

PART VI

Synthesis

On the origin of Amazonian landscapes and biodiversity: a synthesis

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Abstract

In northern South America the Cenozoic was a period of intense tectonic and climatic interaction that resulted in a dynamic Amazonian landscape dominated by lowlands with local and shield-derived rivers. These drainage systems constantly changed shape and size. During the entire Cenozoic, the Brazilian and Guiana Shields were stable mountainous areas. Andean-derived river systems increased in importance especially in the Neogene. A remarkable feature in western Amazonian history is the waxing and waning of large lake systems and embayments. By the Late Miocene (about 11 Ma), the Andes were connected with the Atlantic through an incipient Amazon River, and from c. 7 Ma Andean-derived river systems became fully established in central and eastern Amazonia and the modern landscape configuration had developed. Rainforests already existed in northern South America during the Paleogene, but the modern rainforests – with resemblance to the Present forest – only developed during the Miocene. The western Amazonian Miocene record contains very diverse aquatic faunas (molluscs, ostracods, turtles, crocodiles, fishes) as well as terrestrial mammals. Remarkable gigantic forms thrived in Amazonian ecosystems at the time. Since the Late Miocene, edaphically heterogeneous lands emerged in western Amazonia in areas previously occupied by lake systems. At the same time nutrient-rich deposits spread over central and eastern Amazonia, an event that, based on molecular phylogenetic studies on extant taxa, coincided with diversification of terrestrial taxa. Molecular-based time estimates confirm the steady diversification and mostly pre-Quaternary origin of extant Amazonian taxa. A significant portion of the current species richness is attributed to a combination of relatively constant wet and warm climates and a heterogeneous edaphic substrate. The Quaternary was a time of distribution shifts, but can no longer be considered a time of diversification in Amazonia.

Introduction

Amazonia comprises the world's largest rainforest and river system. It is the stage for a staggering diversity of life. With an estimated two to three thousand species, the Amazonian fish fauna

makes up more than 20% of freshwater fish species in the world (Lundberg *et al.* 2000; Reis *et al.* 2003). Floristic diversity is enormous, with up to 473 tree species occurring in a single hectare of lowland Ecuadorean rainforest (Valencia *et al.* 1994). Not only are the high species numbers in Amazonian ecosystems remarkable, but also the ecological and evolutionary interactions among these species are equally surprising. For example, insects and other small animals evading swarming raids of the army ant *Eciton burchelli* form the main diet of several species of antbirds (Thamnophilidae), a group of birds highly and sometimes exclusively specialized for such a behaviour (Brumfield *et al.* 2007). The Amazon forests and rivers are rife with such extraordinary expressions of life.

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Until the 1990s not even the approximate timing of the origin of modern Amazonia was known, nor was the time of origin of the modern highly diverse biota (Antonelli 2008). Diversification in long-term stable rainforest (e.g., Raven & Axelrod 1974) as well as Quaternary ice-age perturbations (Haffer 1969) and even more complex interacting processes on a variety of timescales (Bush 1994) were used to explain the origin of Amazonian diversity. The diversity patterns themselves were poorly understood on all scales. Nelson *et al.* (1990) showed that presumed biodiversity hotspots in lowland Amazonia were an almost perfect match with the location of biological field stations and biological expeditions. The combination of poorly mapped or interpolated diversity patterns, together with incomplete insights into the geological history of the Amazon region, has allowed for the creation of grandiose but often poorly data-supported theories about the origin of modern Amazonian ecosystems and biodiversity, some of which continue to dominate the debate about Amazonian origins.

In the past few years many new and relevant insights into the development of Amazonian landscapes and biodiversity have been gained from a range of sources. The Miocene timing of the onset of the Amazon River system (Dobson *et al.* 2001; new data presented in Figueredo *et al.* 2009), the nature of former Amazonian landscapes and river systems (Hoorn 1994a; Hoorn *et al.* 1995; Lundberg *et al.* 1998), the development of past rainforest floras (Hoorn 1994a; Jaramillo *et al.* 2006) and faunas (e.g., Wesselingh & Salo 2006; Latrubesse *et al.* 2007) and their relationship with floras and faunas of areas currently outside Amazonia (Albert *et al.* 2006) became more clear. Furthermore, the nature and impact of tectonic events (Espurt *et al.* 2007; Mora *et al.* 2008) on Amazonian landscape evolution became increasingly appreciated. Substantial progress has been made with the documentation and modelling of species richness and biodiversity (see references in Ruokolainen *et al.* 2007 and Chapter 21). These studies permitted insight into the relationships between diversity and environmental factors such as edaphics, which in turn has allowed consideration of the development of edaphic heterogeneity in Amazonian history (Ruokolainen *et al.* 2007 and references therein; Arbelaez *et al.* 2008). Finally, the advent of molecular phylogenetic work in the 1990s has provided additional independent insights into the timing of the origin of Amazonian diversity (Lovejoy *et al.* 1998; see also Chapter 24 and references therein). Together, all these recent developments have led to considerable advances in our understanding of the causes underlying the origin and evolution of Amazonian biodiversity.

By combining insights from scientific areas as diverse as sedimentology, molecular phylogeny, climatic modelling and palaeontology, we aim to sketch an outline of the timing and context of the origin of Amazonian ecosystems and diversity. Parallels among insights from the various disciplines presented in this book are explored. This chapter ends with an updated chronology of Amazonian history (see also Plates 14–16).

