity, we clearly did not create it.

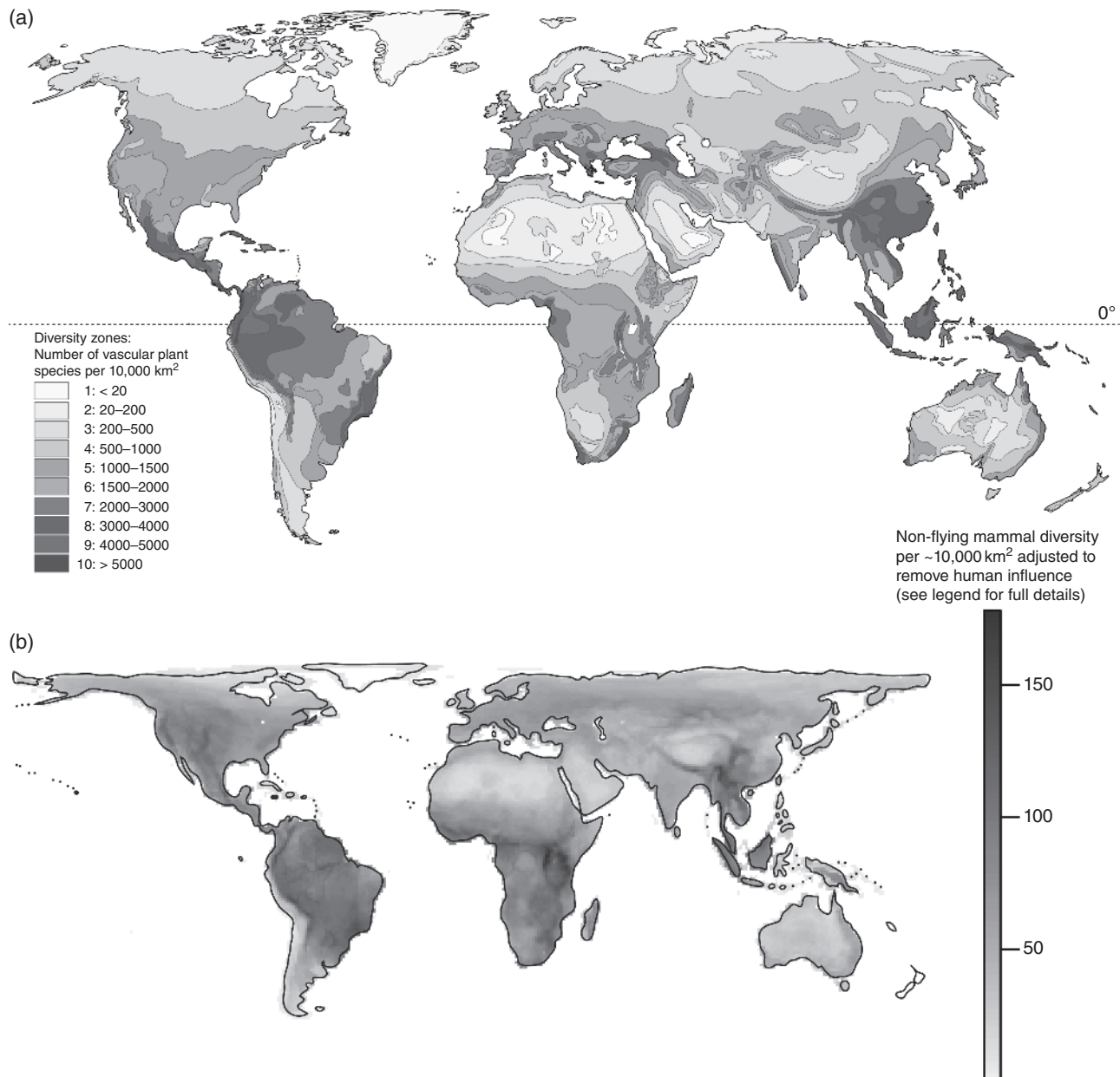


Figure 1.4 (a) Global plant diversity measured by estimated number of vascular plant species per 10,000 km². *Source:* Barthlott et al. (1996, 2007), with permission from Wilhelm Barthlott and Jens Mutke. (b) Estimated patterns of species diversity for terrestrial mammals. This map was constructed using estimated natural species ranges without human influences, and plotted using an equal-area Behrmann projection with colors proportional to the number of expected species. Several mountain regions have noticeably higher diversity than surrounding areas (e.g., the Rocky Mountains and Sierra Nevada in North America, the Andes in South America and, in particular, the East African Rift System). *Source:* Modified from Faurby & Svenning (2015), with permission from Søren Faurby. See also Plate 4 in color plate section.

1.3 The Physiography of Mountains and Patterns of Biodiversity

Mountains are natural barriers, characterized by their elevation gradients, their physiographic complexity and the changes in climate and environment that they cause through time. These factors influence the distribution

and diversification of species, and also make mountains suitable for maintaining biodiversity over time. This is particularly pronounced in the tropics, where a species only needs to move relatively small distances to remain within its preferred niche space during periods of rapid climate change, as compared to species in the lowlands (Sandel et al. 2011; Condamine et al. 2016).

By the 19th century, Alexander von Humboldt had already recognized the important relationship between plant diversity, complex topography and climate (Figure 1.1) (Mutke 2010). Over the course of the 20th century, however, the role of geological processes was gradually segregated from biodiversity research, with paleontology, geology and biogeography seldom considered in ecological theory (Ricklefs 1987, 2004). In spite of this general trend, certain themes were recognized and expanded on during the 20th century, which can now be integrated in order to provide a better understanding of the complex biodiversity patterns in mountains.

