



# AMAZONIA: LANDSCAPE AND SPECIES EVOLUTION

A LOOK INTO THE PAST

EDITED BY  
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# **Amazonia: landscape and species evolution**

## **A look into the past**

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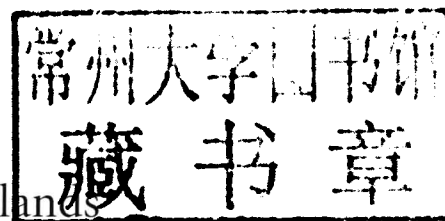
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# *Dedication to Thomas van der Hammen*

We dedicate this book to the life and work of Professor Thomas van der Hammen who is one of the most prominent Dutch geoscientists, making many links between geology, biology and archaeology. The study of altitudinal vegetation distributions in the northern Andes is a red line through his work and it has served studies of the Neogene uplift history of the northern Andes as well as studies of pollen-based Pleistocene climate change. During more than two decades he lectured at the University of Amsterdam and inspired generations of Dutch students. Since his retirement in 1989 he has lived in Colombia where, with his never-ending enthusiasm, he continues to motivate large numbers of Colombian students.

Carina Hoorn, Frank P. Wesselingh (editors)

Henry Hooghiemstra, Hubert Vonhof, Salomon Kroonenberg  
(editorial advisors)



## **Biography**

Thomas van der Hammen was born in The Netherlands in 1924 and had an innate interest and love for nature. After the Second World War he studied geology at Leiden University. He was trained as a palynologist by Professor F. Florschütz but also had regular contact with other founding fathers of this discipline such as J. Iversen and R. Potonié. His PhD dissertation was on '*Late*

*glacial flora and periglacial phenomena in the Netherlands*', a subject that would remain of interest to him for the rest of his life. In 1951 he started working for the Geological Survey in Colombia and did pioneering research on Cretaceous and Cenozoic sediments. Through his trademark multidisciplinary approach he unravelled the stages of tectonic uplift of the Andes. Later, he and his co-workers were able to make a link with the evolution of the montane forest and *páramo* vegetation of the Northern Andes.

In 1959 Thomas returned to The Netherlands and worked at the Department of Geology of Leiden University. He developed a research line in palaeoecology and climate history in the eastern part of The Netherlands while continuing his research in tropical palynology, often in cooperation with the geologist Lex Wijmstra, and focusing on exploratory studies in Guyana, Suriname and the Amazon Basin. In 1966 Thomas moved to the University of Amsterdam where he was appointed as a Professor in Palynology. A suite of both Dutch and Colombian (PhD) students were trained in topics such as geology, archaeology, biostratigraphy, climate history and vegetation analysis, and conducted field work in areas located in Brazilian Amazonia, Colombian Amazonia, the Colombian Andes and Venezuela. During the late 1970s and early 1980s he designed the large 'Ecoandes Project' and the 'Tropenbos Colombia Programme' respectively. The Ecoandes Project focused on integrated palaeo/actuo-ecological research of transects across different sectors of the Colombian Andes. These unprecedented studies resulted in seven volumes in the series *Studies of Tropical Andean Ecosystems*, published at Cramer/Borntraeger in Germany. The Tropenbos Colombia Programme studies focused on a wide variety of subjects, ranging from fishery, plant systematics, floristic inventories, sociogeographical studies, anthropology, palaeoecology, geology and tropical vegetation ecology. These studies resulted in 20 volumes of the series *Studies on Colombian Amazonia*, published at Tropenbos-Colombia office in Bogotá. To promote distribution of scientific results among Colombian institutes and colleagues around the world in 1973 he started the series *El Cuaternario de Colombia* [*The Quaternary of Colombia*], which he edited up to volume 20 (1995).

Perhaps his most valuable contribution to science was to increase our understanding of the history of Pleistocene climate change. His training in the climate history of Western Europe

enabled him to show us that the Neotropics also had a dynamic history of climate change. Thomas van der Hammen discovered the immense value of the pollen archives in the deep intra-Andean sedimentary basins. He studied the first deep boreholes in the Bogotá Basin and the Fúquene Basin, and created a basis for later studies on long continental pollen records from Colombia. During the decades that Thomas lectured in The Netherlands he played an active role in Dutch nature conservation and in developing international structures for nature assessment studies. His contributions to the advancement of science were rewarded by her Majesty Queen Beatrix with a knighthood.