Landscape evolution and driving factors

The outline of the Amazon River has existed since c.11 million years ago (Ma) (Figueredo *et al.* 2009). Prior to the establishment of the Amazon River, the region also contained fluvial regimes,

but these had completely different watershed boundaries and mostly lacked Andean rivers (Hoorn *et al.* 1995; Lundberg *et al.* 1998; see also Chapter 7). Also, huge lake/wetland systems and marginal marine embayments occurred, especially in western Amazonia (Hoorn 1994b; Wesselingh *et al.* 2002). While lowlands experienced drastic changes, the shields in the east were by comparison ultrastable landscapes characterized by very slow denudation. Amazonian history is disproportionately represented in the geological record of intracratonic and sub-Andean basins as well as the Andes itself. Geological evidence from deeply altered and/or non-depositional central-eastern lowland Amazonia and the Shield areas is subtle at best. The available geological evidence points to two partially interacting factors that drove Cenozoic evolution of Amazonian landscapes, namely tectonics and climate.

Tectonism

Andean uplift is closely related to landscape evolution in Amazonia. However, many other tectonic processes have been identified that influenced Amazonian landscape development (Table 26.1).

An approximately 5° northward displacement of the South American continent since the Early Miocene shifted the position of lowland Amazonia with respect to the Equator. Before that, the Equator was positioned in central Colombia and the Guianas. It is therefore likely that the centre of convective rainfall, as well as the presence of warm and wet conditions, also would have had a more northerly position. Cenozoic Andean uplift changed the nature of connections between Amazonia and the Pacific and Caribbean coastal realm (Hoorn *et al.* 1995; Lundberg *et al.* 1998) as well as with drainage systems currently located within the Andes.

A major shift from fine-grained lacustrine depositional settings towards very coarse-grained fluvial depositional systems occurred in the Llanos Basin at around 10–11 Ma (Cooper *et al.* 1995), and was related to increased uplift of the Eastern Cordillera. This shift marked the closure of the northern connection between Amazonia and the Caribbean, which had existed for almost the entire Cenozoic. This coincided with geochemical signals that represent the arrival of Andean-derived sediments at the Amazon submarine fan (Figueredo *et al.* 2009) and the Ceara Rise (Dobson *et al.* 1997), recording the onset of the transcontinental drainage system. The shift of major depocentres from western Amazonia to the Amazon submarine fan at around 7.5 Ma coincided with overfill of the foreland basins (see Chapters 4 & 5), which in turn coincided with an episode of major uplift in the central Andes (Garzzone *et al.* 2008). Even in the ultrastable shield areas uplift had its effect, but was far more subtle. Low denudation rates in the shields must have been compensated by slow uplift in order to maintain the high mountains.

Uplift zones in lowland Amazonia (often referred to as arches) have played diverse roles in the history of the landscape and drainage development (see Chapter 7). However, their role has not been fully appreciated in the past. Uplift structures are transient features in geological time (a clear example is the migration of the El Baúl Arch in Venezuela as depicted by Pindell *et al.* 1998). Furthermore, the actual locality of some of the arches is still very

Table 26.1 Tectonic processes and their role in the evolution of Amazonian landscapes.

Tectonic process	Roles in landscape evolution	References
(sub-)Andean uplift	Fragmentation of drainage systems	Hoorn <i>et al.</i> 1995; Lundberg <i>et al.</i> 1998; Albert <i>et al.</i> 2006 and references therein; Espurt <i>et al.</i> 2007; see also Chapters 6 & 25
	Creation of rain shadows/wetspots	See Chapters 4 & 14
	Generation of erosive products/nutrients	Wesselingh <i>et al.</i> 2006b; Martin-Gombojav & Winkler 2008; see also Chapter 5
	Increasing landscape heterogeneity	Chapter 5
Foreland basin subsidence	Accommodation space for wetland development	Wesselingh <i>et al.</i> 2006b; see also Chapter 5
	Development of megafans	Chapter 10
	Enabling stream avulsions	Räsänen <i>et al.</i> 1987, 1992; see also Chapter 14
	Creation of pathways for marine influence	Villamil 1999; Bayona <i>et al.</i> 2007, 2008
Intracratonic subsidence	Accommodation space for fluvial systems and wetlands	Chapters 3 & 5
	Pathway for nutrient-rich Andean rivers and cratonic influx	Figueiredo <i>et al.</i> 2009; Chapters 3 & 11
Cratonic uplift	Permitting/blocking marine influence	Hoorn <i>et al.</i> 1995; Bayona <i>et al.</i> 2007, 2008; see also Chapter 9
	Fragmentation of drainage systems	Figueroa <i>et al.</i> 2009; see also Chapters 2 & 8
Plate motion	Shift of latitudes/climate zones	Pardo-Casas & Molnar 1987
	Waxing/waning of island arcs and landbridges	Lundberg <i>et al.</i> 1998; Verzi & Montalvo 2008

problematic (Wesselingh & Salo 2006). On regional scales, tectonic uplift did shape drainage systems and influenced development of biodiversity in lowland Amazonia (Roddaz *et al.* 2005; Wesselingh *et al.* 2006a; Espurt *et al.* 2007; see also Chapter 6). According to Espurt *et al.* (2007) drainage basins became fragmented by the low-domed Fitzcarrald uplift during the Pliocene. Such fragmentation caused the isolation of riverine biota and should have promoted allopatric divergence. Domal uplift also exposed geological strata with very different textures and compositions and, therefore, contributed to increased edaphic heterogeneity in the region. An example of this is the Iquitos-Araracuara region (Wesselingh *et al.* 2006a). Edaphic heterogeneity has been considered a key factor in creating and sustaining high diversity of the western Amazonian floras (Ruokolainen *et al.* 2007 and references therein; see also Chapters 21 & 22).