It has been known since the 19th century that physiography relates to species richness, but the relevance of this notion has become eclipsed over time. Inspired by the theory of island biogeography proposed by MacArthur and Wilson (1963, 1967), Ricklefs (1977) coined the term “environmental heterogeneity” (EH), reviving the idea that a species can be excluded from a region due to environmental or evolutionary change. Ricklefs’ (re)introduction of EH was a revolutionary step in ecology, as it renewed the debate on the relevance of geological processes in time and space as drivers for species richness and distribution. Later, Ricklefs (1987, 2004, 2005) concluded that despite long-term resistance to the idea from ecologists, large-scale regional and historical processes influence regional biodiversity, and that regional and local diversity are directly connected. Previously, large-scale processes had been considered too weak to influence the equilibrium that was achieved by local processes. Nevertheless, Ricklefs explained that patterns of biodiversity can only be properly interpreted within the broad context of regional and historical influences.

Many studies now recognize the importance of EH (see Tews et al. 2004 and Stein & Kreft 2015 for overviews) – including variation along the elevational gradient (EG) – in mountain biodiversity. The EG consists of gradual changes in the environment with increasing elevation along a mountain slope. Along an EG, biodiversity can be quantified in relation to hydrological, geochemical, climatological, topographical and edaphological factors, among others (Hughes & Eastwood 2006; Kreft & Jetz 2007; Kupfer 2010; Mutke 2010; Mutke et al. 2011; Moeslund et al. 2013; Flantua et al. 2014; Stein & Kreft 2015). However, the taxonomic coverage of a study is important to its interpretation. Recently, Peters et al. (2016) showed that at community level, temperature came out as the strongest driver for species diversity along the EG on Mount Kilimanjaro. Although spatial EH and EG are now well studied, their changes through time and parallel impact on mountain biodiversity remain poorly understood.

Early naturalists, such as Humboldt, Linnaeus and also Tournefort, recognized the importance of the EG as an abiotic determinant of biodiversity in mountain regions. This gradient is most pronounced in the tropics and loses its dramatic effect at higher latitudes. As Janzen (1967) stated, “In respect to temperature, valleys may be figuratively deeper to an organism living on the ridge top in the tropics than in a temperate area”. The EG is characterized by a consistent decrease in temperature and air pressure as one moves upslope, whereas other climatic variables – such as solar radiation and precipitation – have a less consistent pattern (Körner 2003, 2007; McCain & Grytnes 2010). This differentiation in physical parameters along the EG is reflected in vegetation zones or belts.

Mountains often are conical, decreasing in area upslope (but see Elsen & Tingley 2015). The original concept derived from the south-western USA, where forested mountain peaks – or “sky islands” – were separated from a “sea” of desert; it is now expanded to include other regions with similar contrasting settings (McCormack et al. 2009). Although the classical species/area relationship would demand a decline in species towards the top of a mountain (see Lomolino 2000), in reality this does not occur. Meta-analyses of large floral and faunal data sets show that repeated isolation and connectivity between biomes favors endemism and colonization in sky islands (e.g., Steinbauer et al. 2016). In spite of this, the highest biodiversity is found in mountains at mid-elevation, where species of lower and higher altitudes meet (see Lomolino et al. 2010).

Mountains directly affect regional climate, because of the orographic barrier effect (Houze 2012). The orographic barrier redirects atmospheric masses, often by directing clouds upslope. At higher altitudes, these clouds cool, leading to precipitation. This process is particularly well studied in the Andes, where the South Monsoon and the South American Low-Level Jet are associated with the high Andes (e.g., Garreaud et al. 2008; Poulsen et al. 2010; Rohrmann et al. 2016). The effects of orographic rains extend into the tropical lowlands, leading to drainage modifications and high biodiversity (Hoorn et al. 2010). Mid-elevations in mountains are especially exposed to orographic rainfall, which makes them a suitable home for cloud forests rich in ferns (Kessler et al. 2016). For further details on mountain climatology in relation to modern plant assemblages and distribution, we refer the reader to Körner (2003, 2012) and Scherrer & Körner (2010).

Biota are not just passive recipients of physical and chemical changes in the environment and can also substantially influence the local and regional climate. These feedback effects occur through increases or decreases in albedo and evapotranspiration, and by fixing carbon