After his retirement he implemented his valuable experience in Colombia and, in collaboration with national research institutes such as the Geographical Institute (IGAC), the Geological Institute (Ingeominas), the Archaeological Institute, and the Von

Humboldt Biodiversity Institute, he helped to promote many collaborative studies. Thomas van der Hammen was the author of more than 100 international peer-reviewed publications and contributed much to our understanding of tropical ecology and tropical climate history. His contributions to the training of Colombian scientists, and to the development of nature conservation and awareness of infrastructural issues in Colombia are highly valued. For the latter Thomas received the Colombian *Order of San Carlos*, which he received out of the hands of the Colombian President. Thomas's enthusiasm, charisma, vision and ability to make people work together made him a most inspiring person and a true leader.

Henry Hooghiemstra and Carina Hoorn

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# Prologue

It is now almost 60 years since I arrived in Colombia for the first time to start investigations for a geological survey. I had one great desire: to work in Amazonia. Very soon afterwards, early in 1952, this desire was fulfilled; for one month I was able to work in one of the most remote and undisturbed areas of Western Amazonia, the middle to lower Apaporis River, to study the flora and the geology. This was possible because of the help of the (ethno)botanist Dick Schultes, who had good relations with the rubber trade company in Soratama. The company had a base there and collected rubber from the local Indian tribe. Once a month this rubber was sent to Bogotá with the Catalina (a small airplane) but – on request – it occasionally also transported researchers.

An assistant, two local Indians and I set off in a tree-canoe equipped with two hammocks, a plant-press, sample bags and some food. We travelled several hundreds of kilometres along the Apaporis and Cananari Rivers to study the rainforest and the outcrops. We climbed the table mountains, measured the cross-bedding in the old *tepui* sandstone formations and established that in early (Palaeozoic) times the rivers ran to the northwest, instead of to the modern southeasterly direction. We also encountered the younger Tertiary sediments, and concluded that the presence of iron oölite and manganite could only indicate one thing: that lacustrine and brackish-water conditions had once ruled in the heart of Amazonia.

After a month of fieldwork in the area I came back to Soratama to wait for the plane; Schultes also arrived from another expedition at the same time, and so we had some days together. We were out of food and lived on what was available in Soratama. One day Schultes said to me: 'I have still a tin with plum-pudding, let's go into the forest and eat it together!' And so we did: Christmas pudding in March, in the jungle. I was 27 years old then and at the beginning of a life lived in pursuit of understanding the composition and evolution of the forests through time in the Andes and in Amazonia.

It was some 25 years after our first Amazonian survey that I again saw samples from this area. This time they came in the form of bagged clays that were collected during an extensive Colombian survey, the Proradam project (1974 to 1979). The question that came with the bags was whether the age and environment could be established through palynology. A Neogene

age was soon evident, and the presence of abundant pollen of mangrove trees (*Rhizophora*) for the first time confirmed the presence of saline or brackish waters in ancestral Amazonia.

Around this time two other major geological and geographical surveys were carried out in Brazil: the RadamBrasil survey and the coal exploration project by the Companhia de Pesquisa de Recursos Minerais (CPRM). The latter project drilled close to 50 cores in the subsurface of Brazilian Amazonia, and so far constitutes the best register of Neogene Amazonian history. In addition, the Brazilian oil company Petrobras drilled numerous cores though the Lower to Middle Cretaceous, which permitted the reconstruction of the floral history of that period. There were of course also groups of dedicated researchers who spent most of their life in Amazonia. One of them was Harald Sioli, who recently died but is much remembered through both his research papers and his autobiography.

Another 10 years passed and in the 1980s Tropenbos International, an initiative of the Dutch government, established a large research project with the Amazonian ecosystem as its focal point. Within this project, Carina Hoorn carried out a much more extensive and profound geological, palynological and environmental study of the Miocene of western Amazonia. This coincided with a renewed interest in Amazonia by several other countries, which all greatly increased our knowledge of the Neogene history.