As shown by the aforementioned examples, tectonic processes have unquestionably played a major role in shaping the development of Amazonian landscapes and biota, on a variety of temporal and spatial scales.

Climate

The suggested influence of climate on the development of Amazonian landscapes is summarized in Table 26.2.

The Amazonian hydrological cycle (the 'water cycle' of Salati & Vose 1984) is believed to be responsible for the wet conditions in

the Amazon region. The cell brings in moist air from the tropical Atlantic and precipitation is recycled westwards until it meets the Andean barrier (Salati & Vose 1984). Modelling results (see Chapter 13) indicate that a lowered Andean mountain chain would not cause reduced precipitation in the Amazon region as a whole. However, it would have increased the differences between dry and wet seasons. A major shift from more seasonal to more permanent wet conditions seems to have taken place in western Amazonia around the Oligocene-Miocene boundary (Wesselingh *et al.* 2006b), but a possible link with Andean uplift remains to be investigated.

Depositional regimes in floodplains and fans are strongly determined by drastically increased precipitation during El Niño-Southern Oscillation (ENSO) events (see Chapter 14). ENSO-type conditions date back into the Pliocene (Molnar & Cane 2007). Increased erosion and sediment transport through the Amazonian river systems must have taken place since that time. Indeed, such an increase is in agreement with increased sediment fluxes during the past 3 million years in the Amazon Fan area (Figueiredo *et al.* 2009), as well as increased Andean denudation in that period (Mora *et al.* 2008). The extent to which such an increased sediment transport can be attributed to the establishment of the ENSO or, for example, accelerated Andean uplift, and how both may have interacted (Mora *et al.* 2008), remains to be investigated. Today, as well as in the past, large parts of Amazonia are or have been located at altitudes low enough to be within reach of eustatic sea level changes (see, e.g., Chapter 11) that are ultimately controlled by global temperatures and polar ice cover (Miller *et al.* 2005).

Table 26.2 Climate and the development of Amazonian landscapes.

Climatic factor	Impact(s) on landscape	References
Amazonian hydrological cycle	Permanent wet megathermal (warm) conditions	Salati & Vose 1984; see also Chapters 12 & 13, and references therein
	Erosion of uplifted areas	Mora <i>et al.</i> 1998; see also Chapter 14
	Enabling large and dynamic riverine systems	Chapter 14
	Excess fresh water blocking marine incursions	Chapters 11 & 12, and references therein
	Deep weathering in lowlands and shield areas	Dohrenwerd <i>et al.</i> 1995
El Niño-Southern Oscillation	Episodic increase in denudation	Chapter 14
	Increased dynamic river channel behaviour	Chapter 14
Orbital cyclicity	Glacial-interglacial cooling/warming	Chapters 12 & 20
	Precession-driven changes in precipitation patterns/intensity	Chapters 12 & 20
	Erosional cycles	Chapters 12 & 14
	Local base-level changes driven by eustasy	Chapter 11, and references therein

The timing and amount of marine influence in Amazonian history have been a contentious issue. In Chapter 9, Hovikoski *et al.* show that hard geological evidence for marine influence is only available for limited periods of time, such as the Miocene. There is no geological evidence for marine settings in lowland Amazonia during the Quaternary (see also Chapter 11). The very strong precipitation surplus prevented marine influence extending into the low-lying Amazon river system. The low altitude of Amazonia is best exemplified by the base of the Negro River near Manaus, located about 2000 km from the mouth of the Amazon River and situated some 70 m below sea level. The magnitude of Cenozoic sea level change, often considered to be in the order of 100–200 m (Haq *et al.* 1987), was probably much lower than this (Miller *et al.* 2005) (Fig. 26.1).

Many new insights about Quaternary climate dynamics and its effect on vegetation cover in Amazonia have emerged in the past decade (see references in Maslin *et al.* 2005, and in Chapters 12 & 20). During the Quaternary, glacial cycles mostly affected temperature regimes, whereas precession cyclicity affected precipitation regimes in lowland Amazonia. Significantly drier conditions, or more seasonal conditions with a prolonged dry season, occurred mostly at the fringes of lowland Amazonia and parts of eastern lowland Amazonia. The core of lowland Amazonia has remained moist throughout the ice ages (see also Colinvaux & Oliveira 2000).

In the past decade it has become clear that Amazonian landscape development is the result of an interplay between different tectonic and climatic processes that interacted on various temporal and spatial scales. Increased stratigraphic knowledge of Cenozoic deposits has provided a better understanding of the location and timing of major landscape events. A synopsis of landscape evolution and biotic development is provided at the end of this chapter.

Evolution of Amazonian biodiversity: the message from DNA

Improved understanding of the timing and nature of landscape evolution in Amazonia allows assessment of the causes and processes underlying the diversification of its aquatic and terrestrial biota. In the past 15 years, the use of molecular techniques has opened a whole new avenue for investigating the origins of modern biodiversity. By reconstructing phylogenies and applying molecular clock methods, crude age estimates of major divergences became available. The basic assumptions underlying molecular clock estimates, such as stable molecular divergence rates, have been broadly questioned (see, e.g., Chapters 23 & 25). Even so, a clear message from molecular dating studies is that the outstanding biodiversity found today in Amazonia is evidently not the result of a single, time-limited event.