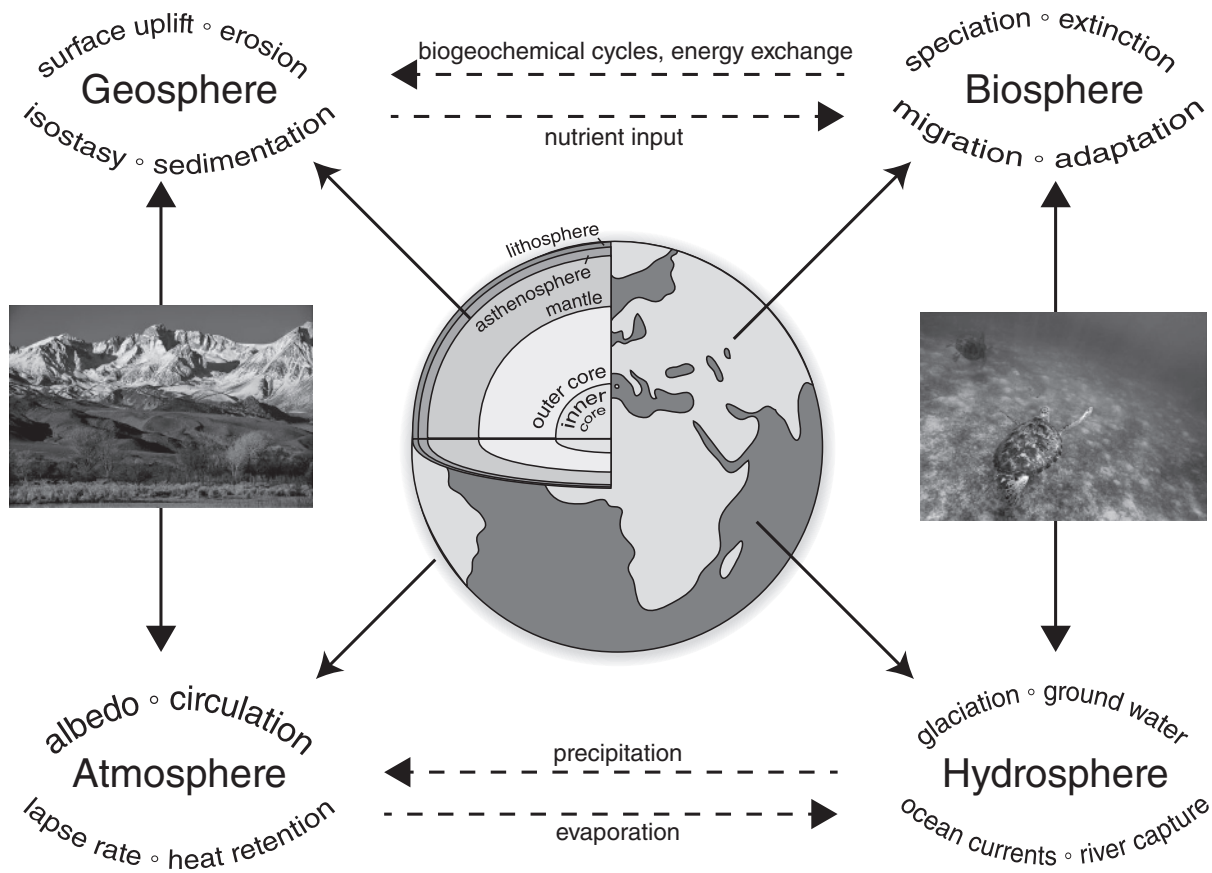


Figure 1.5 Schematic representation of the complex interaction between four of Earth's "spheres": the geosphere, biosphere, atmosphere and hydrosphere. Each sphere is surrounded by a selection of words indicating the terminology and processes associated with it. The Earth's layers are indicated in the cut-out, but are not drawn to scale. The lithosphere comprises the crust and the uppermost solid mantle. *Source:* Adapted from Senckenberg Magazine (2015). See also Plate 5 in color plate section.

(e.g., Malhi et al. 2002). Moreover, species also have a profound effect on the development of soils, on the biogeochemical cycles of nitrogen and other nutrients and on erosion and sedimentation processes (e.g., Durán-Zuazo & Rodríguez-Pleguezuelo 2007). These feedback mechanisms between the atmosphere, hydrosphere, geosphere and biosphere are illustrated in Figure 1.5.

1.4 Plate Tectonics, Mountain Building and the Biological (R)evolution

Plate tectonics are crucial for understanding biogeography and answering the question: *Why aren't all species found everywhere with a suitable habitat?* Although the breakup of the supercontinent Pangea and the later split of Gondwana and Laurasia seem something from the distant past, the biota of the modern world still carry their signatures. For example, they provide a plausible

explanation for why marsupials are found in both South America and Australia, and why penguins are not found on Greenland. Incidentally, both are derived from taxa that originated on the Gondwanan landmass and never dispersed with successful establishment on Laurasian landmasses. This is most evident in the recognition of biotic realms: continent-level regions containing similar sets of organisms at higher taxonomic levels. Their number, placement and limits were mapped by Wallace (1876), and later revised and refined by modern methods and large amounts of data (e.g., Holt et al. 2013).

Alfred Wegener was the first to recognize the relevance of plate tectonics in biological and climatic evolution (Wegener 1912; Köppen & Wegener 1924). Much later, Raven & Axelrod (1974) realized the importance of this global geological mechanism for biological distribution patterns. They presented a comprehensive review in which they evaluated the effects of continental drift on the current distribution of biodiversity, which constitutes a major contribution to the field now known as historical biogeography. More recently, the effect of plate

tectonics on determining deep biological differences among continents was confirmed by spatial regression analyses (Ficetola et al. 2017).

Areas of active tectonics are tightly associated with vicariance and dispersal, two processes by which a taxon comes to exist in its current range. Taxa that passively “rode” the diverging landmasses during continental breakups are considered vicariant, as are those whose distributions were physically disconnected by smaller-scale processes such as river re-routing (e.g., some Amazonian fishes: Albert et al. 2006). Vicariance occurs on both large (e.g., continental) and small (e.g., intra-mountain) scales, and is simply the result of a taxon breaking into several populations due to an emerging physical or ecological barrier, leading often to independent evolution and speciation. In contrast, species that actively or passively colonized novel environments – such as oceanic islands or sky islands, or via migration over land bridges – are said to have dispersed. In addition to these processes, range expansion and contraction, sympatric speciation and local extinction further influence local species richness and diversity.

Mountain building is an important driver of speciation through time and space (Van der Hammen et al. 1973; Raven & Axelrod 1974; Van der Hammen & Cleef 1986). In the past two decades, there has been an increased focus on the role of geological processes in montane biotic evolution (Winkworth et al. 2005; Linder 2008; Antonelli et al. 2009; Potter & Szatmari 2009; Djamali et al. 2012; Särkinen et al., 2012; Heenan & McGlone 2013; Hoorn et al. 2013; Madriñán et al. 2013; Luebert & Weigend 2014; Favre et al. 2015; Hughes & Atchison 2015; Merckx et al. 2015; Craw et al. 2016; Hughes 2016; Lagomarsino et al. 2016; Renner 2016), the effects of which extend well into adjacent continental basins (Gentry 1982; Kohn & Fremd 2007, 2008; Badgley 2010; Finarelli & Badgley 2010; Hoorn et al. 2010; Gates et al. 2012; Jacques et al. 2014) and marine environments (Clague 1996; Renema et al. 2008; Wright & Stigall 2013; Yasuhara et al. 2016).

