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Valentí Rull
Ana Carolina Carnaval
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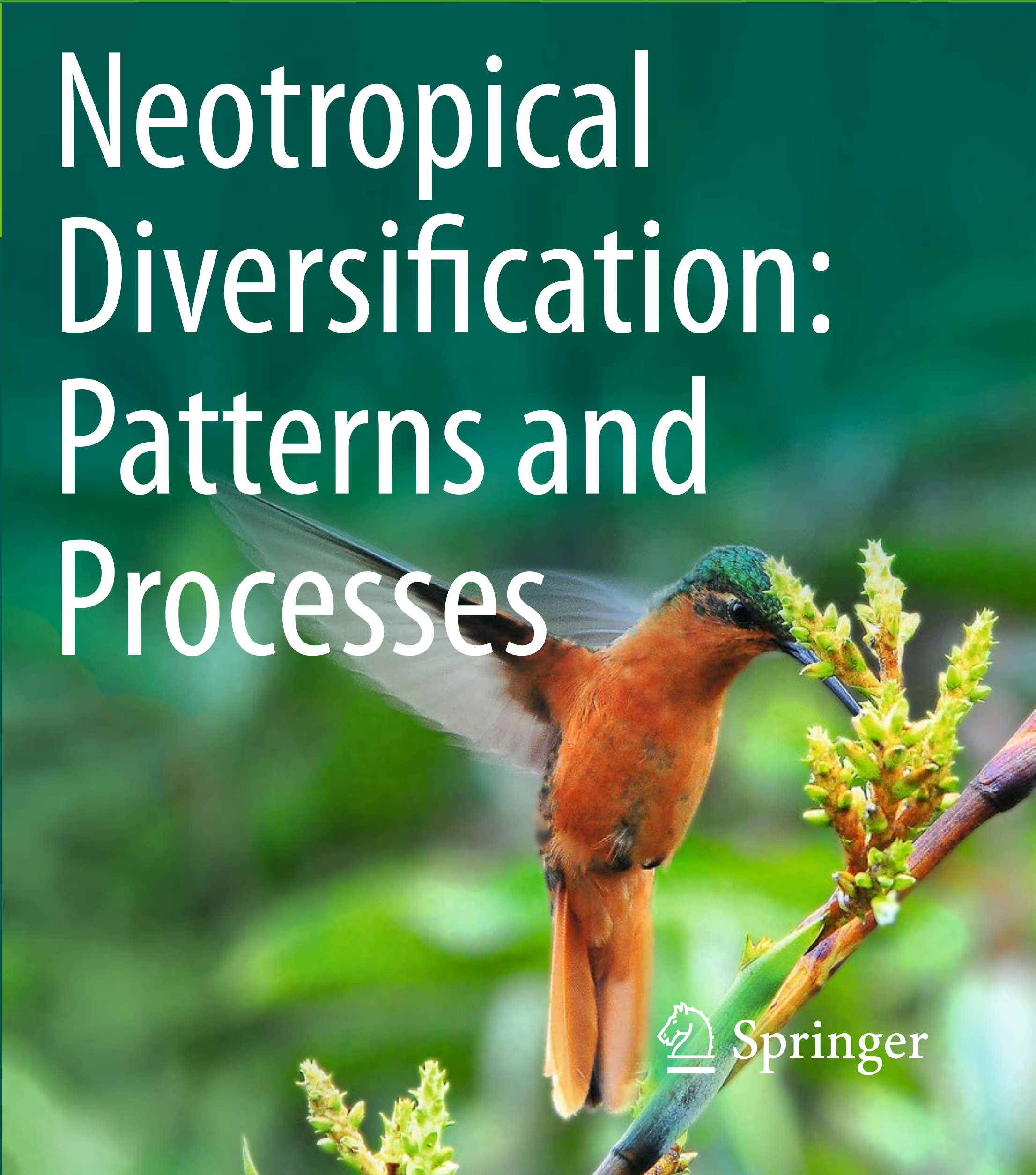
Neotropical Diversification: Patterns and Processes



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Neotropical Diversification: Patterns and Processes

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Editors
Valentí Rull
Laboratory of Paleoecology
Institute of Earth Sciences Jaume Almera (CSIC)
Barcelona, Spain

Ana Carolina Carnaval
Department of Biology
City College of New York
New York, NY, USA

Biology Program, Graduate Center of CUNY
New York, NY, USA

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Chapter 1
Introduction

Valentí Rull and Ana Carolina Carnaval

This book addresses the colossal biodiversity of the Neotropics and provides a range of potential explanations for its origin and maintenance. In general, we use the term "Neotropics" as synonym of "tropical America"—i.e., the part of this continent situated between the tropics of Cancer and Capricorn—rather than of the Neotropical biogeographical realm, which includes also the southern part of South America and excludes the Mexican highlands. However, the geographical distribution of the taxonomic groups studied in some chapters makes necessary to consider certain extratropical areas for a thorough study.

The main differential feature of this book with respect to other compilations and reviews on the same subject is that it is not attached to any particular idea on how the Neotropical biodiversity has originated. Instead, it considers that there is no a single explanation applicable to any Neotropical region or taxonomic group. We (the editors) are convinced that different environmental drivers acting at multiple spatio-temporal scales have led to the complex environmental-evolutionary-ecological interactions that resulted in current biogeographical patterns (Rull 2011), and this compilation is a testimony of that.

For this reason, we have invited scholars who are working on the subject regardless their personal views on Neotropical diversification. Each author has been free to choose the topic of his/her paper and to develop it according to their own preferences, without any formal or conceptual constraint besides the editorial author's instructions. As a result, the book gathers as many views as possible on the

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V. Rull (✉)
Laboratory of Paleoecology, Institute of Earth Sciences Jaume Almera (ICTJA-CSIC), Barcelona, Spain
e-mail: vrull@ictja.csic.es

A. C. Carnaval
Department of Biology, City College of New York, New York, NY, USA

Biology Program, Graduate Center of CUNY, New York, NY, USA

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causes of the extant Neotropical biodiversity, according to the awareness of the editors and the availability of the contributors.

It could be argued that this could create confusion, rather than help the reader to acquire a sound view of the status of the problem. We do not agree with that opinion, for several reasons. After more than three centuries of study, it is clear that the origin of Neotropical biodiversity and of large-scale diversity patterns (e.g., the latitudinal diversity gradients) are not simple problems with a single explanation (Brown 2014). Any attempt to reduce global macroecological patterns to a particular cause runs the risk of being inaccurate or unrealistic. It may be that a general theory on Neotropical biodiversity is just a human expectation or construct, and that explanations should be explored case by case, biome by biome, or region by region (Carnaval et al. 2014). Syntheses such as the presented here may be a good starting point to test these ideas. Avoiding the potential pitfalls of focusing the narrative on one or few sensationalist messages, regardless the soundness of its empirical support—a not unusual practice in current scientific literature—we created space for multiple views and data, allowing the contributing scholars to build and share their own perspective on Neotropical diversity and diversification. We consider this to be more useful for those readers interested in figuring out the true state of the art.