DNA sequence variation has been used to estimate divergence times among Amazonian aquatic taxa (see review in Chapter 25), plants (Antonelli 2008; see also Chapters 20 & 23) and tetrapods (see Chapter 24). The majority of these studies have shown that diversification in the Amazon region was a continuous process (see also Rull 2008) throughout the Cenozoic, with an apparent acceleration during the Miocene for several groups. Most extant lineages are too old to have been formed during the Pleistocene, which should be considered a period that affected distributional patterns and caused genetic differentiation at the level of populations, rather than a period when most species radiations took place, a long-held paradigm (Maslin *et al.* 2005; Antonelli 2008; Rull 2008; see also Chapters 20 & 24). Therefore, in the Amazonian lowlands in the Quaternary should possibly be considered as a period of net loss of diversity (Van der Hammen & Hooghiemstra 2000). For instance, molecular investigations resulted in Miocene age estimates for the origin of particular complex Amazonian life

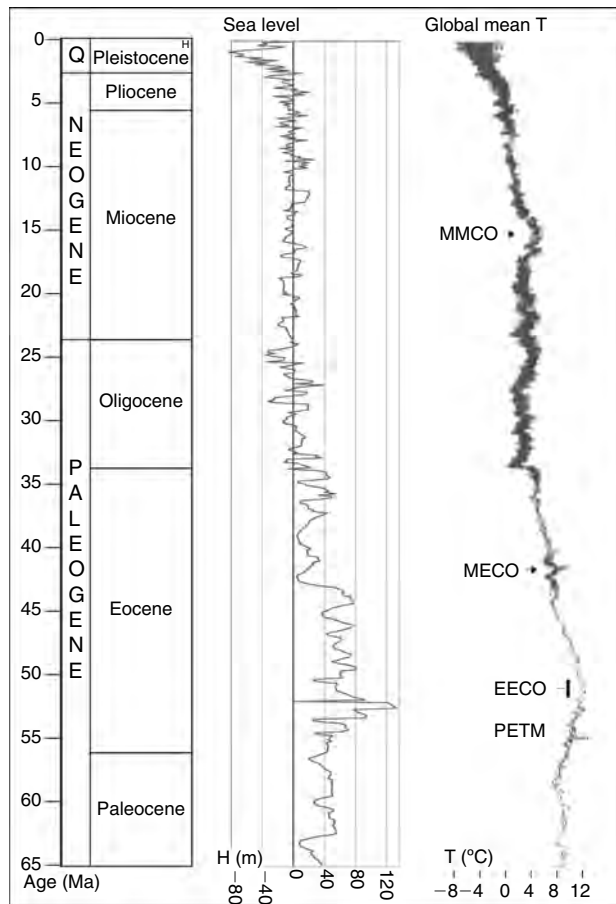


Fig. 26.1 Global climate and sea level during the Cenozoic. The sea-level curve is based on 100 thousand-year averages of data of Miller *et al.* (2005). The temperature (T) proxies derive from Zachos *et al.* (2008). MMCO, Middle Miocene climate optimum; MECO, Middle Eocene climate optimum; EECO, Early Eocene climate optimum; PETM, Paleocene-Eocene thermal maximum; Q, Quaternary; H, Holocene. Stratigraphic framework according to the International Commission on Stratigraphy (www.stratigraphy.org).

forms such as aquatic *Bromelia*-tank beetles and the tank habitat itself (Balke *et al.* 2008) and the development of the aforementioned ant birds (Brumfield *et al.* 2007).

In several cases molecular age estimates for major diversifications could be linked to geological events, although one should bear in mind the message provided by Lundberg *et al.* (1998) that a tendency exists to oversimplify putative relationships between geological events and speciation events, the documentation for both of which is often incomplete. Among several plant and animal taxa, a causal connection between the Andean uplift and diversification has been suggested for both montane and lowland lineages (Antonelli 2008; see Chapter 24). The timing of the evolution of freshwater Amazonian stingrays from a marine ancestor and their diversification coincides with the presence of large wetlands in lowland western Amazonia that acted as an interface with marginal marine settings during the Miocene (Lovejoy *et al.* 1998; see also Chapter 25). The timing of evolution of montane potato parasites

turned out to coincide with estimates of critical elevations of Andean mountains (Picard *et al.* 2007). The Late Miocene diversification of the montane genus *Hedyosmum* also coincided with major Andean uplift (Antonelli 2008).

Molecular phylogenetic methods are only applicable to modern biota. For areas lacking a fossil record, such as the Amazonian shield areas, they are the only way to estimate ages of biotic origins. The methods provide an estimate of the approximate ages of diversifications, but must be constrained by geological evidence and are not always consistent with fossil occurrences. Molecular age estimates give little insight into the geo-ecological context of speciation and the total diversity through time, as extinct taxa are excluded from such analyses. For that we must rely on geological evidence and, in particular, the fossil record.

Amazonian biodiversity and the fossil record

The Amazonian fossil record is unevenly developed. Miocene coastal formations in eastern Amazonia contain marine and continental fossils. However, large tracts of central and eastern lowland Amazonia and the shield regions are almost devoid of fossils. Western Amazonia and the Andean region, in contrast, have a very good fossil record that permits the reconstruction of diversity throughout geological history. In the current volume insights from plants, aquatic invertebrates, reptiles, fish, mammals and birds are reviewed.