The mechanisms of mountain building and their effect on geomorphology and on peripheral sedimentary basins are further summarized in Owens & Slaymaker (2004) and Johnson & Harley (2012).

1.5 Mountains, Climate and Biodiversity: A Short Overview

This book is divided into three parts. The first two deal with processes and theory, while the third presents location-specific examples from around the world. Part I primarily addresses geological and hydrological processes, and biological mechanisms are incorporated in Part II. Part III is made up of chapters that apply concepts from

the first two parts to exemplify how – by combining mountains, climate and biodiversity – we can arrive at a more holistic view of how montane biodiversity evolved.

Part I begins with a review of mountain and volcanic arc formation and isostasy – the equilibrium between the Earth’s crust and mantle – and how these processes control continental elevation (Chapters 2 and 3). Climate, weathering and erosion are important factors that continuously reshape relief and promote uplift, particularly in the past 3 million years (Chapter 4). The methods used to quantify exhumation, surface uplift and mass removal through novel geological techniques and methodologies, such as fission-track and isotope analysis, are introduced (Chapter 5), along with an explanation of stable isotope paleoaltimetry, used to infer past altitudes (Chapter 6). Information gleaned from these techniques, when included in biological models, can lead to novel insights into the coupling (and timing) of abiotic and biotic processes. In addition to geochemical methods, fossil leaves also make excellent indicators of past precipitation and temperature (Chapter 7), which give insights into past topographic complexity, altitudes and climatic gradients. Mountains alter the regional climate and have distinct climatic gradients along their slopes that are directly connected to biotic evolution (Chapter 8). On an even larger scale, global drivers of climatic change through time include the Earth’s surface reflectiveness (albedo), incoming solar radiation and atmospheric greenhouse gas contents, as they change over decades to million-year time scales (Chapter 9). The implications of this for the modern landscape and for biotic evolution are not yet well understood, but must be enormous.

In Part II, the key connections between topographic complexity, EG and biodiversity are explored. The concept of geodiversity underpins this part, and it is broadly defined and explored (Chapter 10). This is followed by a methodological introduction to geodiversity analysis and examples of how it can be used to predict biodiversity (Chapter 11). Over time, the highly diverse nature of mountains can be explained in a more process-oriented manner, focusing on the importance of shifting connectivity between mountain peaks during climatic change in the Pleistocene (Chapter 12). Different facets of EH and how isolation drives diversification patterns across mountains over shorter time scales play a major role (Chapter 13). High geodiversity is linked to high levels of biodiversity. The effects of the landscape and climate on past and future rates of diversification are explored in North American mammals (Chapter 14), and the components of this process are further decoupled by the separate estimations of speciation and extinction rates, as these do not necessarily respond similarly to environmental changes (Chapter 15). However, the time scales on which geological and evolutionary processes act may

differ by several orders of magnitude, and broad correlations of regions with similar geodiversity over time do not always have presently analogous patterns of biodiversity (Chapter 16). With this in mind, the focus moves to the relationship between biota and physiography. When looking at global-scale patterns, climatic stability directly relates to those areas with the highest overall endemism in bird taxa (Chapter 17), whereas for hummingbirds specifically, it is instead temperature that correlates best with speciation rates over time (Chapter 18). As topography changes, catastrophic events leave their mark on major features, with equally major effects on the local biodiversity. River capture is a rare but significant result of physiographic change, and can lead to increased diversity in lowland river basins, which are already among the most species-dense ecosystems on Earth (Chapter 19). Finally, the key concepts and pitfalls in measuring biodiversity across regions are explained (Chapter 20), leading in to the theory behind how species distributions are estimated and projected across space and time (Chapter 21), which can be used to forecast the effects of climate change and the potential of mountains as climate refugia.

Part III is organized following the historical landmasses – Gondwana and Laurasia – and presents case studies from mountain systems around the world. The large-scale relationships between mountains, climate and biodiversity become apparent. The selected mountain systems are mostly young, formed in the Cenozoic. However, examples of older systems, such as the tepuis in South America and the Transantarctic Mountains, are also included. The geologically recent uplift of the Isthmus of Panama led to the Great American Biotic Interchange, and united former Laurasian and Gondwanan elements: North and South America, respectively. However, the timing of the biotic interchange does not directly coincide with the uplift, as there was significant habitat disparity between the newly uplifted region and the areas it connected (Chapter 22). Likewise, the biodiversity found on top of the table-like tepui of northern South America does not entirely match with the expected “Lost World” scenario once envisioned: despite significant endemism in the region, there is also evidence of ongoing biotic exchange with surrounding ones (Chapter 23). Antarctica became an isolated continent starting about 50 million years ago. Once disconnected from South America and Australia, the temperate (almost tropical) setting in the Paleogene changed into the icy, biologically depleted environment of the present. The montane and alpine biota in the Transantarctic Mountains are a relic from a biodiverse past (Chapter 24). Another Gondwanan fragment, New Zealand, was mostly submerged after the breakup of the supercontinent. Significant parts of its

landmass did not re-emerge until the late Neogene, and it was around that time that the Southern Alps and their biota formed, as shown by the high rates of speciation in certain taxa (Chapter 25). Africa is the largest continent that derived from Gondwana, and is primarily formed by old continental crust. This stable cratonic crust is, however, breaking up along one of the most striking geological features in the world: the East African Rift System. The geological evolution of this system is intimately connected to the paleoenvironment, climate, biodiversity and human evolution on the continent (Chapter 26). Meanwhile, in the Northern Hemisphere, a close biological connection persisted across Eurasia throughout the Meso-Cenozoic. EGs in the Alps and the mountains of Eastern Asia are well recorded in floral records, and the regions maintained similar biotas until the onset of recent global climate variations. In the past ca. 3 My, climate variations drove many of the European taxa to extinction (Chapter 27). In the wake of the reduction in European taxa, the Tibeto-Himalayan region witnessed a period of diversification (Chapter 28). Likewise, Eastern China and Japan were united by land until relatively recently. Around 10 Ma, rifting separated these regions, but the common history of the mountain biota of Japan and Eastern China is still preserved in the resemblance between their modern floras (Chapters 29 and 30). The book concludes with a review of vegetation dynamics in Southeast Asia, a region that – like New Zealand and Japan – is dramatically deforming at the intersection of two tectonic plates. This region constitutes a crossroads of migration, but also includes long-recognized, distinct biogeographic barriers. Detailed reconstructions of the natural history of this region are now possible through the integration of molecular and geological data (Chapter 31).