Meanwhile Quaternary geologists and palynologists contributed to the knowledge of the younger Pleistocene-Holocene history of the area, indicating that Amazonia passed through periods of drier climate. Moreover, the first reconstruction by the international CLIMAP project (in 1976) of the Last Glacial Maximum indicated lower temperatures for Amazonia. It was Jürgen Haffer who in 1969 published his theory of speciation of Amazonian forest birds and his theory of glacial forest refugia. For many years his ideas had an enormous influence and caused deep controversies and forthright discussions, which, as more data become available, gradually became less extreme. The time necessary for the formation of subspecies or species may have been much longer than originally was assumed, but still the place and functions of the centres of endemism and their history continue to be a key point in the scientific debate.

The first palynological data that showed the glacial time transition of rainforest to grass-savanna (in Rondônia, Brazil), were published in 1972. These were followed by data showing the more or less continuous presence of forest in other areas (Lake Pata, in the north of Brazilian Amazonia), the drying up of lakes during the Last Glacial Maximum and/or the replacement of forest by open vegetation (Carajas, Brazil). Other areas (Rio Branco) in the northern part of Brazil show a well-dated glacial time and early Holocene extension of dune fields. Vegetation maps of the possible – or probable – situation during the Last Glacial Maximum, based on the available data and the use of present rainfall patterns, have been published, and are open to corrections – if and when more data become available.

Not all problems and discussions on Amazonia's past have been resolved, and the cause of its enormous biodiversity is one of the great mysteries that still need an explanation. Nevertheless, our knowledge has advanced considerably since 60 years ago, and the time seems to be right for a major effort to gather all our present knowledge on Amazonia's history and evaluate the problems and existing controversies, whilst reflecting on the gaps that still exist in our knowledge. Altogether this book will form a solid base to direct future research.

One of the most promising avenues of future research that can resolve some of our current questions is the study of genetics and the use of the molecular clock as an indicator of the separation of subspecies and species. This could enable us not only to compare geological and climatic history with the present climatic pattern, but also to assess the differences within Amazonia and the earlier proposed centres of endemism, as suggested by Haffer, Prance and others. These centres of endemism are, at least in part, related to geographical and climatic patterns that existed since the Late Miocene, Pliocene and the Quaternary. In particular, during

the glacial periods the differences may have become much more pronounced because of the resulting changes of vegetation.

It now seems more than probable that new species and subspecies were formed over millions of years; there are even strong indications that biodiversity was greater during the Miocene than at Present. This suggests that the speciation–extinction balance may have become negative during the Pleistocene glaciations, when the lower temperatures and drier climate intervals led to higher extinction rates (but eventually to the appearance of certain new subspecies).

The importance of the Amazonian rainforest and its enormous biodiversity for the conservation of the environmental equilibrium of the earth can only be underestimated. Moreover, the expected negative effect of the disappearance of a major part of the forest on both Amazonia and Earth as a whole, would affect us all. Therefore a better understanding of this sensitive ecosystem and its dynamics over a range of timescales is important to the global scientific and political community. The conservation of Amazonia, and a better understanding of its plant, animal and human life, is doubtlessly related to the future well-being of our planet.

This book may therefore be considered as a very important contribution to the knowledge of Amazonia, but also to science in general. It concludes a period of intensive investigations but also might herald the beginning of a new era of investigations that will hopefully lead us to the answers of many of the questions that for long have remained unanswered, and to more definite guidelines that will ensure the future of our Earth and its living inhabitants.

Thomas van der Hammen  
Chía (Colombia), July 2009

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# Introduction: Amazonia, landscape and species evolution

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## Motivation

The Amazon drainage basin covers over 8 million km<sup>2</sup> and has the largest rainforest on earth (Sioli 1984). The Amazon River is 6400 km long, from its source in the Andes to its mouth in the Atlantic, and the drainage basin includes a variety of landscapes such as the enigmatic *tepui* in the north, the forested slopes at the foot of the Andes in the west, and the wide tracts of rainforest in the central part of the basin.

The region is renowned for its great biodiversity, both aquatic and terrestrial. Exact figures to quantify this diversity do not yet exist, and estimates of species numbers are still increasing. This incomplete understanding of species numbers makes any firm estimate impossible; nevertheless, the region is thought to harbour no less than 7500 butterfly species (possibly about 40% of the world butterfly species), 1500 species of birds (about one-third of the world total) and an estimated 11,200 tree species (Hubbell *et al.* 2008).