Plants

Rainforests have existed in the Amazon region at least since 55 Ma, and even some rainforest biomes dominated by non-angiosperm plants have been identified in Cretaceous deposits of Colombia (Maslin *et al.* 2005; Jaramillo *et al.* 2006; see also Chapter 19). Pollen data from the northern Andes (Jaramillo *et al.* 2006) show that the angiosperm-dominated Paleocene rainforests were characterized by a low diversity. Species numbers (as inferred from pollen types: Weng *et al.* 2006) increased considerably during the Eocene, when almost all modern plant families were present. Diversity levels were higher than that of present-day Amazonia. In the Late Eocene plant diversity gradually declined and dropped steeply at the Eocene-Oligocene boundary, coinciding with a major global cooling event (Zachos *et al.* 2001, 2008; Jaramillo *et al.* 2006) (see Fig. 26.1). The pollen record from western Amazonia indicates that during the Early Miocene, forests resembled modern Amazonian forests on a generic level and were possibly more diverse than at Present (Hoorn 1994a; see Chapter 19). Further diversifications occurred in the Late Neogene in lowland Amazonia at the same time as rainforests disappeared to the north in Venezuela. The composition of the lowland Amazonian rainforests changed throughout the glacial cycles of the Quaternary, and the fringes of the forest were severely affected (Freitas *et al.* 2001), but total diversity and the overall nature of these forests remained very similar (see Chapters 19 & 20). There is no evidence from the pollen record supporting the proposition that speciation was more important than extinction during the Quaternary: a net increase in diversity has not been substantiated. However, species richness of montane plant species did increase in

the Andes during the Quaternary (Hooghiemstra & van der Hammen 2004).

Aquatic invertebrates

Fluvial mollusc faunas dominated by pearly freshwater mussels and freshwater cerithioidean snails have been present in the Amazon region throughout the Cenozoic (see Chapter 18). During the Miocene, however, two additional groups of invertebrates became established in western Amazonia. In short episodes, species with marginal marine affinity were present including several molluscs, ostracods, foraminifers, barnacles and crustaceans, the latter leaving characteristic trace fossils (see Chapters 9 & 18). More prominently, during the Early and Middle Miocene, large diversifications of endemic freshwater ostracod and mollusc faunas occurred in huge lake-swamp systems of the Pebas mega-wetland (see Chapters 8 & 18). These endemic faunas disappeared with the termination of the Pebas system around the Middle-Late Miocene transition, some 11 Ma. Late Miocene invertebrate faunas are very rare, and to date only freshwater mollusc fossils have been found as well as freshwater to brackish-water trace fossils of crustaceans. The modern diversity of Amazonian aquatic molluscs is remarkably low (Fittkau 1981), in contrast to the modern Amazonian decapod faunas.

Aquatic vertebrates

The Miocene Amazonian crocodile and turtle fauna (see Chapter 16) is the most diverse ever found, both in species numbers as well as in disparity. The fauna of major wetlands in the Early-Middle Miocene suggests only very limited marine influence, but a Late Miocene change to fluvial dominated faunas is observed. Among the aquatic reptiles, the diversity of slender snouted gharials and the huge size of the caiman *Purussaurus* (up to 12 m) and the turtle *Stupendemys* (possibly up to 4 m) are remarkable features (see Chapter 16 and references therein).

The Amazonian fish fauna evolved steadily throughout the Cretaceous and Cenozoic (Lundberg *et al.* 1998; see also Chapter 25). By the Middle Miocene it was essentially a modern fauna, with all major modern clades present (see Chapter 17). Subsequently, local extirpation occurred as well as modest speciation. Fish faunas have been very important in efforts to reconstruct the changing outlines of Amazonian aquatic ecosystems. During the Paleogene and Neogene these systems included areas currently located in Andean and Orinoco drainage basins. The separation of these peri-A Amazonian areas from lowland Amazonia in the Late Miocene led to additional allopatric speciation as well as extinction (Albert *et al.* 2006; see also Chapters 17 & 25).

Manatees and freshwater dolphins, two very conspicuous groups of aquatic mammals, have an Amazonian fossil record that extends back at least to the Miocene (see Chapter 15).

Terrestrial vertebrates

The Paleogene terrestrial vertebrate record in northern South America is very poor, with the exception of the Santa Rosa locality

of Peruvian Amazonia (Campbell 2004). The fauna of that locality hints at the existence of a diverse South American mammal fauna around the Eocene–Oligocene transition (see references in Campbell 2004). In contrast, the Amazonian Miocene mammal record is very rich (see Chapter 15). A diversified South American fauna with, for example native ungulates, existed during the Middle Miocene. Especially the Late Miocene faunas from the Acre region are very rich in species and include remarkable gigantic forms. The Acre fauna contains a highly diversified terrestrial fauna of South American groups in which xenarthrans (including sloths) and toxodontids (hoofed herbivorous mammals) were especially diversified. In the latest Miocene, some 6 Ma, North American immigrants related to the Great American Biotic Interchange (GABI) appeared in South America (see references in Stehli & Webb 1985; Verzi & Montalvo 2008; and Chapter 15). The arrival of these immigrants appears to be related to the severe decline of native South American mammals during the Pliocene and Quaternary, the gigantic species amongst them.