1 Book Plan

The book has been subdivided into three main parts: (I) Neotropical diversity and diversification, (II) regional biodiversity patterns and diversification processes, (III) taxon-based studies at the local and regional scales. An epilogue links the topics discussed here with the conservation of Neotropical biodiversity. The first part examines diversity patterns and diversification processes at a Neotropical scale using multitaxon approaches or broad taxonomic categories, such as plants, diatoms or birds, among others. The second part gathers chapters focused on more specific but large-scale Neotropical regions. Diversity patterns and diversification processes have been most intensely studied in the Amazon, and this region is often used as the preferred model for discussing the origin and maintenance of Neotropical biodiversity. In Part II, however, we ensured to include areas that go beyond the Amazon basin, considering, for example, the Atlantic rainforests, the Mexican forests, and the Caribbean, a region that is rarely contemplated in studies about Neotropical diversification. The third section of the book includes studies of particular taxonomic groups (amphibians, reptiles, flightless birds, angiosdperm families) on specific Neotropical areas such as the Guayanan and the Andean highlands, or selected river catchments. Below, we briefly summarize the content of chapters of the main book sections.

Part I: Neotropical Diversity and Diversification
This part is composed of eight chapters.

Rull introduces the focus area of this book, and discusses Neotropical diversification from historical and conceptual perspectives. Four historical steps are recognized, namely the discovery of the latitudinal biodiversity gradients, the biogeographic phase, the paleoecological phase, and the phylogeographical phase. Conceptually, this chapter explores the main handicaps that have hindered the progress towards an explanation for the comparatively high Neotropical biodiversity, with emphasis on the shifting from one paradigm to another, the geographical and taxonomic extrapolation of particular case studies, the selection of biased evidence to support different hypotheses, the identification of Pleistocene diversification with the refugial hypothesis, and the inference of diversification mechanisms from solely diversification timing. Some solutions are proposed to circumvent these drawbacks.

Baker et al. follow Rull's opening by revisiting the Haffer's refuge hypothesis in light of the paleoclimatic evidence gathered during the last 50 years. Their message to us is that the role of Quaternary climatic changes on Neotropical diversification should be reevaluated. The authors emphasize two main features that should be considered in addition to the glacial-interglacial cyclicity, namely the existence of an east-west precipitation dipole due to precessional cycles of ~20-kyr period, and the occurrence of phases of anomalously high rainfall of ~1500-y recurrence consistent with cold North-Atlantic stadials (Dansgaard-Oeschger cycles). The combination of these climatic modes conform a much more complex scenario of climatic change in time and space than originally proposed by the refuge hypothesis.

The biological significance of climatic transitions, this time in space, is the focus of the next chapter. Nascimento et al. investigate the effect of the Tropic of Capricorn in the distribution of Neotropical communities, particularly comparing the changes observed in the composition of biological communities in geographical space. By cleaning and analyzing nearly 15 million records of 124,066 species, all available online, they show that only in the cis-Andean region one can observe a latitudinal gradient in the degree of species turnover. Contrary to previous taxon-specific analyses, this chapter suggests that the tropical-subtropical transition does not influence the rate at which turnover indexes change in South America—at least not when data from multiple groups are combined. Although the data indicate that the replacement of species is largely responsible for changes in community composition, the Tropic of Capricorn does not seem to represent a common marker of concerted changes in community turnover at this large scale.

Villalobos et al. also focus on large-scale patterns of biodiversity in geographic space, but they utilize new methods in the field of macroecology to incorporate evolutionary thinking into studies of species ranges. They illustrate these novel approaches with data from the Furnariides, a model group of Neotropical birds. Their contribution shows that multiple metrics now enable the inclusion of speciation and extinction processes into data analyses and provide coherent results and insights. The chapter ends with a discussing of ways to expand the field by incorporating lineage dispersal over evolutionary time as a major contributor to geographic diversity gradients, and the promise of simulation studies in historical inference.

Similar to Nascimento et al., Maestri and collaborators combine data from thousands of species and explore possible correlates of biodiversity patterns at a continental scale. Yet, they specifically explore how the spatial distribution of evolutionary history compare across major groups of organisms. For that, they combine phylogenetic data and occurrence information from 1100 + species of vertebrates whose evolutionary histories are primarily confined to the Neotropics. They find that the spatial patterns of phylogenetic dissimilarity between areas are very similar across groups, despite the fact that they have different ecological requirements and ages. Their analysis also suggests that biogeographical relationships across regions explain phylogenetic similarity patterns better than present-day environments.

Nores discusses the biogeographical patterns observed in the birds of tropical and subtropical South America. Using range data, he introduces and discusses major geological and climatic events in the Neogene and the Pleistocene that are believed to have impacted these fauna, including the uplift of the Andes (splitting pan-Amazonia into a trans- and a cis-Andean regions, and leading to the formation of large Amazonian rivers), and the closing of the Isthmus of Panama (allowing for faunal interchange, increase in diversity, and new radiations). He argues that Amazonia and other tropical forests remained predominantly forested over time, even during glacial periods, and claims that marine transgressions in the Tertiary and lower Quaternary, tied to Amazonian rivers, were important by fragmenting species ranges and leading to speciation. Nores ends this chapter alerting us to the significant drop in species diversity and abundance recently observed in South America, particularly in protected areas of Amazonia, the lower Eastern Andean slopes, and the Pacific Forest—and likely tied to anthropogenic climate change.

Brower and Garzón-Orduña also explore the history of another widespread group of animals—Neotropical butterflies—but through the use of molecular data. Because the fossil record is too scarce to study the age of origin of these species, the authors estimate time of speciation through phylogenetic trees calibrated with relaxed molecular clocks. Brower and Garzón-Orduña compile clock-based age estimates for six butterfly families, at a Neotropical level, containing ~800 species in ~100 genera. The authors conclude that crown ages, that is, the ages of the initial diversification of the genera, range from Oligocene to Miocene, whereas species pairs diverged mostly during the Pleistocene. The analysis suggest that Neotropical butterflies are relatively young, and that Pleistocene climate changes likely played a significant role, whereas biogeographically significant geological events in the Miocene only set the stage for their subsequent evolution.

While studies on the diversity and community composition of macroorganisms are abundant, this is not the case for microorganisms, especially in the tropics, where this type of surveys are particularly scarce. Benito and Fritz fill this gap in our book, reviewing the diversity and distribution of Neotropical diatoms using a newly created database for tropical South America, which also includes geoclimatic and limnological parameters, as environmental drivers of community change. Using island biogeography and metacommunity approaches, the authors identify several aspects that may influence biogeographical patterns in diatoms, notably differences in regional floras, latitudinal gradients in species richness, dispersal ability, and environmental filtering. They also emphasize the need for incorporating diatoms into macroecological frameworks for studying community assembly in the Neotropics.