1.6 Outlook

Biodiversity loss through climate change and the destruction of habitats is seen as a major societal challenge (Rockström et al. 2009). On humanity’s time scale, spanning hundreds to thousands of years, our actions are a threat to biodiversity through both landscape and climate changes. A large part of Earth’s biodiversity may be destroyed before we have even begun to understand its origins and evolution. Even though we are not the only players shaping the world around us, we must strive to understand our impact on global processes before it is too late.

The effect of current climatic and landscape changes on biodiversity is a hot topic in international scientific research and political agendas. Large amounts of funding have been devoted to reconstructing the relationship

between climate and biological diversity in order to make accurate projections of future scenarios. However, while climate is a dominant process that is visibly changing during our lifetimes, it is not the only mega-scale process affecting biodiversity. Over a longer time scale, spanning millions of years, processes such as plate tectonics, global climate and environmental changes have formed the world that we know, and these must be considered in order to properly understand present diversity and ongoing changes.

Biodiversity is transient and evolves continuously over different temporal and spatial scales (Benton 2009). Abiotic, mega-scale geodynamic processes, including mountain building, operate on the scales of entire continents and millions of years, heavily influencing the three major processes responsible for determining biodiversity: migration, speciation and extinction.

This book presents a compilation of contributed chapters from researchers in a variety of fields, studying different organisms and systems, who are all working towards the common goal of promoting a broader, combined view of geologic, climatic and biological processes and how these shape diversity. The advances showcased in this book permit us to develop a more informed and

comprehensive view on the topic, and to expand on the early ideas proposed in the 19th and 20th centuries by the pioneers of biogeography. Taken as a whole, *Mountains, Climate and Biodiversity* is intended as a handbook for current and future students, a reference and an inspiration for how the field can grow and develop.

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References

- Albert, J., Lovejoy, N.R. & Crampton, W.G.R. (2006) Miocene tectonism and the separation of cis- and trans-Andean river basins: evidence from Neotropical fishes. *Journal of South American Earth Sciences* **21**, 14–27.
- Antonelli, A. (2015) Multiple origins of mountain life. *Nature* **524**, 300–301.
- Antonelli, A., Nylander, J.A.A., Persson, C. & Sanmartin, I. (2009) Tracing the impact of the Andean uplift on Neotropical plant evolution. *Proceedings of the National Academy of Sciences* **106**, 9749–9754.
- Antonelli, A., Hettling, H., Condamine, F. et al. (2016) Towards a Self-Updating Platform for Estimating Rates of Speciation and Migration, Ages, and Relationships of Taxa (SUPERSMART). *Systematic Biology* syw066.
- Badgley, C. (2010) Tectonics, topography, and mammalian diversity. *Ecography* **33**, 220–231.
- Badgley, C., Smiley, T.M., Terry, R. et al. (2017). Biodiversity and topographic complexity: modern and geohistorical perspectives. *Trends in Ecology & Evolution* **32**, 211–226.
- Barthlott, W., Lauer, W. & Placke, A. (1996) Global distribution of species diversity in vascular plants: towards a world map of phytodiversity. *Erdkunde* **50**, 317–327.
- Barthlott, W., Mutke, J., Rafiqpoor M.D. et al. (2005) Global centers of vascular plant diversity. *Nova Acta Leopoldina NF* **92**, 61–83.
- Barthlott, W., Hostert, A., Kier, G. et al. (2007) Geographic patterns of vascular plant diversity at continental to global scales. *Erdkunde* **61**, 305–315.
- Benton, M.J. (2009) The Red Queen and the Court Jester: species diversity and the role of biotic and abiotic factors through time. *Science* **323**, 728–732.
- Clague, D.A. (1996) The growth and subsidence of the Hawaiian-Emperor volcanic chain. In: Keast, A. & Miller, S.E. (eds.) *The Origin and Evolution of Pacific Island Biotas, New Guinea to Eastern Polynesia: Patterns and Processes*. Amsterdam: SPB Academic Publishing, pp. 35–50.
- Condamine, F., Leslie, A.B. & Antonelli, A. (2016) Ancient islands acted as refugia and pumps for conifer diversity. *Cladistics* **33**, 69–92.
- Craw, D., Upton, P., Burrridge, C.P., Wallis, G.P. & Waters, J.M. (2016) Rapid biological speciation driven by tectonic evolution in New Zealand. *Nature Geoscience* **9**, 140–144.
- Djamali, M., Baumel, A., Brewer, S. et al. (2012) Ecological implications of *Cousinia* Cass. (Asteraceae) persistence through the last two glacial–interglacial cycles in the continental Middle East for the Irano-Turanian flora. *Review of Palaeobotany and Palynology* **172**, 10–20.
- Durán-Zuazo, V.H. & Rodríguez-Pleguezuelo, C.R. (2007) Soil-erosion and runoff prevention by plant