The fossil record shows that the Amazonian fauna and flora were diverse during Eocene and especially Neogene times. The approximate timing and magnitude of several immigration and extinction events has been established. In the Neogene, extinction rates appear to have been low (see, e.g., Chapter 17, for fish) contributing to the high diversity in the region. Amazonian extinction events identified from the fossil record include floral extinctions in the Late Paleocene and at the Eocene–Oligocene boundary, the demise of the endemic Pebasian invertebrate faunas in the early Late Miocene, and the disappearance of many endemic mammal species during the Pliocene and Quaternary due to the arrival of North American immigrants, and eventually anthropogenic activity. The fossil record indicates that a highly diverse rainforest biota existed in northwestern Amazonia in the Eocene, and that modern forest and aquatic biotas already existed during the Miocene. Fossil evidence matches well with molecular evidence of a continued increase of diversity (positive speciation–extinction balance) throughout the Cenozoic and discards the Quaternary as a major period of speciation.

Cenozoic Amazonian landscapes and the development of its biota: an outline

The complete data set presented in this book permits us to sketch an outline of the evolution of Amazonian landscapes and biota. The chronology below is an update and summary primarily based on the paper by Lundberg *et al.* (1998), focusing on Amazonia. The reader is referred to that work, as well as to the different chapters of this book for more details and primary literature references. The evolution of Amazonian landscapes is summarized in Plates 14–16.

Cretaceous–Early Eocene (83–43 Ma): marine settings disappear, cratonic river systems dominate

During the Late Cretaceous, western Amazonia was a retroarc basin that sustained predominantly marine settings with a discontinuous proto-Andean island arc located to the west.

A major drainage divide was initially located at the eastern end of the modern Amazon valley (the so-called Gurupá high; Figueiredo *et al.* 2004; see also Chapter 7), dividing short drainage systems eastwards from the transcontinental east–west-running precursor of the Amazon system. The drainage divide shifted westwards to the Monte Alegre high, also in eastern Amazonia, during the Late Cretaceous (Figueiredo *et al.* 2004; see also Chapter 7). The major Amazonian river systems probably emptied into the sea in the current Peruvian and Ecuadorean sub-Andean basins.

From the Late Cretaceous until the Early Eocene, the Andean island arc became a more permanently uplifted feature and marine settings retreated northwards. The accompanying transformation of the retroarc basin into the sub-Andean foreland basins was completed by the Late Paleocene (some 59 Ma). A short-lived but widespread marine incursion covered most of the foreland basin during the late Early Paleocene (some 60–61 Ma). The newly formed foreland basin zone entrenched a major south–north fluvial system that had its headwaters in central Argentina. The river system ran all the way to northern Colombia/western Venezuela. Shield areas were positive landscape features and remained so throughout the Cenozoic.

The marine settings in the Cretaceous part of this period have produced a variety of fossiliferous marine strata that are nowadays located throughout the Andean and sub-Andean zones. Low-diversity non-angiosperm-dominated rainforests existed in Brazil during the Cretaceous (see Chapter 19). Angiosperm-dominated low-diversity rainforests developed in northern Andean areas during the Paleocene (Burnham & Johnson 2004; Jaramillo *et al.* 2006). During the Late Paleocene, rainforests diversified but almost at once underwent a major drop in diversity. During the Early Eocene, Amazonian rainforest diversity increased and reached levels of species richness that are greater than today's. Wetlands similar to those found today in the Pantanal have been reconstructed in more southerly areas, currently located in Bolivia. Very little is known about the impact of the Yucatan meteorite at the K–T (Cretaceous–Paleogene) boundary on lowland Amazonia, but given its comparative proximity it would be logical to suppose that the biota suffered badly from this event. Between 56 and 59 Ma, a land connection or closely spaced island arc connection existed between North and South America, facilitating dispersal of boreotropical/holarctic taxa into and tropical taxa out of South America (Iturralde-Vinent & Macphee 1999).

Middle Eocene–Early Oligocene (43–34 Ma): Andean closure and episodic marine incursions into western Amazonia

During this time interval, the south–north-trending fluvial system located in the Andean foreland basins dominated much of northern South America. The southernmost river systems were sequestered during this period, and the major Amazonian and Paraná continental divide shifted northwards from present-day Argentina into Bolivia. The divide between the eastern- and western-flowing Amazonian rivers was possibly still located at the Monte Alegre high in eastern Amazonia. During this time interval, the northwestern Amazonian lowlands were invaded by the

sea, developing large, partially brackish marine embayments (Santos *et al.* 2008; Lundberg *et al.* 1998 and references therein). The marine incursions were episodic, and these western lowlands also were occupied by continental and freshwater environments. Major Andean exhumation has been reported from the Ecuadorean Cordillera Real and the sub-Andean zone between 30 and 43 Ma (Martin-Gombojav & Winkler 2008) related to the break-up of the Farallon Plate. Shield areas were positive landscape features and experienced humid tropical climates, resulting in the development of deep lateritic soils (Theveniaut & Freyssinet 2002).

During the Late Eocene, diversity in rainforests of the northern Andean zone decreased (Jaramillo *et al.* 2006). A major drop in diversity occurred around the Eocene–Oligocene boundary, coinciding with a major global cooling event (Zachos *et al.* 2001). Pollen and organic-walled microfossils (Santos *et al.* 2008) as well as foraminifers (Tschopp 1953; Burgos 2006) are evidence of marine influence in western Amazonia. A terrestrial assemblage of Late Eocene/Oligocene age in eastern Peru (Campbell 2006) hints at the existence of a diverse endemic tropical megafauna. The Amazonian fossil record of this period is otherwise very poor. Between 35 and 33 Ma, biotic interchange between the boreotropical region (southern Laurasia) and South America occurred over the proto-Greater Antilles/Aves Ridge, a semicontinuous land bridge or closely spaced island arc (Iturralde-Vinent & Macphee 1999; Antonelli 2008; Verzi & Montalvo 2008).