Part II: Regional Biodiversity Patterns and Diversification Processes
This part has 11 chapters that are sorted geographically.

Cracraft et al. revisit Amazonian diversification in relation to the origin of modern landscape features modeled by tectonic activity, drainage evolution, and climatic change. These authors observe that, although current Amazon landscapes were shaped during the last 4–5 million years, much of bird, mammal and butterfly diversity, at species level, originated during the last 1–2 million years. Therefore, the more significant landscape changes for the evolution of the current Amazon biota should have occurred over the last 1–2 million years. Cracraft et al. conclude that many mysteries still remain in relation to the origin of current Amazonian biodiversity, and that further research should be transdisciplinary and integrative, thus avoiding simplistic explanations. Phylogeographic analyses of individual clades should be replaced by among-clade studies that consider a wider spatial context and the differential action of landscape changes on different clades.

To address this question at a smaller geographic scale, Capurucho and collaborators focus on an under-explored region of Amazonia: the White Sand Ecosystems (WSE). These are nutrient-poor, quartz-rich sandy soils patchily distributed in areas of low elevation areas. Gathering data on community composition and the phylogeny of birds and plants, the authors demonstrate that the WSE present a unique assemblage of species. Although these areas pre-date the Quaternary, the molecular data suggest that their Pleistocene history has been dynamic. In the face of anthropogenic change, the authors emphasize that the WSE's low resilience to disturbance, as inferred through their historical analysis, ought to be incorporated into conservation planning.

Many traditional studies of the origin of Amazonian biodiversity, like Cracraft et al. and Capurucho and collaborators', have focused on the action of natural drivers such as tectonic or climatic changes—but largely disregarded the contribution of human activities on local biodiversity patterns. Montoya et al. analyze the potential impact of pre-Columbian anthropogenic activity on today's diversity of Amazonian plants, based on a review of the recent literature. Pre-Columbian human influence began with plant domestication and possibly megafaunal extinction, and remained until European contact, as shown by several types of evidence, including landscape transformations (i.e., savanna expansions) and changes in forest composition and soil properties. However, most studies developed to date are of local nature and are unable to account for the high spatial heterogeneity of the Amazon region. The authors conclude that more transdisciplinary interaction is needed for a proper understanding of human contribution to the Amazonian biodiversity, with emphasis on the last few millennia.

Azevedo and collaborators focus on the history of another key Neotropical ecosystem: the South American savannas. By combining data from the fossil record, paleoenvironmental proxies, and phylogenetic information of plants and animals, the authors claim that the phenomenal diversity of the South American Neotropical savannas did not emerge from a long history of stability. Paleoenvironmental data indicate that appropriate environmental conditions for the occurrence of savannas were in place since the middle Miocene, in agreement with phylogenetic analyses that recovered that as the beginning of the diversification phase of C4 grasses. However, the review finds that woody plants diversified only a few millions year later. This time lag, say the authors, may indicate that trees adapted to the fire-prone savannas reached ecological dominance only after the emergence of open habitats and their associated fauna.

Colevatti et al. review the biogeographic patterns and the diversification timing of Angiosperms of the South American Dry Diagonal (SADD), an open vegetation belt extending from northeastern Brazil to northern Argentina that includes several xeric biomes. The main goal is to unravel whether the Neogene tectonic/paleogeographic events or the Quaternary climatic changes were the main responsible for biotic diversification. Despite the low proportion of species studied, the authors highlight some regular patterns, notably that major lineage divergences occurred during the Pliocene but most intraspecific divergence took place during the Early and Middle Pleistocene. This suggests that Quaternary climate changes played a significant role but the authors emphasize that species responded differently to these environmental shifts and challenge the hypothesis of glacial refugia and the Last Glacial Maximum (LGM) on the diversification of the SADD Angiosperms.

Guedes et al. discuss the role of the major Non-Andean South American mountain ranges as biodiversity cradles and museums, emphasizing the Serra do Mar Range, the Mantiqueira Mountains, the Espinhaço Mountains, the Northeastern Highlands, the Central Brazilian Highlands, and the Pantepui region. Data published to date show that the Neogene and the Quaternary were important periods for the diversification for many terrestrial groups, resulting in the high endemism that today characterizes the non-Andean mountains. They also discuss how biotic interchange among the mountain ranges themselves, and the Andes, resulted in the patterns observed today.

Peres et al. zooms into the patterns of diversity and endemism of the ecosystem that encompass three of the mountain ranges discussed by Guedes and collaborators: the Brazilian Atlantic rainforest. Their review indicates that higher species richness is often found in the topographically complex coast of Rio de Janeiro and São Paulo, including the Mar and Mantiqueira ranges discussed by Guedes, though not exclusively (e.g. coastal Bahia). Data from multiple groups of plants and animals demonstrate striking differences in the composition of communities in the northern vs. the southern half of the forest, although the exact point of community turnover varies among groups. Several areas of unique taxonomic composition and endemism have been consistently identified across plants and animals, and those defined by organisms with low dispersal ability, such as terrestrial invertebrates, are nested within the areas identified by groups of higher ability to disperse, like birds. By contrasting regional diversity patterns and the processes that led to them, the authors argue that both climate and landscape changed acted in combination to lead to the astonishing diversity of this hotspot. They also argue that while the spatial patterns of species and genetic diversity are similar across plants and animals, the processes that led to them—and their timing—are widely different.

Silveira et al. argue that the study of Neotropical diversity has largely focused on relatively recent geological environments such as Amazonia or the Andes, whereas older and extremely nutrient-poor settings have been traditionally overlooked, despite their outstanding biodiversity and endemism patterns. This is the case of the so called Old Climatically-Buffered Infertile Landscapes (OCBILs) and, specifically, of the Brazilian "campos rupestres", which Silveira et al. use to propose a theoretical diversification framework including mechanistic explanations that link ecological and evolutionary processes to vegetation patterns and functional traits. This example is proposed as a model to demonstrate how the OCBIL theory and its predictions can help understanding the complex history of Neotropical plant diversification and inform their conservation.

Rull and Vegas-Vilarrúbia focus on another area included within the OCBIL category, as is the biogeographical province of Pantepui, formed by the assemblage of flat summits of the Guiana table mountains (tepuis), situated in the confluence of the Amazon and the Orinoco basins, between approximately 1500 and 3000 m elevation. Pantetui is one of the few pristine areas remaining on Earth and has been considered a natural laboratory for the study of Neotropical biodiversity. The diversity and endemism patterns of Pantepui are outstanding and its biota and ecosystems are unparalleled across the planet. The authors use the most recent update on the biodiversity of Pantepui, including algae, bryophytes, vascular plants, aquatic insects, butterflies, scorpions, land snails, amphibians, reptiles, birds, mammals and vertebrate parasites, to take the first steps towards a biogeographical, ecological and evolutionary synthesis on the origin of Pantepui biota and ecosystems. Direct (notably fire) and indirect (global warming) threats to Pantepui biodiversity are also analyzed.