The Amazon system plays a significant role in the world's climate as it produces about 20% of the world's oxygen supply. Nutrients delivered by the Amazon River to the Atlantic Ocean help to foster oceanic life that sequesters globally relevant amounts of carbon (Subramaniam 2008), and in the terrestrial realm the Amazon rainforest is responsible for 10% of the net primary productivity of the whole terrestrial biosphere (<http://earthobservatory.nasa.gov>). Therefore, Amazonia is of the greatest concern to us all.

In spite of Amazonia's importance the number of studies on species composition and their distribution is still limited. Diversity hotspots seemingly coincide with biological field stations and specific large-scale biological expeditions (Nelson *et al.* 1990), and indicate just how much basic research still is required. Even the classification of habitats in Amazonia is far from straightforward (e.g. Kalliola *et al.* 1993) as major parts of the region are hardly accessible and remote sensing techniques cannot grasp the variety without substantial 'ground-truthing'.

If our knowledge of Amazonia's present is limited, this is even more so for its past. When did the Amazonian landscape and

jungles arise? What climatic, chemical, geological and other non-biological processes were involved in the development of these ecosystems and sustain them now, and what part did they play in the previous episodic demise of these ecosystems? In order to assess ecosystem resilience it is imperative to understand the historical (i.e. geological) processes that have shaped Amazonian landscapes and their biota.

For decades scientists have speculated about the evolution of species and biodiversity. However, the scientific debate was mostly dominated by biologists and geomorphologists using species and geomorphology as a basis for their theories (Haffer 1969; Ab'Sabr 1982; Absy *et al.* 1991; Colinvaux *et al.* 2000, 2001; Haffer & Prance 2001; see also Chapter 26) and few geologists were involved in this discussion. Scientists are now increasingly aware that the geological substrate in Amazonia, and the relatively young age of the Andes and the Amazon River, were of paramount importance in species evolution and distribution of diversity hotspots (e.g. Salo *et al.* 1986; Hooghiemstra & Van der Hammen 1998; Lundberg *et al.* 1998; Lovejoy *et al.* 1998; Van der Hammen & Hooghiemstra 2000; Nores 2002; Wesselingh and Salo 2006; Tuomisto 2007; Antonelli 2008) yet an undisputed theory about the timing and context of Amazonian diversifications – in the light of geological evidence – still has to materialize.

Geology only recently started playing a role in the debate on the origin of biodiversity as it was hampered by the same obstacles as the biological and geomorphological sciences – the lack of firm evidence due to the difficult access to the terrain. However, in the past two decades geological studies in Amazonia quickly followed one another. The sedimentary environments in Amazonia and their age (e.g. Räsänen *et al.* 1987; Hoorn 1993; Wesselingh *et al.* 2002; Hovikoski 2006), the ancient nature of rainforests (e.g. Morley 2000; Jaramillo *et al.* 2006), the importance of soil heterogeneity and distribution in relation to floristic biodiversity (e.g. Kalliola & Flores-Paitan 1998; Ruokolainen *et al.* 2007), past climate dynamics (Sugden 2000; Bush & Flenley 2006; Bush *et al.* 2007) and the exact age of the establishment of the Amazon River (Dobson *et al.* 2001; Figueiredo *et al.* 2009) are but a few of the thrilling insights that were obtained.

Simultaneously, a relatively young branch of science, DNA studies, increasingly suggested that the origin of extant biodiversity dates back well before the Quaternary (Antonelli 2008;

Rull 2008) and may have coincided with regional geological events (see Chapters 23–25). Consequently, at the turn of the millennium, geology and biology were drawn to each other in a concerted effort to explain the origin of Amazonian biodiversity and landscapes.

### A journey through the geological history of Amazonia

The scientific advances of the past two decades, and the newly gained perception that biotic and abiotic evolution might be intimately related, demanded an interdisciplinary, multinational effort to summarize the state of the art in Amazonian geological sciences. This book attempts to fulfil this role. It not only presents an outline of the geological history, but also assesses the implications of the geological past for landscape evolution and biotic diversity. The contributors show that the development of Amazonian diversity is intimately linked to landscape evolution, and that modern Amazonian ecosystems were formed during the geodynamic processes of the Cenozoic. The implication of this work is that before the Quaternary there were periods with even more diverse ecosystems.