Oligocene (34–24 Ma): sub-Andean trunk river and denudation in the shield areas

Amazonia was mostly part of the south–north-trending river drainage. On its western margin, white-water tributaries draining the emergent Andes delivered substantial amounts of sediments. On the eastern side, cratonic and lowland rivers ran into this south–north trunk river system. Although the exact timing is uncertain, the major drainage divide between west- and east-flowing Amazonian rivers may have shifted from the Monte Alegre high in eastern Amazonia to the Purus Arch in central Amazonia during the Oligocene. In the Llanos Basin and western Venezuela this river system emptied into the marine Carboneras–Roblecito embayment. The drainage divide with the Paraná system to the south was located at the Chapare buttress in central-eastern Bolivia (Lundberg *et al.* 1998). Major uplift occurred in the Central Andes as well as in the Northern Andes (e.g. Garzzone *et al.* 2008; Parra *et al.* 2009). In the Eastern Cordillera in Colombia for instance, uplift is registered around 30 Ma (Parra *et al.* 2009). In the shield areas the formation of lateritic soils continued, but the Oligocene is also a period when part of the deeply weathered sediment cover was stripped (Theveniaut & Freyssinet 2002). This period of continental uplift may be possibly related to the break-up of the Farallon Plate.

In western Amazonia, the climate regime was probably more seasonal than today, with a more prolonged dry season (Wesselingh *et al.* 2006b). Rainforest diversity in the northern Andes was low (Jaramillo *et al.* 2006). The fossil record of the Oligocene in Amazonia is very sparse but includes rodents, marsupials and notoungulates (see Chapters 15 and 24). It permits only limited insights into the flora and fauna during that period.

Early-Middle Miocene (24–11 Ma): Pebas mega-wetland and the establishment of modern rainforests

During the Early and Middle Miocene, the South American continent drifted several degrees northwards (Pardo-Casas & Molnar 1987). The Pebas mega-wetland (see Chapter 8) extended from the northern sub-Andean basins eastwards and occupied part of western Amazonia during the Early Miocene, and most of it during the Middle Miocene. At its maximum this vast network of lakes and swamps covered an area of over one million km². Aquatic habitats were more or less continuous, but their configuration must have changed with base-level changes. The Pebas system was open to marine settings towards the north. Several episodes of increased marine influence are found in Miocene deposits in the Colombian Llanos Basin (Bayona *et al.* 2007, 2008), which can probably be matched with episodes of increased marine influence in the Pebas system. Short-lived lowland connections between Amazonia and the Pacific coast also may have occurred (Steinmann *et al.* 1999). From the west, the Pebas system was fed by short rivers draining the emergent Andes. Much of the erosive products of these rivers were deposited in a narrow wedge on the west side of the Pebas lake system (see Chapter 5). During the Early-Middle Miocene, Andean uplift continued. In the Bolivian-Peruvian segment, uplift progressed northwards. Further north, major uplift occurred in the Colombian Central Cordillera and areas in Eastern Cordillera and the Venezuelan Andes. The marine Roblecito embayment had vanished and lowland corridors between the Llanos Basin and the Caribbean shifted towards the East Venezuela Basin (Wesselingh & Macsotay 2006). Direct lowland aquatic connections between the Llanos Basin and the Falcon Basin also persisted. Rivers draining Central Amazonian lowlands and the adjacent shield areas west of the Purus Arch flowed into the Pebas system. In shield areas a major episode of deep lateritic soil development (Theveniaut & Freyssinet 2002) indicates humid tropical settings. Drainage systems in the higher parts of the Guiana Shield remained in place for millions of years (Dohrenwerd *et al.* 1995). The major drainage divide between eastern and western Amazonia was located at the Purus Arch in Brazil. Lowland Amazonia east of the Pebas wetlands was a cratonic-riverine landscape with poor and deeply leached soils. Along the Guyana and northeastern Brazilian coasts carbonate platforms developed.

The climatic record (see references in Chapter 12) indicates that lowland Amazonia experienced wet-tropical climates similar to the Present. The Amazon hydrological cycle was already in place. To the north (Llanos and Magdalena regions, Colombia) and south (Chaco, Bolivia), conditions were more seasonal, like at Present. The wetlands of western Amazonia were surrounded by tropical rainforests (Hoorn 1994a). These forests probably entirely covered lowland Amazonia, including eastern Amazonia (see references in Chapter 19). Diversity levels, as provisionally reconstructed from pollen records, are comparable with the Quaternary records, and at some stratigraphic levels are even more diverse (see Chapter 19). Carbonate environments of the coastal Marajó region, near the modern Amazon mouth, indicate the absence of Andean rivers at the time. However, there are indications of cratonic fluvial input. The aquatic ecosystems of western Amazonia hosted a highly varied aquatic fauna that included diverse crocodylian, turtle and

fish faunas as well as mostly endemic mollusc and ostracod faunas. In adjacent forests a diverse mammalian community was present. The wetlands were fringed by extensive palm swamps dominated by *Mauritia*-like palms. During the Miocene, potamotrygonoid stingrays evolved from marine ancestors into the Amazonian freshwater systems (Lovejoy *et al.* 1998).