Reginato and Michelangeli explore the data emerging from rich, well-curated, and digitized plant collections from Eastern Brazil to advance on the review provided by Peres and collaborators and identify areas of unique community composition (or bioregions). To enable analyses across groups with striking different dispersal abilities, diversity and endemism, they provide three levels of grouping—and the small, intermediate, and large spatial scales. The intermediate-level analysis splits E Brazil into 10 bioregions, which cluster into 5 super-bioregions at the larger scale, and which can be further subdivided into 23 sub-regions, at the smaller scale. High diversity and endemism is flagged both in the mountain ranges of the Serra do Mar and Mantiqueira discussed by Guedes and collaborators, but also in the campos rupestres system introduced by Silveira et al., and lowland areas of Bahia, as described by Peres et al. The rasters of the inferred bioregions are available for download and use by the scientific community at large.

Figueroa-Rangel and collaborators transport us north to Central America. Two major types of Mexican forests have been recognized: the Neartic forests, in the north, and the Neotropical forests, in the south, separated by a transition zone called the Trans-Mexican Volcanic Belt (TMVB). Figueroa-Rangel et al. review the long-term plant diversity changes along an altitudinal transect of the TMVB and the

Neotropical forests, ranging from sea level to the highlands (~3900 m). For that, they use a variety of diversity indices applied to Holocene pollen records. The results reveal that Neotropical forests are more diverse than forests with Holarctic affinities, and that Holocene climate change has been decisive for the shaping of these diversity patterns.

Finally, Roncal et al. discuss an important but often overlooked Neotropical biodiversity hotspot: the Caribbean archipelago. The origins of the high diversity observed in this area is very poorly understood. Roncal et al. use a combination of time-calibrated phylogenetic studies and biogeographical inferences to test the main hypotheses erected to explain Caribbean plant diversity, namely Late Cretaceous vicariance, Oligocene GAARlandia colonization, recurrent Cenozoic long-distance colonization, and in situ speciation. The authors conclude that plants repeatedly colonized the Caribbean islands during the last 60 million years (roughly, the Cenozoic) by long-distance dispersal from the American mainland, especially from Central and South America. They also raise doubts on the existence of GAARlandia, a hypothetical emerged land connecting the present Greater Antilles (Cuba, Hispaniola, Puerto Rico, Jamaica), which would have promoted plant migration among them.

Part III: Taxon-Based Studies at the Local and Regional Scales
This part has eight chapters, each devoted to a unique taxonomic group and its diversification history in a key Neotropical region.

Señaris and Rojas-Runjaic describe and discuss diversity patterns of the herpetofauna (amphibians and reptiles) of the Venezuelan Guayana (also Guiana), one of the largest wilderness areas on the planet. They document how species richness decreases, and endemism increases, with elevation: 34% (amphibians) and 22% (reptiles) of the local fauna is endemic to upland areas, whereas widespread species, or forms with an Amazonian-Guianan distribution, dominate the lowland fauna. This distribution pattern makes conservation particularly difficult in the region, especially in the face of climate change—a topic discussed by the authors.

Exploring a similar topic, Cadena and Céspedes zoom into the processes leading to species turnover along elevational gradients, but they use the Andes as a model system. Combining phylogenetic and occurrence data from a group of passerine birds, they find that most species have small elevational ranges and that those taxa that are more closely related to each other have similar elevational distributions across mountains. Conversely, those species that replace each other along a mountain are distantly related. Based on this pattern, the authors propose that speciation happened mostly in allopatry, across mountains, instead of not along environmental gradients within mountains—suggesting that species accumulation in montane environments largely reflects colonization instead of in situ divergence.

Leubert and collaborators also study patterns of species distributions, this time with the aim of understanding niche evolution in South America. Specifically, they use data from ten plant clades to study a well-documented disjunction: that between the southern Andes (SA) and southern Brazil (SB). These areas tend to have higher precipitation relative to their intervening areas, where no species of the disjunct clades occur. Comparing divergence times between SA and SB, obtained from phylogenetic studies, they show a wide range of split times across groups—from 27 to 1 Ma. This, they argue, demonstrates that SA-SB disjunctions reflect different clade histories as opposed to a single explanation behind the common pattern observed—much like Peres et al.'s findings for coastal Brazil. Comparing the realized climatic niches of species across SA and SB, however, they find that they do not overlap—suggesting that niche evolution may have occurred across multiple groups. This hypothesis, however, remains to be tested.

Moraes and collaborators transport us to a very distinct environment to investigate the potential role of another environmental barrier on the distribution of local diversity—the Tapajós River, in Amazonia. Using molecular data from 16 species of amphibians and reptiles, sampled from across the Tapajós river basin, the authors find that most groups show spatial patterns of genetic diversity that are consistent with the present-day location of the river: they observe high levels of genetic divergence across river banks. However, much like Leubert et al., the range of riverine-associated divergence times is wide and continuous—suggesting a dynamic history and multiple events of vicariance or colonization.

Recoder and Rodrigues focus on another Neotropical river system to test how changes in geomorphology and climate may have impacted local patterns of diversification—the São Francisco. Located within the domain of the semi-arid Caatinga, the São Francisco river is known for its extensive paleodunes and for the spectacularly diverse sand-dwelling fauna endemic to the dune region. The authors compile existing and new data from local reptiles to ask whether a paleolacustrine vicariant diversification hypothesis, once proposed to explain the origin of this endemic fauna, agrees with current patterns of diversification. That hypothesis suggested that the river flowed into an interior lake during the last glacial maximum, but later made its way out into the Atlantic, isolating populations on opposite margins. The phylogenetic data gathered here show that this model is not sufficient to explain all pattern observed: divergence times differ across species, and some splits pre-date the Pleistocene. Again, Neotropical history is complex and cannot be attributed to a single event.

Ignacio de La Riva calls attention to the diversitication processes impacting high-Andean direct-developing frogs, particularly focusing on species occurring from Colombia to Bolivia. Through his review, he clarifies how similar life histories and ecological niches are associated with a particular morphology: local frogs are small-bodied, have short legs, and simple digital tips, likely reflecting adaptions to live in humid mossed habitats of the cloud forests and paramos. According to the author, new studies indicate that this is a convergent morphology across distantly related groups, and that the limited information available about these species render inferences about their evolutionary history, and the history of these unique Neotropical high-elevation areas, tentative at best.

Olave and collaborators also discuss morphological evolution, but are able to incorporate extensive molecular data available for the Liolaemini—the most diverse lizard group of the southern half of South America—in their chapter. Combining molecular and morphological data, they identify different patterns of diversification among the three genera that compose the clade. They propose that the richness of one of the genera, the species-rich *Liolaemus*, is associated with low extinction rates over time—while the opposite is observed in *Phymaturus*. Based on their analyses, they also argue that natural selection is tied to body size evolution and net diversification in this group, but notice that the trajectories and processes are different across the genera studied.