- covers. *A review. Agronomy for Sustainable Development* **28**, 65–86.
- Elsen, P.R. & Tingley, M.W. (2015) Global mountain topography and the fate of montane species under climate change. *Nature Climate Change* **5**, 772–776.
- Faurby, S. & Svenning, J.-C. (2015) Historic and prehistoric human-driven extinctions have reshaped global mammal diversity patterns. *Biodiversity Research* **21**, 1155–1166.
- Favre, A., Päckert, M., Pauls, S.U. et al. (2015) The role of the uplift of the Qinghai-Tibetan Plateau for the evolution of Tibetan biotas. *Biological Reviews* **90**, 236–253.
- Ficetola, G. F., Mazel, F. & Thuiller, W. (2017) Global determinants of zoogeographical boundaries. *Nature Ecology and Evolution* **1**, 0089.
- Finarelli, J.A. & Badgley, C. (2010) Diversity dynamics of Miocene mammals in relation to the history of tectonism and climate. *Proceedings of the Royal Society B* **277**, 2721–2726.
- Flantua, S.G.A., Hooghiemstra, H., Van Boxel, J.H., Cabrera, M., González-Carranza, Z. & González-Arango, C. (2014) Connectivity dynamics since the last glacial maximum in the Northern Andes. In: *Paleobotany and Biogeography: A Festschrift for Alan Graham in his 80th Year*. Monographs in Systematic Botany from the Missouri Botanical Garden 128, Missouri Botanical Garden, St. Louis, pp. 98–123.
- Flantua, S., Hooghiemstra, H., Grimm, E.C. et al. (2015) Updated site compilation of the Latin American Pollen Database; challenging new research. *Review of Palaeobotany and Palynology* **223**, 104–115.
- Forest, C.E. (2007) Paleoaltimetry: a review of thermodynamic methods. *Reviews in Mineralogy & Geochemistry* **66**, 173–193.
- Garreaud, R.D., Vuille, M., Compagnucci, R. & Marengo, J. (2008) Present-day South American climate. *Palaeogeography, Palaeoclimatology, Palaeoecology* **281**, 180–195.
- Gates, T.A., Prieto-Marquez, A. & Zanno, L.E. (2012) Mountain building triggered Late Cretaceous North American megaherbivore dinosaur radiation. *PLoS ONE* **7**, e42135.
- Gentry, A. (1982) Neotropical floristic diversity: phytogeographical connections between Central and South America, Pleistocene climatic fluctuations, or an accident of the Andean orogeny? *Annals of the Missouri Botanical Garden* **69**, 557–593.
- Gosse, J.C. & Stone, J.O. (2001) Terrestrial cosmogenic nuclide methods passing milestones toward paleoaltimetry. *Earth and Space Science News* **82**, 82–89.
- Gray, M. (2004) Defining Geodiversity. In: Grey, M. (ed.) *Geodiversity*. Chichester: John Wiley & Sons Ltd., pp. 1–9.
- Heenan, P.B. & McGlone, M.S. (2013) Evolution of New Zealand alpine and open-habitat plant species during the late Cenozoic. *New Zealand Journal of Ecology* **37**, 105–113.
- Herman, F. & Champagnac, J.-D. (2015) Plio-Pleistocene increase of erosion rates in mountain belts in response to climate change. *Terra Nova* **28**, 2–10.
- Herman, F., Seward, D., Valla, P.G. et al. (2013) Worldwide acceleration of mountain erosion under a cooling climate. *Nature* **504**, 423–426.
- Holt, B.G., Lessard, J.-P., Borregaard, M.K. et al. (2013) An update of Wallace's zoogeographic regions of the world. *Science* **339**, 74–78.
- Hoorn, C., Wesselingh, F.P., ter Steege, H. et al. (2010) Amazonia through time: Andean uplift, climate change, landscape evolution and biodiversity. *Science* **330**, 927–931.
- Hoorn, C., Mosbrugger, V., Mulch, A. & Antonelli, A. (2013) Mountain building and biodiversity. *Nature Geoscience* **6**, 154.
- Houze, R.A. (2012) Orographic effects on precipitating clouds. *Reviews of Geophysics* **50**, RG1001.
- Hughes, C.E. (2016) The tropical Andean plant diversity powerhouse. Commentary on Lagomarsino et al. *New Phytologist* **210**, 1152–1154.
- Hughes, C.E. & Atchison, G.W. (2015) The ubiquity of alpine plant radiations: from the Andes to the Hengduan Mountains. *New Phytologist* **207**, 275–282.
- Hughes C.E. & Eastwood R. (2006) Island radiation on a continental scale: exceptional rates of plant diversification after uplift of the Andes. *Proceedings of the National Academy of Sciences USA* **103**, 10334–10339.
- Humboldt, A. & Bonpland, A. (1807) *Geographie der Pflanzen in den Tropenländern*. Paris: Tübingen.
- Jacques, F.M.B., Su, T., Spicer, R.A. et al. (2014) Late Miocene southwestern Chinese floristic diversity shaped by the southeastern uplift of the Tibetan Plateau. *Palaeogeography, Palaeoclimatology, Palaeoecology* **411**, 208–215.
- Janzen, D.H. (1967) Why mountain passes are higher in the tropics. *The American Naturalist* **101**, 233–249.
- Johnson M.R.W. & Harley, S. (2012) *Orogenesis: The Making of Mountains*. Cambridge: Cambridge University Press.
- Kessler, M., Karger, D.N. & Kluge, J. (2016) Elevational diversity patterns as an example for evolutionary and ecological dynamics in ferns and lycophytes. *Journal of Systematics and Evolution* **54**, 617–625.
- Kohn, M.J. & Fremd, T.J. (2007) Tectonic controls on isotope compositions and species diversification, John Day Basin, central Oregon. *PaleoBios* **27**, 48–61.
- Kohn, M.J. & Fremd, T.J. (2008) Miocene tectonics and climate forcing of biodiversity, western United States. *Geology* **36**, 783–786.
- Köppen, W. & Wegener, A. (1924) *Die Klimate der geologischen Vorzeit*. Berlin: Verlag von Gebrüder Borntraeger.