Late Miocene (11–7 Ma): the Acre mega-wetland and the transcontinental aquatic corridor

Around 11 Ma the transcontinental drainage was established (Figueroa *et al.* 2009). Until some 7.5 Ma, marine influence reached western Amazonia, almost certainly through the Amazon trunk valley. Andean sediments were mostly captured in the foreland basins, occupied by large fluvio-tidal landscapes termed the Acre mega-wetland (see Chapter 8) (see Plates 14–16). The presence of a transcontinental corridor is shown by geochemical signals of Andean origin in deep-sea sediments in the Amazon submarine fan and the Ceará Rise. During the Late Miocene, the Orinoco system became separated from the Amazon system, and additionally small drainage systems in the Andean zone were separated from the Orinoco and Amazon systems. Uplift in the Central and Northern Andes accelerated, most noticeably in the Eastern Cordillera and the Venezuelan Andes (Garzzone *et al.* 2008; see also Chapter 4).

The Guiana Shield and presumably also the Brazilian Shield remained under tropical humid conditions, as deep lateritic soils suggest. The geochemistry of Amazonian-derived sediments in the Ceará Rise also implies the presence of predominantly wet tropical climates throughout lowland Amazonia (Harris & Mix 2002). Vegetational reconstructions from scarce pollen data from Acre, which at the time was located at the southern rim of the Amazon region, indicate that rainforests existed but that herbs (and thus more open landscapes) also occurred (Latrubesse *et al.* 2007; see also Chapter 19). Molecular phylogenetic studies of plants and tetrapods (Antonelli 2008; see also Chapter 24, and references therein) indicate a major diversification in Amazonia during the Late Miocene extending into the Pliocene. The diversification appears to be partially linked to major uplift of the Eastern Cordilleras of the northern and central Andes (Gregory-Wodzicki 2000; Garzzone *et al.* 2008), from where newly formed plant lineages dispersed to the lowlands and underwent rapid radiations (Antonelli 2008).

Late Miocene-Pliocene (7–2.5 Ma): onset of the modern Amazon River system

During the Late Neogene, Andean uplift increased. In many areas altitudes similar to today's were reached by the Late Pliocene (Garzzone *et al.* 2008; Mora *et al.* 2008; see also Chapter 4 and references therein). In the course of the Pliocene, uplift in western lowland areas, such as the Fitzcarrald Ridge in southwestern Amazonia, caused compartmentalization and entrenchment of the upper part of the Amazonian river system. During this period, aquatic biota in Andean and Amazonian systems became separated (see Chapter 25).

At about 7.5 Ma the sub-Andean basins were overfilled and sedimentation shifted towards the Amazon submarine fan. Marine influence had disappeared from lowland Amazonia, and the transcontinental Amazon River system became a fully fledged river system. The entire sub-Andean zone became the focus of thick accumulations of coarse-grained clastic deposition, partially in megafan systems, fed by the rapidly emerging Andes (see Chapters 4 and 10). The early lowland Amazon River system may have been different from today. In many areas, the rivers were less entrenched in valleys, and courses may have been widely shifting. Shield areas were stable cratonic landscapes, with the exception of the lower western margin of the Guiana Shield, which probably was gently uplifted.

ENSO climate conditions were established during the Pliocene (Molnar & Cane 2007). Precipitation anomalies associated with this phenomenon are disproportionately responsible for erosion and transport of sediments in the Amazon system (see Chapter 14). During the Pliocene, the amount of Andean sediments reaching the Amazon submarine fan increased dramatically (Figueroa *et al.* 2009) causing a rapid progradation along the Guyana coast. Almost no fossil floras and faunas are available from the Late Miocene and Pliocene in Amazonia. From regions to the south of the Amazon we know that the earliest North America immigrants related to the Great American Biotic Interchange (GABI) started to occur around 6 Ma (Verzi & Montalvo 2008), before the final emergence of the Panama land bridge about 3.5 Ma (Briggs 1994; Molnar 2008).

Quaternary: ice ages in Amazonia (<2.5 Ma)

The climatic oscillations of the Quaternary caused altitudinal shifts in biomes and changing communities within the rainforest (see Chapter 20 and references therein). Major landscape features in Amazonia were established by the beginning of the Quaternary. The Amazon trunk river became increasingly entrenched into valleys as a result of slow continental uplift and strong erosion (see Chapter 11). During each glacial cycle the Amazon River and tributaries experienced a depositional cycle of headward erosion during glacial lowstands, submergence during sea-level rise, and sedimentary infill during interglacial highstands, the so-called 'Irion cycle' (F.P. Wesselingh & C. Hoorn 2009). The recurring erosion of fluvial deposits along the main Amazon River during glacial lowstands resulted in the deposition of large quantities of sediment in the Amazon submarine fan and contributed to the fringes of Amazonia experiencing recurring drier conditions at precession timescales (c. 20 ka; see Chapter 20). In the Andes and Guiana highlands, plant communities shifted up and down slopes and their composition changed (Hooghiemstra & van der Hammen 2004; Rull 2004, and references therein). Forests in lowland eastern Amazonia were at times more open, and 'edaphic' savannas may have developed in some regions. However, the major part of the Amazon rainforest remained intact (Maslin *et al.* 2005; see also Chapter 20). During the Quaternary many conspicuous large-bodied South American mammals became extinct, possibly as a result of the arrival of North American immigrants, including, ultimately, humans. Over the course of the past five centuries the entire ecosystem has been increasingly threatened. Currently, large tracts

of forests are being emptied of their valuable timber. Animal life in many places is hunted down and large areas are being converted to agricultural land. Amazonian ecosystems face challenges at a magnitude and rate unseen throughout their entire Cenozoic history.

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