In the last chapter of Part III, Vargas and Dick focus on a group of 10 genera (ca. 232 species) of Lechytidaceae—the third most abundant family of trees in Amazon forests. Using a time-callibrated phylogeny of more than 100 species, they discuss the diversification history of this important group. Their results suggest that these plants dispersed from the Paleotropics long after the Gondwana break-up, and that most clades diversified in the Miocene. The analysis places the Guayana floristic region as ancestral to several clades, agreeing with Señaris and Rojas-Runjaic about the evolutionary relevance of that area. The results also suggest that this clade diversified through a pattern of steady accumulation of species, as opposed to well-marked pulses in response to specific geomorphological or climatic events.

Epilogue

Closing our book, Carnaval compiles several conservation-relevant messages discussed throughout this volume. Although not the main goal of this contribution, the author argues that one can and should leverage the large, heterogeneous and collective body of knowledge presented in these chapters to inform and guide conservation in the tropical Americas. She emphasizes some of the messages that we are about to hear in the chapters to come, particularly those about the status and patterns of diversity in the Neotropics, along with the authors' insights about the ecological and evolutionary process, and the biological mechanisms, that underscore them. This understanding, she argues, may allow us to better anticipate the behavior of the Neotropical biota as we move forward—a step which will require us not only to integrate data and insight across the biological and physical sciences, as we have done here, but also to reach out to the social sciences. But that is a topic for another book.

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Part I
Neotropical Diversity and Diversification

Chapter 2
Neotropical Diversification: Historical Overview and Conceptual Insights

Valentí Rull

Abstract Studying the causes of biological diversification and the main environmental drivers involved is useful not only for the progress of fundamental science but also to inform conservation practices. Unraveling the origin and maintenance of the comparatively high Neotropical biodiversity is important to understand the global latitudinal biodiversity gradients (LBGs), which is one of the more general and conspicuous biogeographical patterns on Earth. This chapter reviews the historical development of the study of Neotropical diversification, in order to highlight the influence of methodological progress and to identify the conceptual developments that have appeared through history. Four main steps are recognized and analyzed, namely the discovery of the LBGs by pioneer naturalists, the first biogeographic studies, the inception of paleoecology and the recent revolution of molecular phylogeography. This historical account ends with an update of the current state of the study of Neotropical diversification and the main conceptual handicaps that are believed to slow progress towards a general theory on this topic. Among these constraints, emphasis is placed on (1) the shifting from one paradigm to another, (2) the extrapolation from particular case studies to the whole Neotropics, (3) the selection of biased evidence to support either one or another hypothesis, (4) the assumption that Pleistocene diversification equals to refuge diversification, and (5) the straightforward inference of diversification drivers from diversification timing. The main corollary is that the attainment of a general theory on Neotropical diversification is being delayed by conceptual, rather than methodological causes. Some solutions are proposed based on the Chamberlin's multiple-working-hypotheses scheme and a conceptual research framework to address the problem from this perspective is suggested.

Keywords Latitudinal biodiversity gradients · Diversification drivers · Historical developments · Conceptual insights · Biogeography · Paleoecology · Phylogeography

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V. Rull (✉)
Institute of Earth Sciences Jaume Almera (ICTJA-CSIC), Barcelona, Spain
e-mail: vrull@ictja.csic.es

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1 Introduction

This paper reviews the historical development of research on the origin of Neotropical biodiversity under a conceptual perspective, in an attempt to identify the main factors that have hindered the attainment of a holistic theory on this subject. The Neotropics, or the American tropics, are among the most biodiverse regions in the world. A synthetic perspective on the origin and maintenance of such diversity would be relevant to understand the global Latitudinal Biodiversity Gradients (LBGs), one of the most pervasive global macroecological patterns on Earth (Lomolino et al. 2010; Cox et al. 2016). In addition, understanding how extant biodiversity and its major geographical patterns have been generated and sustained is needed for better informed conservation and restoration practices (Winter et al. 2013; Dietl et al. 2015).

The review emphasizes the environmental drivers and the evolutionary processes that have contributed to the origination of Neotropical species, ecological mechanisms favoring species' coexistence and biodiversity maintenance will be addressed when appropriate but are treated in more depth elsewhere (Wright 2002; Mittelbach et al. 2007; Cannon and Lerdau 2015; Usinowicz et al. 2017). Following the definitions of Pielou (1975), the measure of diversity employed in this paper is species diversity, that is, the number of species in a given geographical context. Other measures such as ecological diversity, which also considers the relative abundance of each species, are not analyzed. Species richness is here considered at local (α-diversity) and regional (γ-diversity) levels; diversity trends along environmental gradients or across regions or ecosystems/biomes (β-diversity) and other spatial patterns (Anderson et al. 2011; Wiegand et al. 2017) are not under scrutiny.

Technical or specialized jargon and concepts have been avoided or appropriately explained, due to the transdisciplinary character of the topic, the variety of research fields and methodological approaches involved and the general interest that the topic may have for a wide scientific audience, including advanced students. However, basic knowledge on general disciplines (as for example geology, evolution, ecology, biogeography or genetics, among others) is required. It should also be stressed that, given the great amount of literature available on Neotropical diversification and the continued publication of numerous papers on this subject, the literature provided here is by no means exhaustive but a selection aimed to be, at least, representative. The use of papers on diversification studies of particular taxonomic groups and/or geographical regions has been kept to a minimum; emphasis is placed on general studies, revisions, meta-analyses and other synthetic views that address the problem of Neotropical diversity from more general perspectives. It should also be stressed that evidence-based studies and models are preferred. Top-down modelling approaches using flawed biological assumptions, as for example species' equivalence—i.e., the purported irrelevance of specific biological traits and particular niche features—to favor previously established stochastic processes (e.g., Colwell and Hurt 1994; Hubbell 2001; Scheffer et al. 2018), are not analyzed. This paper is mainly a personal approach to the problem and uses data, concepts and arguments already published by the author elsewhere, in which case the corresponding references are provided in order to avoid self-plagiarism and eventual double-publication claims (Gutiérrez and Block 2013; Rozensweig and Schnitzer 2013). This is the only reason why own author's citations are overrepresented with respect to others.

The paper has been subdivided into four sections for more clarity. In order to provide a worldwide perspective, the first part briefly summarizes the issue of the LBGs and their potential causes. The second part emphasizes the comparatively higher Neotropical biodiversity with respect to other tropical areas and how this has been framed in global conservation strategies. The third section provides a historical account on the development of hypotheses about Neotropical diversification and the nature of the evidence used to propose and to test them. The fourth section emphasizes several conceptual and methodological constraints that have slowed the progress towards a synthesis on the origin and maintenance of Neotropical diversity and proposes some potential solutions. Finally, some hints are provided on the possible future research trends on Neotropical diversification, with emphasis on the mentioned conceptual constraints.