The contributions to this book are grouped into five themes, corresponding to the book's five parts. The first of these themes discusses the origin, architecture and stratigraphic and tectonic relationships of the major geological units of the eastern Andes and Amazonia. The second theme focuses on the Amazonian sedimentary record from the Mesozoic era to the Quaternary period. This record is subdivided into cratonic and Andean-driven depositional systems although Neogene and Quaternary systems are a combination of both Andean and cratonic fluvial systems. In addition, megafan depositional systems in western Amazonia are also reviewed. Climatic evolution and the implications for the Amazonian region during the Miocene are assessed in the third part. The Amazonian palaeontological record of the aquatic and terrestrial realms constitutes the fourth part of the book. Despite the uneven concentration of fossiliferous deposits in western Amazonia and the adjacent Andes, the palaeontological chapters provide an in-depth insight into the development of Amazonian floras and faunas. The final, fifth, part of the book is concerned with modern perspectives on the origin of Amazonian biodiversity. The book concludes with a chapter by Wesselingh *et al.*, who summarize the highlights of each chapter and provide a synopsis of the Cenozoic history of Amazonia. The best localities for observing the outcrops and fossils are shown in Fig. 1.1.

### Main geological processes shaping Amazonia through time

The geography of Amazonia was shaped during three principal geological phases. The first was a Proterozoic phase (3–1 Ga [gigayears]) of cratonic formation dominated by magmatism, continental accretion and tectonic processes (see Chapter 2 by Kroonenberg & de Roever). The craton forms most of eastern Amazonia and consists of ultrastable basement with landscapes that date back to the Cretaceous and Paleogene. In terms of biodiversity these areas are relatively poor compared to the nutrient-rich, Andean-dominated western part of Amazonia (see Chapters 21 & 22). At the end of the Proterozoic a series of east–west

orientated intracratonic sedimentary basins were formed, which acted as fluvial conduits. Throughout geological history basement reactivation formed 'arches' that, at different times, created drainage divides. Seismic data and new stratigraphic charts from the Brazilian oil company Petrobras illustrate the development of these sedimentary basins in Brazilian Amazonia (see Chapter 3 by Wanderley Filho *et al.*).

The second major geological phase was characterized by rifting and break-up of the supercontinent Pangaea. This period also saw the opening of the Atlantic (Jurassic, c. 195 Ma) during which the Americas became fully separated from Europe and Africa. The separation was completed during the Cretaceous after which sedimentation of the intracratonic basins was resumed (c. 120 Ma). The third and final geological phase was determined by changes in plate configuration along the Pacific. This plate activity was an aftermath of the continental break-up and ultimately responsible for the uplift of the Andean Cordilleras that was initiated during the Cretaceous.

Pulses of uplift continued throughout the Cenozoic; however, Andean tectonism only reached a climax during the Late Miocene and Pliocene (c. 10–4 Ma). This resulted in intense denudation, increased subsidence in the sub-Andean zone and progression of the sedimentary wedge into Amazonia, and ultimately connected the inland drainage system with the Atlantic Ocean creating the Amazon River (see Chapters 4 & 5 by Mora *et al.* and Roddaz *et al.*; Figueredo *et al.* 2009).

