ONE

Introduction: Amazonia, landscape and species evolution

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Motivation

The Amazon drainage basin covers over 8 million km^2 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 *tepuis* 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; Figuereido *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;

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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.*; Figuereido *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^2 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

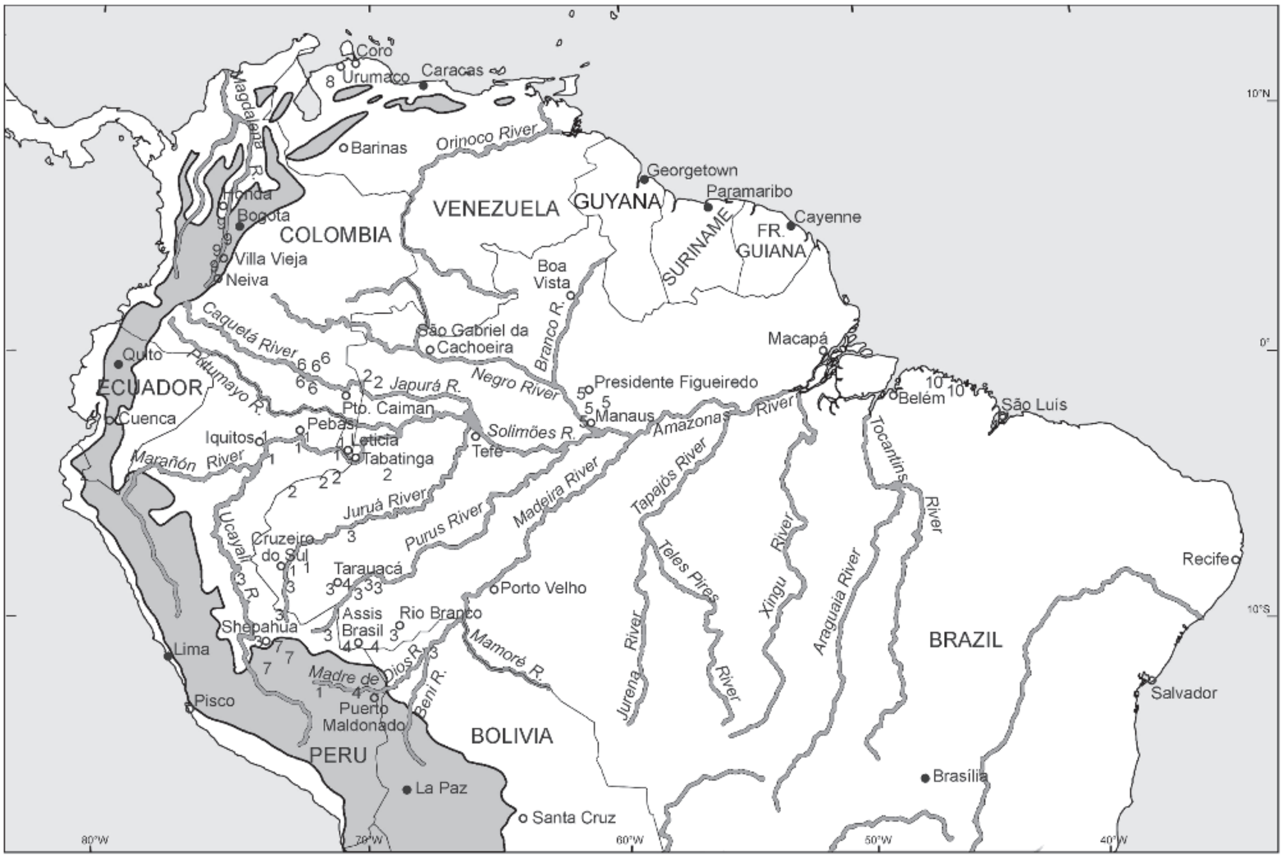

Fig. 1.1 This map represents the principal Amazonian rivers and outcrops of Cretaceous and Cenozoic origin in Amazonia that are referred to in the various chapters of this book. The locations are represented as numbers and either indicate the author or the common name of the locality. (1) Pebas/Solimões 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 (Sao 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.

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