2 The Latitudinal Biodiversity Gradients

The occurrence of Earth's biodiversity gradients from the species-rich tropics to the almost barren poles is a classical biogeographical topic since the late eighteenth century, when the first biogeographical explorations took place (Lomolino et al. 2010). Johann Forster, who travelled around the world with the famous Captain James Cook, was the first to note the latitudinal trends in plant diversity attributing this fact to the increased intensity of heat towards the tropics (Forster 1778). Since then, the LBGs have been recognized in many terrestrial and marine organisms, as well as in total biodiversity patterns, and is now considered a first-order biogeographical pattern (Rozenzweig 1995; Willig et al. 2003; Hildebrand 2004; Krug et al. 2009; Yasurara et al. 2012). The LBGs do not seem to be only a present-day-only feature; paleontological studies have shown that similar patterns were already present during several Paleozoic and Cenozoic phases, especially those characterized by global cooling or 'icehouse' phases. Contrarily, the Mesozoic 'greenhouse' phase seems to have been characterized by reverse patterns characterized by depleted tropical biodiversity and extra-tropical richness peaks (Mannion et al. 2014). Understanding the environmental drivers and the ecological and evolutionary processes and mechanisms involved in the generation and maintenance of the LBGs is still challenging (Mittelbach et al. 2007; Lomolino et al. 2010; Brown 2014).

In general terms, the LBGs are considered to be generated and maintained by coupled ecological and evolutionary processes. Geographical differences in origination (speciation), extinction and dispersal (*s. l.*) over evolutionary timescales seem to have been essential (Krug et al. 2009; Mannion et al. 2014). Ecological mechanisms related to predation, competition, colonization ability, mating behavior, germination, differential growth or habitat heterogeneity, among others, would have been responsible for minimizing extinction and favoring species coexistence thus contributing to the maintenance of a high biodiversity (Wright 2002; Mittelbach et al. 2007; Stein et al. 2014; Cannon and Lerdau 2015; Usinowicz et al. 2017). Stebbins (1974) asked whether the tropics are more diverse due to higher speciation rates (cradle hypothesis) or lower extinction rates (museum hypothesis). Others consider that net diversification—the balance between speciation and extinction—is higher in the tropics (Mittelbach et al. 2007). In addition to speciation and extinction, dispersal has also been considered crucial to explain the LBG (Jablonski et al. 2006). Whatever the case, the environmental drivers and the ecological and evolutionary processes involved in speciation, extinction and dispersal trends in both time and space are the object of intense debate.

Some hypotheses favor the dominant action of single factors of worldwide extent, as for example the energy-gradient hypothesis, according to which, the increasing solar energy from the poles to the equator would be responsible for increased tropical productivity thus promoting higher diversity (Connell and Orias 1964; MacArthur 1965). Others emphasize the combined action of environmental and ecological factors by assuming that higher tropical diversity is due to more stable climates, which favor ecological interaction and niche diversification, whereas lower extra-tropical diversity is due to the depleting action of harsh climates, notably the Pleistocene glaciations (Fischer 1960; Pianka 1966; Slobodkin and Sanders 1969). The time-area hypothesis proposes that the tropics have accumulated more species than the temperate zones because they are bigger and have remained in its present geographical location for more time (Farrell et al. 1992; Ricklefs and Schluter 1993). The niche-conservatism hypothesis considers that tropics are both a cradle and a museum and, as a consequence, their older species largely retain their ancestral traits and niches (Wiens and Donoghue 2004). The out-of-the-tropics hypothesis contends that the tropics are more diverse because most taxa originated in the tropics and migrated toward higher latitudes but still remaining in the tropics (Jablonski et al. 2006; Jansson et al. 2013). At local and regional scales, migration—the dispersal across hospitable terrains (Pielou 1979)—can be important, either as species' input (immigration) or output (emigration) (Gaston and Spicer 2005).

Until recently, these and other hypotheses about the origin and maintenance of the LBGs were tested using mainly present-day biogeographical evidence (sometimes coupled with paleontological and paleoecological data) and theoretical modelling. Yet, the recent development of molecular phylogenetic tools has revolutionized the field. Empirical testing using these new methods has supported a number of the existing hypotheses or combination of them (Brown 2014; Kerhoff et al. 2014; Antonelli et al. 2015; Fine 2015; Schluter 2016) but the debate continues. According to Hurlbert and Stegen (2014) and Jablonski et al. (2017), the tendency to focus on single causal factors and processes is blocking progress towards a general LBG theory, which needs a more synthetic and integrative approach. Such synthesis should consider habitat and niche features, ecological interactions, evolutionary trends and biogeographical shifts, as well as their variability along environmental gradients and across temporal scales (Pontarp et al. 2019). Whittaker et al. (2001) and Willis and Whittaker (2002) question the possibility of attributing global

Table 2.1 A hierarchical framework for processes influencing biodiversity (simplified from Willis and Whittaker 2002)

Spatial scale	Species richness	Environmental variables	Temporal scale
Local	Within communities and habitat patches	Fine-scale biotic and abiotic interactions	1–100 years
Landscape	Between communities	Soils, elevation, peninsula effect	100–1000 years
Regional	Within continents	Radiation budget, water availability, area, latitude	Last 10,000 years
Continental	Across continents	Pleistocene glacial/interglacial cycles, mountain-building events, ardification	Last 1–10 million years
Global	Between continents and geographical realms	Continental drift, sea-level changes	Last 10–100 million years

biodiversity patterns to a single causal explanation and propose a hierarchical framework that considers the more influential processes and their corresponding spatio-temporal scales (Table 2.1).

3 The Neotropics

In the American continents, the LBG is particularly apparent (Fig. 2.1). This paper is concerned with the tropical part of these continents, the ecozone known as the Neotropics (Schultz 2005), lying between the tropics of Cancer and Capricorn (Fig. 2.2). Therefore, the term 'Neotropical' used here refers to the Neotropics and should not be confused with the Neotropical biogeographic realm, encompassing not only the tropical Americas but also the whole South America (Lomolino et al. 2010). Defined in this way, the Neotropics range from central Mexico and the Greater Antilles, to the north, to the southern end of Bolivia, to the south. The Neotropics exhibits a complex topography, ranging from the sea level to above 5000 elevation (Fig. 2.2) and encompasses a varied range of biomes, from the driest deserts to the more humid forests on earth (Fig. 2.3).