- Körner, C. (2003) *Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems*. Berlin: Springer Science & Business Media.
- Körner, C. (2007) The use of “altitude” in ecological research. *TRENDS in Ecology and Evolution* **22**, 569–574.
- Körner, C. (2012) *Alpine Treelines: Functional Ecology of the Global High Elevation Tree Limits*. Berlin: Springer-Verlag.
- Körner, C. & Ohsawa, M. (2006) Mountain systems. In: Hassan, R., Scholes, R. & Ash, N. (eds.) *Ecosystems and Human Well-Being: Current State and Trends*, 1. Washington, DC: Island Press, pp. 681–716.
- Körner, C., Paulsen, J. & Spehn, E.M. (2011) A definition of mountains and their bioclimatic belts for global comparisons of biodiversity data. *Alpine Botany* **121**, 73–78.
- Körner, C., Jetz, W., Paulsen, J., Payne, D., Rudmann-Maurer, K. & Spehn, E.M. (2016) A global inventory of mountains for bio-geographical applications. *Alpine Botany* **127**, 1–15.
- Kreft, H. & Jetz, W. (2007) Global patterns and determinants of vascular plant diversity. *Proceedings of the National Academy of Sciences* **104**, 5925–5930.
- Kupfer, J.A. (2010) Theory in landscape ecology and its relevance to biogeography. In Millington, A., Blumler, M. & Schickhoff, U. (eds.) *The SAGE Handbook of Biogeography*. Thousand Oaks, CA: Sage, pp. 57–74.
- Lagomarsino, L.P., Condamine, F.L., Antonelli, A. et al. (2016) The abiotic and biotic drivers of rapid diversification in Andean bellflowers (Campanulaceae). *New Phytologist* **210**, 1430–1442.
- Linder, H.P. (2008) Plant species radiations: where, when, why? *Philosophical Transactions of the Royal Society B* **363**, 3097–3105.
- Lomax, B.H., Fraser, W.T., Harrington, G. et al. (2012) A novel palaeoaltimetry proxy based on spore and pollen wall chemistry. *Earth and Planetary Science Letters* **353**, 22–28.
- Lomolino, M.V. (2000) Ecology’s most general, yet protean pattern: the species-area relationship. *Journal of Biogeography* **27**, 17–26.
- Lomolino, M.V., Riddle, B.R., Whittaker, R.J. & Brown, J.H. (2010) *Biogeography*, 4th edn. Sunderland, MA: Sinauer Associates.
- Luebert, F. & Weigend, M. (2014) Phylogenetic insights into Andean plant diversification. *Frontiers in Ecology and Evolution* **2**, 27.
- MacArthur, R.H. & Wilson, E.O. (1963) An equilibrium theory of insular zoogeography. *Evolution* **17**, 373–387.
- MacArthur, R.H. & Wilson, E.O. (1967) *The Theory of Island Biogeography*. Princeton, NJ: Princeton University Press.
- Madriñán, S., Cortés, A.J. & Richardson, J.E. (2013) Páramo is the world’s fastest evolving and coolest biodiversity hotspot. *Frontiers in Genetics* **4**, 192.
- Malhi, Y., Meir, P. & Brown, S. (2002) Forests, carbon and global climate. *Philosophical Transactions of the Royal Society of London A* **360**, 1567–1591.
- McCain, C.M. & Grytnes, J.-A. (2010) Elevational gradients in species richness. In: *Encyclopedia of Life Sciences*. Chichester: John Wiley & Sons Ltd.
- McCormack, J.E., Huang, H. & Knowles, L.L. (2009) Sky islands. In: Gillespie, R. & Clague, D. (eds.) *Encyclopedia of Islands*. Berkeley, CA: University of California Press, pp. 841–843.
- McElwain, J.C. (2004) Climate-independent paleoaltimetry using stomatal density in fossil leaves as a proxy for CO₂ partial pressure. *Geology* **32**, 1017–1020.
- Merckx, V.S.F.T., Hendriks, K.P., Beentjes, K.K. et al. (2015) Evolution of endemism on a young tropical mountain. *Nature* **524**, 347–350.
- Moeslund, J.E., Arge, L., Bøcher, P.K. et al. (2013) Topography as a driver of local terrestrial vascular plant diversity patterns. *Nordic Journal of Botany* **31**, 129–144.
- Molnar, P. (2015) Mountain (landform). Available from: <https://www.britannica.com/science/mountain-landform> (last accessed September 1, 2017).
- Molnar, P. & England, P. (1990) Late Cenozoic uplift of mountain ranges and global climate change: chicken or egg? *Nature* **346**, 29–34.
- Morlon, H., Lewitus, E., Condamine, F.L. et al. (2016) RPANDA: an R package for macroevolutionary analyses on phylogenetic trees. *Methods in Ecology and Evolution* **7**, 589–597.
- Mulch, A. (2016) Stable isotope paleoaltimetry and the evolution of landscapes and life. *Earth and Planetary Science Letters* **433**, 180–191.
- Mutke, J. (2010) Biodiversity gradients. In: Millington, A., Blumler, M. & Schickhoff, U. (eds.) *The SAGE Handbook of Biogeography*. Thousand Oaks, CA: Sage, pp. 170–190.
- Mutke, J., Sommer, J. H., Kreft, H. et al. (2011) Vascular plant diversity in a changing world: global centres and biome-specific patterns. In: Zachos, F.E. & Habel, J.C. (eds.) *Biodiversity Hotspots – Evolution and Conservation*. Berlin: Springer-Verlag, pp. 83–96.
- Myers, N., Russell A. Mittermeier, R.A. et al. (2000) Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858.
- Owens, P.N. & Slaymaker, O. (2004) *Mountain Geomorphology*. Oxford: Oxford University Press.
- Peters, M.K., Hemp, A., Appelhans, T. et al. (2016) Predictors of elevational biodiversity gradients change from single taxa to the multi-taxa community level. *Nature Communications* **7**, 13736.
- Polissar, P.J., Freeman, K.H., Rowley, D.B. et al. (2009) Paleoaltimetry of the Tibetan Plateau from D/H ratios of lipid biomarkers. *Earth and Planetary Science Letters* **287**, 64–76.