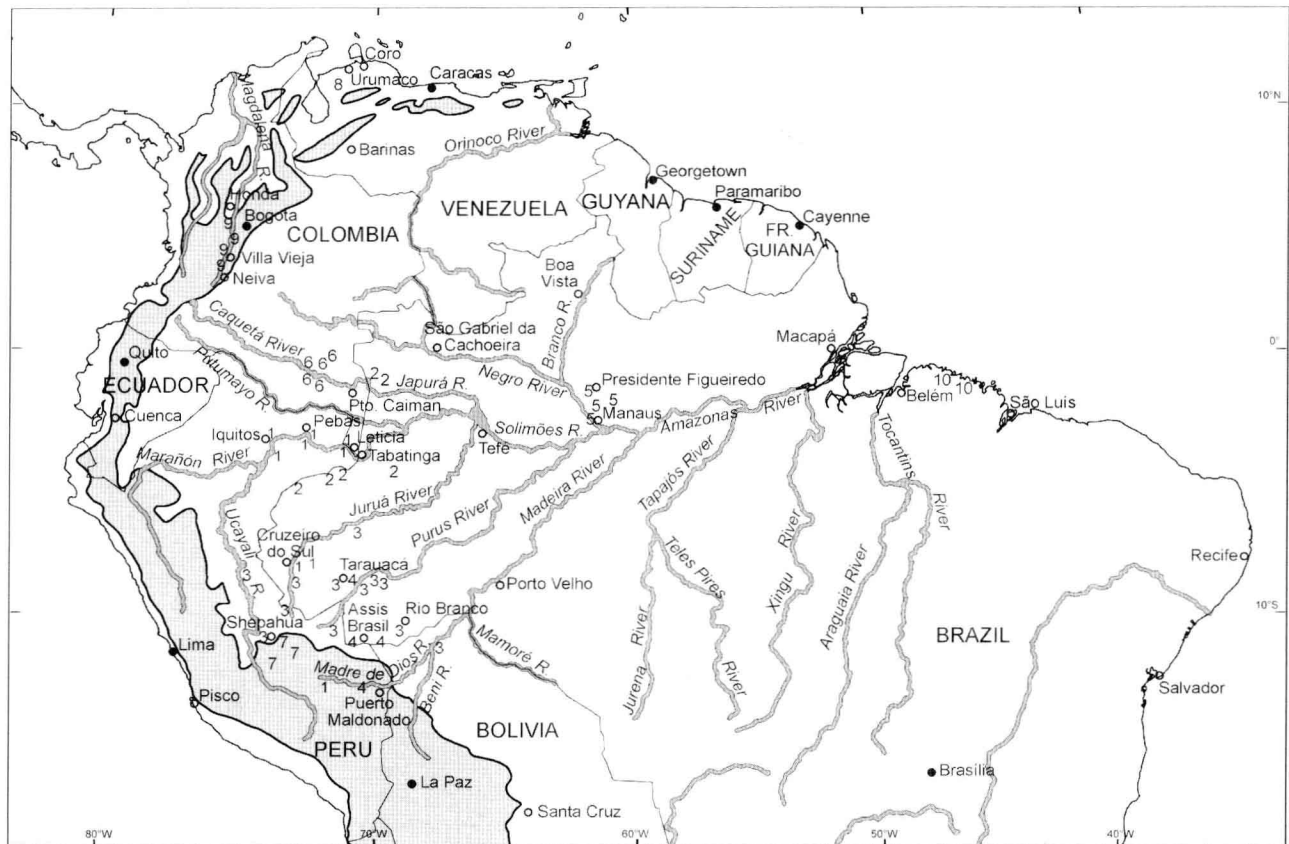
Andean uplift remained high during the Pliocene while subduction of the Nazca Ridge caused tectonic uplift of the Fitzcarrald Arch (southeastern Peru and adjacent Brazil). As a consequence the western Amazonian lowlands, which during the Miocene formed continuous aquatic habitats, became fragmented and dissected (see Chapter 6 by Espurt *et al.*). A final marker event in the geological history of northern South America was the closure of the Panama isthmus around 3 Ma. Although tectonism is ongoing, this concluded the Present geographical configuration of the South American continent, its landscape and modern drainage systems (see also Chapter 26).

### Cratonic and Andean-driven depositional systems

River systems of cratonic descent or local lowland origin have dominated Amazonian landscapes throughout their history. In this book we review the Mesozoic and Cenozoic cratonic fluvial systems by comparing four different fluvial formations that range in age from Cretaceous to Late Neogene (see Chapter 7). From the Oligocene onwards Andean-driven depositional systems dominated the sub-Andean zone and western Amazonia. These systems extended to at least 1.5 million km<sup>2</sup> during the Miocene and were characterized by very large lakes and wetlands and occasional marine influence. During the Early and Middle Miocene a lake- and wetland-dominated system occurs (Pebas phase) whereas in the Late Miocene the newly formed Amazon River introduces a fluvial element into this otherwise wetland-dominated system (Acre phase) (see Chapter 8). Andean drainages are crucial for the soil development and distribution of species-diverse vegetation on nutrient-rich Andean-derived substrate. Instead relatively species-poor vegetation develops on the craton-derived substrate.