The amazing biodiversity of the Neotropics, as compared to the rest of the planet, is well illustrated by higher plants, which have been considered as surrogates of general biological diversity. For example, it has been estimated that Amazonian forests contain more tree species diversity in a square kilometre than do all the temperate forests of Europe, North America, and Asia combined (Usinowicz et al. 2017). The Netropics has also been considered the more species-rich tropical region, with ca. 100,000 species of seed plants, almost 40% of the world's total (Antonelli and Sanmartín 2011). These patterns are similar for many animal species including amphibians, mammals, birds, butterflies and reptiles, among others (Antonelli et al. 2015). Therefore, the Neotropics could be considered the most biodiverse region of

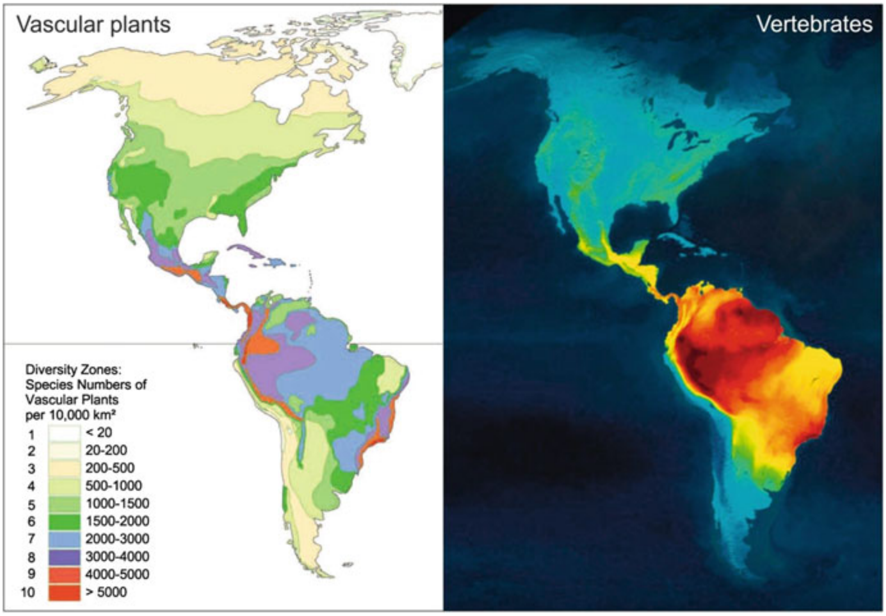

Fig. 2.1 Latitudinal distribution of species richness among vascular plants (left) and vertebrates (right) across the American continents. Vascular plant biodiversity is expressed in species number per unit area (adapted from Mutke and Bathlott 2005) and vertebrates as the total number of species, which is maximum at the brown side of the color spectrum and minimum at the blue side of the color spectrum (adapted from Mannion et al. 2014)

the world and, therefore, a well suited place to study the drivers, processes and mechanisms involved in the generation of the LBGs.

The Neotropics is also a keystone region for biodiversity conservation as manifested, for example, in the occurrence of six of the 25 world's biodiversity hotspots considered as conservation priorities, namely the Caribbean, the Mesoamerican, the Atlantic forest, the Cerrado, the Tropical Andes and the Chocó/Darién/Western Ecuador areas (Fig. 2.4). A hotspot has been defined as a region holding exceptional biodiversity levels, mainly of vascular plants and vertebrates, and suffering exceptional rates of habitat loss (Myers et al. 2000). The Amazon rainforests are not included in this classification because, despite their amazing biodiversity, they have not been considered to be under exceptional risk of habitat loss. However, given the current rates of rainforest destruction in Amazonia, this region might eventually be included in the list. If so, the whole Neotropics would be considered a mega-biodiversity hotspot. In addition, the Neotropics encompasses 6 of the 17 world's countries defined as megadiverse, namely Brazil, Colombia, Ecuador, Mexico, Peru and Venezuela (Fig. 2.5). As a whole, these 17 countries account for ~70% of the total world's biodiversity and bear at least 5000 endemic species, thus deserving special conservation priorities (Mittermeier et al. 1997).

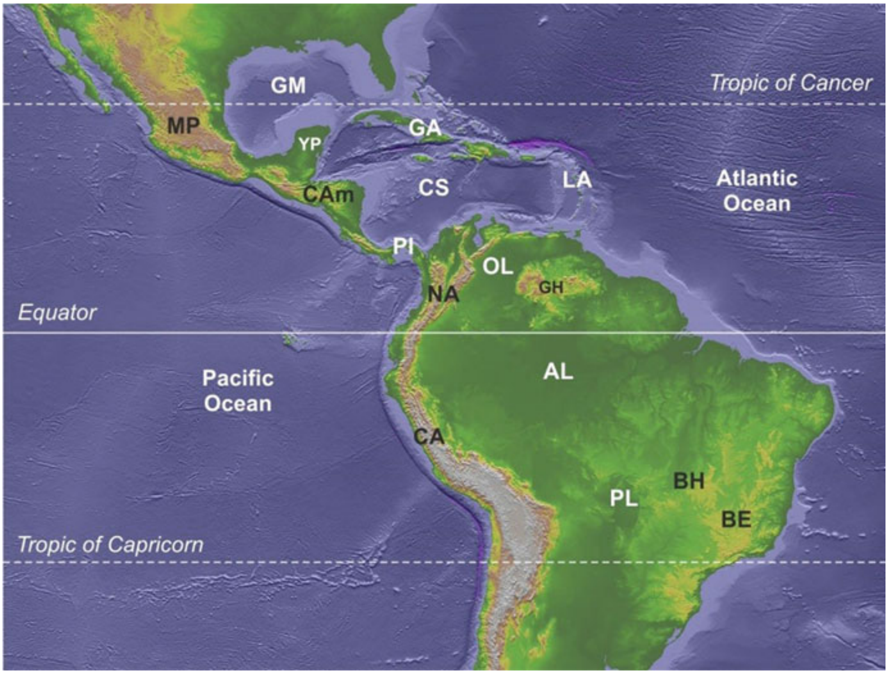

Fig. 2.2 Topographic/bathymetric map of the Neotropics with the main physiographical regions. *AL* Amazon Lowlands, *BE* Brazil East Coast Range, *BH* Brazilian Highlands, *CA* Central Andes, *Cam* Central America, *CS* Caribbean Sea, *GA* Greater Antilles, *GH* Guiana/Guayana Highlands, *GM* Gulf of Mexico, *LA* Lesser Antilles, *MP* Mexican Plateau, *NA* Northern Andes, *OL* Orinoco Lowlands, *PI* Panamá Isthmus, *PL* Pantanal, *YP* Yucatán Peninsula. Base map: NOAA National center for Environmental Information (https://ngdc.noaa.gov/mgg/topo/globega2.html)

Therefore, although the purely academic study of the ecological and evolutionary causes of the high Neotropical biodiversity makes sense by itself, it also has fundamental practical significance in the face of direct (e.g., deforestation and other forms of habitat destruction) and indirect (notably anthropogenic global warming) threats resulting from human activities. This makes of Neotropical biodiversity research a central activity, from basic and applied perspectives, towards a more sustainable use of natural resources.