- Potter, P.E. & Szatmari, P. (2009) Global Miocene tectonics and the modern world. *Earth-Science Reviews* **96**, 279–295.
- Poulsen, C.J., Ehlers, T.A. & Insel, N. (2010) Onset of convective rainfall during gradual Late Miocene rise of the Central Andes. *Science* **328**, 490–493.
- Raven, P.H. & Axelrod, D.I. (1974) Angiosperm biogeography and past continental movements. *Annals of the Missouri Botanical Gardens* **61**, 539–673.
- Reiners, P.W. & Brandon, M. (2006) Using thermochronology to understand orogenic erosion. *Annual Review of Earth and Planetary Sciences* **34**, 419–466.
- Renema, W., Bellwood, D., Braga, J.-C. et al. (2008) Hopping hotspots: global shifts in marine biodiversity. *Science* **321**, 654–657.
- Renner, S. (2016) Available data point to a 4-km-high Tibetan Plateau by 40 Ma, but 100 molecular-clock papers have linked supposed recent uplift to young node ages. *Journal of Biogeography* **43**, 1479–1487.
- Ricklefs, R.E. (1977) Environmental heterogeneity and plant diversity: a hypothesis. *The American Naturalist* **111**, 376–381.
- Ricklefs, R.E. (1987) Community diversity: relative roles of local and regional processes. *Science* **235**, 167–171.
- Ricklefs, R.E. (2004) A comprehensive framework for global patterns in biodiversity. *Ecology Letters* **7**, 1–15.
- Ricklefs, R.E. (2005) Historical and ecological dimensions of global patterns in plant diversity. *Biologiske Skrifter* **55**, 583–603.
- Rockström, J., Steffen, W., Noone, K. et al. (2009) A safe operating space for humanity. *Nature* **461**, 472–475.
- Rohrmann, A., Sachse, D., Mulch, A. et al. (2016) Miocene orographic uplift forces rapid hydrological change in the southern central Andes. *Scientific Reports* **6**, 35678.
- Sandel, B., Arge, L., Dalsgaard, B. et al. (2011) The influence of Late Quaternary climate-change velocity on species endemism. *Science* **334**, 660–664.
- Santos, J. C., Coloma, L.A., Summers, K. et al. (2009) Amazonian amphibian diversity is primarily derived from late Miocene Andean lineages. *PLoS Biology* **7**, e56.
- Särkinen, T., Pennington, R.T., Lavin, M. et al. (2012) Evolutionary islands in the Andes: persistence and isolation explain high endemism in Andean dry tropical forests. *Journal of Biogeography* **39**, 884–900.
- Scherrer, D. & Körner, C. (2010) Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. *Journal of Biogeography* **38**, 406–416.
- Senckenberg Magazine (2015) *Senckenberg – World of biodiversity/Blick in die Zukunft – Senckenberg geobiodiversitätsforschung*.
- Silvestro, D., Zizka, A., Bacon, C.D. et al. (2016) Fossil biogeography: a new model to infer dispersal, extinction and sampling from palaeontological data. *Proceedings of the Royal Society B* **371**, 20150225.
- Spehn, E.M., Rudmann-Maurer, K., Körner, C. & Maselli, D. (2010) *Mountain Biodiversity and Global Change*. Basel: GMBA-DIVERSITAS.
- Spehn, E.M., Rudmann-Maurer, K. & Körner, C. (2011) Mountain biodiversity. *Plant Ecology & Diversity* **4**, 301–302.
- Stein, A. & Kreft, H. (2015) Terminology and quantification of environmental heterogeneity in species-richness research. *Biological Reviews* **90**, 815–836.
- Steinbauer, M.J., Field, R., Grytnes, J.-A. et al. (2016) Topography-driven isolation, speciation and a global increase of endemism with elevation. *Global Ecology and Biogeography* **25**, 1097–1107.
- Tews, J., Brose, U., Grimm, V. et al. (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography* **31**, 79–92.
- Töpel, M., Zizka, A., Caliό, M.F. et al. (2016) SpeciesGeoCoder: fast categorisation of species occurrences for analyses of biodiversity, biogeography, ecology and evolution. *Systematic Biology* syw064.
- Van der Hammen, T. & Cleef, A. M. (1986) Development of the High Andean Paramo flora and vegetation. In: Vuilleumier, F. & Monasterio, M. (eds.) *Tropical Biogeography*. New York: Oxford University Press, pp. 153–201.
- Van der Hammen, T., Werner, J.H. & Van Dommelen, H. (1973) Palynological record of the upheaval of the Northern Andes: a study of the Pliocene and Lower Quaternary of the Colombian Eastern Cordillera and the early evolution of its high-Andean biota. *Review of Palaeobotany and Palynology* **16**, 1–122.
- Wallace, A.R. (1876) *The Geographical Distribution of Animals*. London: Macmillan.
- Wegener, A. (1912) Die Entstehung der Kontinente. *Geologische Rundschau* **3**, 276–292.
- Winkworth R.C., Wagstaff, S.J., Glenny, D. & Lockhart, P.J. (2005) Evolution of the New Zealand mountain flora: origins, diversification and dispersal. *Organisms, Diversity & Evolution* **5**, 237–247.
- Wright, D.F. & Stigall, A.L. (2013) Geologic drivers of Late Ordovician faunal change in Laurentia: investigating links between tectonics, speciation, and biotic invasions. *PLoS ONE* **8**, e68353.
- Yasuhara, M., Iwatani, H., Hunt, G. et al. (2016) Cenozoic dynamics of shallow-marine biodiversity in the Western Pacific. *Journal of Biogeography* **44**, 567–578.