The presence and extent of marine influence in the history of Amazonia has been a hotly debated topic. In Chapter 9, Hovikoski





**Fig. 1.1** This map represents the principal Amazonian rivers and outcrops of Cretaceous and Cenozoic origin in Amazonia that are referred to in the various chapters of this book. The locations are represented as numbers and either indicate the author or the common name of the locality. (1) Pebas/Solimões outcrops (Hovikoski *et al.*, see Chapter 9). (2) Pebas/Solimões outcrops (Hoorn *et al.*, see Chapter 8). (3) Fossil mammals (Negri *et al.*, see Chapter 15). (4) Localities of both Negri *et al.* and Hovikoski *et al.* (the localities close to the city of Assis Brasil are situated on the margins of the Acre River, which is not represented here). (5) Cretaceous-Paleogene Alter do Chão (source Petrobras, in Hoorn *et al.*, see Chapter 7). (6) Neogene fluvial deposits of cratonic origin (Hoorn *et al.*, see Chapter 7). (7) Fitzcarrald mammal fauna (Negri *et al.*, see Chapter 15). (8) Lower Miocene Castillo Formation – other important Venezuelan localities are placed close to/into the cities of Urumaco (Upper Miocene Urumaco Formation) or Barinas (Middle Miocene Parángula Formation) – see Riff *et al.*, Chapter 16. (9) Middle Miocene Honda Group (La Venta Fauna), Magdalena Valley. (10) Atalaia Beach (Salinópolis city) and Ilha de Fortaleza (São João de Pirabas city), Lower Miocene Pirabas Formation (see Riff *et al.*, Chapter 16). Map made by D. Riff and J. van Arkel.

*et al.* argue that in the past 30 Ma well-documented episodes of marine influence in Amazonia are limited to the Miocene. However, there is no evidence for fully established marine corridors ('seaways') throughout the South American continent in the Cenozoic.

The Cenozoic Andean uplift and increased denudation rates further resulted in megafan systems along the Andean foothills (see Chapter 10 by Wilkinson *et al.*). Megafans are low-gradient river systems choked by sediments, which force them to continuously change their courses. Understanding their dynamic behaviour sheds light on the development and distribution of aquatic biota. The extent of megafan depositional systems in the history of Amazonia is greatly underestimated.

Late Neogene and Quaternary fluvial systems are further explored in Chapter 11, by Irion & Kalliola. They outline the fluvial depositional environments and processes from the foreland basins in the west to the mouth of the Amazon in the east, and

consider the resulting landforms, which dominate a major part of the surface of lowland Amazonia. Quaternary fluvial systems along the trunk Amazon River have been dominated by strong eustatic-driven base-level changes.

### Amazonian climate

Although palaeoclimatic data are hard to obtain, isotope data from fossil molluscs and cyclicity in the sediment beds indicate that the modern Amazonian hydrological cycle, which ensures the year-round wet conditions that sustain the rainforests, was in place in the Miocene (see Chapter 12). Experimental climate modelling for a low-elevation Andes and the effect on Amazonian climate is explored by Sepulchre *et al.* in Chapter 13. Based on their model, the role of the Andes in maintaining permanent wet conditions in the lowlands is seemingly less prominent than one would expect.

The wet character of the Amazonian climate is mostly the result of the Amazonian hydrological cycle. However, a lower Andes would create different precipitation patterns than at Present, and the removal of the Andes would increase seasonality.

Another climatic controlling mechanism that affects Amazonia is the El Niño Southern Oscillation (ENSO). In Chapter 14 Bookhagen & Strecker explore the influence of the negative ENSO climatic phenomenon (also known as La Niña) on sediment influx and aggradation in the fluvial systems. The extreme high water levels as a result of high precipitation during the negative ENSO years have a disproportionate effect on denudation and are thus extremely important to the Amazonian river dynamics.

### The palaeontological record in Amazonia

Amazonia has hosted a highly diverse mammal fauna at least since the Paleogene. Recently discovered Eocene-Oligocene faunas and Middle Miocene faunas from the Peruvian-Brazilian border area provide us with detailed information on the faunal composition. However, most noticeable is the rich Late Miocene fauna from Acre (Brazil), which includes species with remarkably large forms (see Chapter 15 by Negri *et al.*). The demise of the giants coincided with the arrival of North American immigrants associated with the emergence of the Panama land bridge (Stehli & Webb 1995).

The Amazonian crocodile and turtle faunas indicate that during the Cenozoic diversification was slow, but culminated in the Miocene fauna with a diversity and disparity that remains unrivalled (see Chapter 16 by Riff *et al.*). This fauna contains the largest crocodile and turtle that ever lived, as well as a remarkable diversity of gharial species. The Pliocene and Quaternary faunas are clearly less diverse, a feature linked by the authors to global cooling and the disappearance of the large productive aquatic ecosystems of the Miocene.