4 Historical Outline

For more clarity, the historical account on the study of the origin of Neotropical biodiversity has been subdivided into four main periods: (1) the discovery of the American LBG by pioneer naturalists, (2) the first attempts to explain this LBG using present-day biogeographical patterns, (3) the incoming of paleoecological

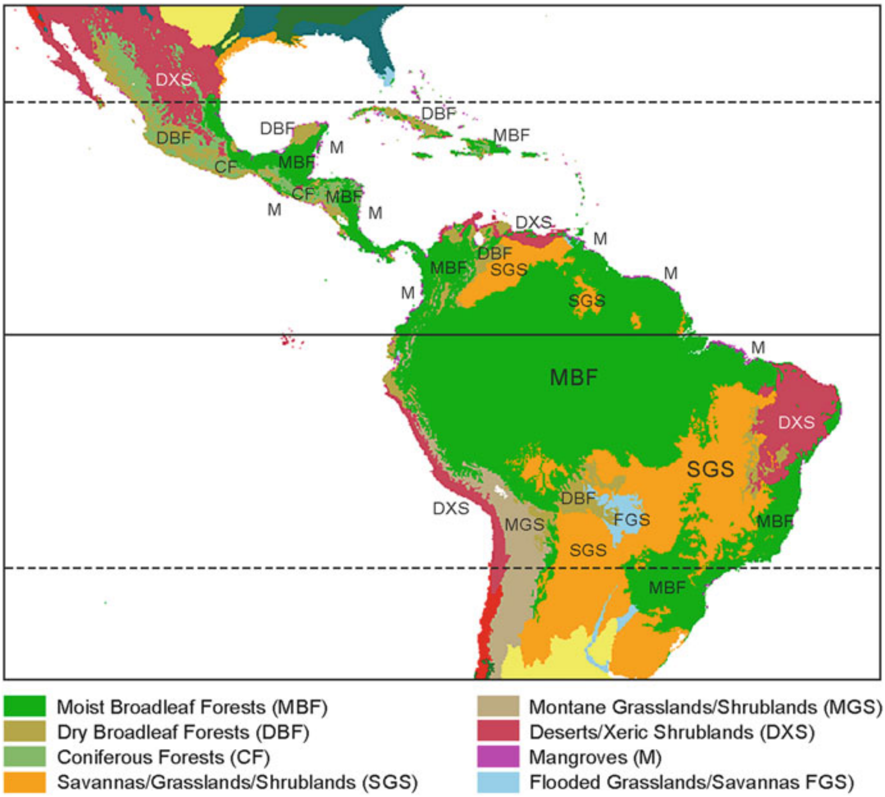

Fig. 2.3 Map of the Neotropics and its major biomes. Redrawn from Olson et al. (2001)

evidence to the investigations and (4) the appearance and the rapid development of molecular phylogenetic and phylogeographic methods. This does not mean that these approaches have replaced one another through history, as a number of them have eventually been combined to obtain a broader picture. This has been especially true in the last years, when some synthetic approaches have been attempted, which is briefly discussed at the end of this section.

4.1 *The Beginnings*

Few decades after the discovery of the general LBGs by Johann R Forster (1778), between 1799 and 1804, Alexander von Humboldt did similar observations in the New World. He noted an increase not only in the number of plant species but also in "structure, grace of form, and mixture of colors, as also in perpetual youth and vigor of organic life" (von Humboldt 1850) towards the tropics, and he attributed this fact to climatic constraints (Hawkins 2001). Humboldt also realized that the latitudinal

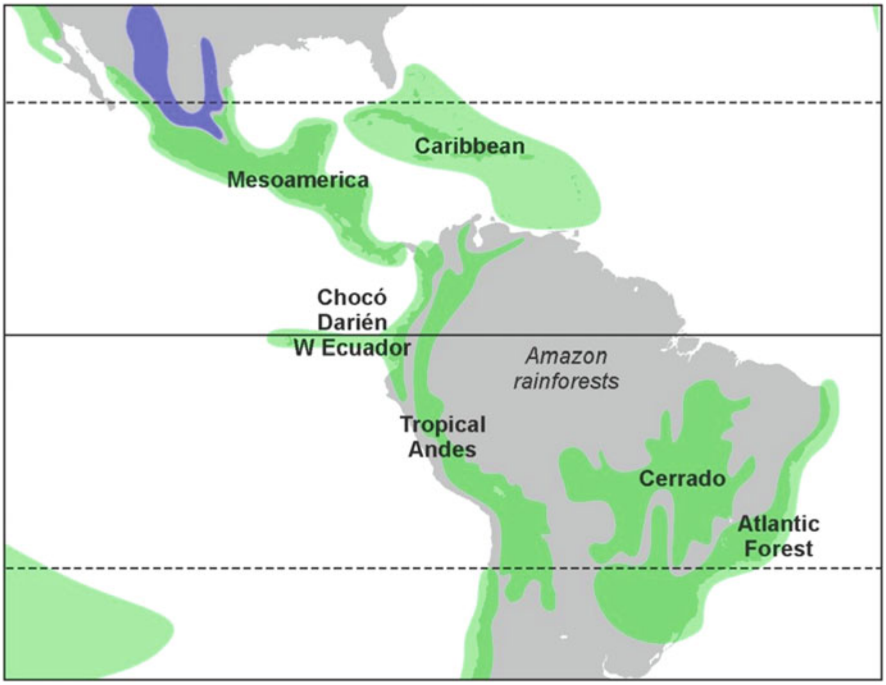

Fig. 2.4 Biodiversity hotspots (green areas) of the Neotropics, according to Myers et al. (2000). The Amazon rainforests are also indicated although they have not yet been considered a biodiversity hotspot (see text). Modified from an original map of Wikimedia Commons (https://en.wikipedia.org/wiki/Biodiversity_hotspot), licensed by Creative Commons 3.0

floristic gradients could be observed at more local scales in the form of elevational gradients across mountains (Lomolino et al. 2010). Charles Darwin (1839) and Alfred R Wallace (1853) also highlighted the luxuriance of plant and animal life in the Neotropics, especially in Amazonia. Wallace (1878) pointed out that these pioneer observations not only revealed a major biogeographical pattern, but also implicitly hypothesized about its potential causes, with emphasis on the increasing climatic severity from the tropics to the poles and the resulting intensification of the struggle for the existence (Lomolino et al. 2010).

Until the 1970s, the Neotropics—and the tropics, in general—were considered climatically stable areas that have been free from the influence of Pleistocene glaciations. In this context, diversification theories considering only rather static latitudinal energy gradients like the present ones dominated the scene. This view changed when widespread evidence of Pleistocene climatic shifts in tropical areas started to accumulate (Damuth and Fairbridge 1970; Emiliani 1971; Ab'Saber 1982). In the Neotropics, these environmental changes were considered to have fostered biotic diversification, mainly through sea-level changes, temperature-driven elevational migrations of montane ecological belts, and intense moisture changes in the lowlands (Simpson 1971). The first general theories about Neotropical