The diverse Amazonian fish fauna, too, has a long history of gradual diversification, as is shown by Lundberg *et al.* in Chapter 17. Already in the Miocene an essentially modern fauna inhabited the Amazonian aquatic ecosystems. The fishes have provided some of the best indications of the changing outline of Amazonian watersheds throughout their Cenozoic history. Especially well reflected in this fauna is the separation, during the Late Neogene, of northern coastal and Andean drainages from Amazonia.

The Miocene invertebrate fauna developed through a large evolutionary radiation of endemic mollusc and ostracod species in the long-lived lakes of the Pebas megawetland (see Chapter 18 by Wesselingh & Ramos). In addition, species associations characteristic for restricted marine conditions occur in some intervals. Nevertheless, since the Late Miocene the Amazonian rivers and lakes have been the domain of a low-diversity fluvial mollusc fauna and a stunningly diverse decapod fauna.

The palynological and palaeobotanical record of plants shows us that modern angiosperm-dominated rainforests existed in Amazonia throughout the Cenozoic (see Chapter 19 by Jaramillo *et al.*). Diversity culminated during the Eocene, and a major extinction occurred at the Eocene-Oligocene transition. Modern genera were already present during the Miocene, when the current rainforest biome developed and diversities were as high, or even

higher, than at Present. In Chapter 20 Behling *et al.* further show that although the Quaternary glaciations affected the distribution of plant species in Amazonia, they did not seem to promote speciation in the Amazonian lowlands. During the Quaternary the fringes of the rainforest were affected at precessional timescales, but the core of lowland Amazonia remained covered by forest. Nevertheless, the composition of forests changed through different parts of the glacial cycle.

### Modern perspectives on the origin of Amazonian biota

In Chapter 21 ter Steege *et al.* present the region-wide diversity patterns and explore their relationships with a range of factors, such as edaphic variation and climate. Although the documentation of biodiversity is notoriously incomplete, the addition of niche modelling has substantially improved our insights, and will do so in future. The importance of edaphic heterogeneity for plant diversity is further illustrated by Duivenvoorden & Duque in Chapter 22, which investigates the relationships between the abiotic environment (geology, geomorphology, soils) and biodiversity.

Recently, many important new insights into the origin of Amazonian biodiversity and biogeography have emerged from molecular studies. In Chapter 23 Pennington & Dick review evidence from plants, while Antonelli *et al.* in Chapter 24 review the development of tetrapods, and the fish are treated in Chapter 25 by Lovejoy *et al.* All contributors caution about hasty interpretation of age estimates from so-called molecular clock studies because of the underlying assumptions. Nevertheless, results clearly indicate that the origination of modern biota has been a steady process that mostly played in the Cenozoic.

### Outlook

New insights and data about the origin of Amazonian landscapes, ecosystems and biodiversity are accumulating even as we compile this book. Further integration of the various biological, geographical and geological disciplines, as well as further technical and conceptual developments within the different fields, will continue to bring new insights about the Amazonian biological system and its resilience, as well as the importance of Amazonia on global processes on a variety of time scales.

As Amazonia is suffering badly from human activities, new and much more ambitious efforts to assess its biodiversity, mostly by time-consuming field-based taxonomic inventories combined with niche modelling, are paramount to get a better sense of the magnitude of species richness and to identify further priorities for conservation. Molecular studies have become an indispensable tool in identifying real species richness.

Further processing of subsurface data, both seismic as well as borehole data and samples, will add to our knowledge of the development of the region and its landscapes. Study of the reaction of biodiversity to previous natural perturbations will bring more insights about ecosystem resilience, at a time when such insights are so badly needed.

Raising awareness of the unique and amazing diversity of life in Amazonia is needed in order to achieve better protection

for the region and its biota. With this book we hope to enhance appreciation of the vast timescales that were needed to create these great ecosystems, which we are challenging so profoundly at this moment in history.

## Acknowledgements

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Finally, we are immensely thankful that Thomas van der Hammen managed to complete the prologue of this book, this in spite of his deteriorating health. Thomas has been our mentor, who inspired us to take on the mighty Amazon. We dedicate this volume to him in admiration of his longstanding commitment to Amazonian research, and hope that this book will inspire young scientists to undertake further research, just as Thomas inspired us to engage in research in wonderful Amazonia. There is still so much to research out there in the virgin rainforest of South America...

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