

Neogene History of the Amazonian Flora: A Perspective Based on Geological, Palynological, and Molecular Phylogenetic Data

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Keywords

palynology, phylogeny, paleobiogeography, climate change, Andes, Amazon

Abstract

The Amazon hosts one of the largest and richest rainforests in the world, but its origins remain debated. Growing evidence suggests that geodiversity and geological history played essential roles in shaping the Amazonian flora. Here we summarize the geo-climatic history of the Amazon and review paleopalynological records and time-calibrated phylogenies to evaluate the response of plants to environmental change. The Neogene fossil record suggests major sequential changes in plant composition and an overall decline in diversity. Phylogenies of eight Amazonian plant clades paint a mixed picture, with the diversification of most groups best explained by constant speciation rates through time, while others indicate clade-specific increases or decreases correlated with climatic cooling or increasing Andean elevation.

Overall, the Amazon forest seems to represent a museum of diversity with a high potential for biological diversification through time. To fully understand how the Amazon got its modern biodiversity, further multidisciplinary studies conducted within a multimillion-year perspective are needed.

- The history of the Amazon rainforest goes back to the beginning of the Cenozoic (66 Ma) and was driven by climate and geological forces.
- In the early Neogene (23–13.8 Ma), a large wetland developed with episodic estuarine conditions and vegetation ranging from mangroves to terra firme forest.
- In the late Neogene (13.8–2.6 Ma), the Amazon changed into a fluvial landscape with a less diverse and more open forest, although the details of this transition remain to be resolved.
- These geo-climatic changes have left imprints on the modern Amazonian diversity that can be recovered with dated phylogenetic trees.
- Amazonian plant groups show distinct responses to environmental changes, suggesting that Amazonia is both a refuge and a cradle of biodiversity.

1. INTRODUCTION

The Amazon rainforest is highly diverse and has an estimated 40,000 plant species (Hubbell et al. 2008). In terms of species richness, the Neotropics, with ca. 118,308 species of vascular plants, is much richer than the Afrotropical region (ca. 56,451 species) or Southeast Asia (ca. 50,000) (Raven et al. 2020). It has long been suspected that geological history played an important role in generating modern biodiversity patterns and gradients (Wesselingh & Salo 2006; Hoorn et al. 2010, 2022a; Higgins et al. 2011). Although the effect of this driver can be clade-dependent (Meseguer et al. 2022), the Earth history effect is well illustrated when the relatively stable geology of the African tropics is compared with the dynamic landscapes of the Amazon and the Indo-Pacific (Hagen et al. 2021).

Climate, hydrology, and geology have fluctuated significantly throughout the history of the Amazon, which reached its present geological configuration during the Neogene, when the uplift of the Andes (Hoorn 1993, Hoorn et al. 2010, Boschman 2021), dynamic topography (Shephard et al. 2010), closure of the Central American Seaway (Montes et al. 2015), and sea level changes (Hoorn 1993, Boonstra et al. 2015, Jaramillo et al. 2017) reshaped the geography of northern South America. During this process, drainages were reconfigured, with the Amazon River reaching its modern course ~10 million years ago (Ma) (Figueiredo et al. 2009, 2010; Hoorn et al. 2017).

The Amazon is limited by the high Andes in the west, which acts as an orographic barrier that cools the westward-directed air masses, causing high precipitation rates and providing an exceptionally large elevational and climatic gradient (Garreaud et al. 2009). The uplift of the Andes also influenced the geological history of the western Amazon through pronounced basin subsidence and by supplying this region with vast volumes of sediments. These sedimentary rocks form the substrate for nutrient-rich soils (Hoorn et al. 2010, Quesada et al. 2012). In turn, the eastern Amazon is drier (Garreaud et al. 2009) and dominated by the Amazon Craton, a fragment of old continental crust consisting of crystalline rocks 3 to 1 billion years (Ga) in age (Wanderley-Filho et al. 2010), leading to nutrient-poor soils (Quesada et al. 2012). This dichotomy of the Amazon is mirrored by a biodiversity gradient with species-rich forests in the west and less diverse forests in the east (Hoorn et al. 2010, Val et al. 2021).

Amazon: the area confined by the Amazon River and its tributaries

Dynamic topography: deflection of Earth's surface (i.e., subsidence or uplift) caused by flow in Earth's mantle

Andean uplift, drainage readjustments, and climate change have affected species composition through time and space. For instance, the western Amazon acted as a biodiversity cradle for fishes and birds, among others, feeding the less diverse eastern Amazon through species interchanges (Oberdorff et al. 2019, Silva et al. 2019, Boschman et al. 2021). Other spatio-temporal developments, such as the transition from Pebas wetland to the Amazon River (~10 Ma) and subsequent entrenchment of the river following global climate cooling during the late Miocene to Pleistocene (6 to 2 Ma), impacted biodiversity history while generating the modern geodiversity in this region. In this context, a comprehensive understanding of the biogeographical history of modern Amazonian biodiversity requires research into its deep time history (i.e., pre-Quaternary).

Here we review the Neogene history of the Amazonian flora by (a) summarizing main geological and climatic events in this region; (b) evaluating changes in the composition of paleofloras based on fossil sporomorph data, and using biostratigraphic schemes as a timeline for evaluating floristic changes; (c) reviewing phylogenetic data sets of predominantly Amazonian clades, and using these data to evaluate changes in speciation rates through time; and (d) providing recommendations for future research on the Amazonian flora.

2. THE MAKING OF THE AMAZON

2.1. Geological History and Landscape Dynamics, from Andes to Amazon

The area where the Amazon stands today (**Figure 1**) has a very long history that began with the formation of the continental crust (craton) in the Proterozoic, at ~3 Ga. New terranes (continental fragments) were subsequently aggregated to the Amazon Craton, leading to the assemblage of the South American continent. The formation of Pangea in the Permian is the final act in the long history of this supercontinent, with South America, Africa, Antarctica, India, and Australia encompassing the mega-continent Gondwana, i.e., the southern half of Pangea. Around 150 Ma, Gondwana started drifting away from the Northern Hemisphere continents (Laurasia). Oceanic spreading in the Proto-Caribbean Ocean separated South America from North America (Pindell & Kennan 2009), while continued rifting in the South Atlantic separated it from Africa, a process that was finalized in the Late Cretaceous, at ~95 Ma (Granot & Dymant 2015). Finally, by 45 Ma, South America detached from the remaining Gondwanan components (Antarctica and Australia), becoming an isolated landmass (for a summary, see Val et al. 2021).

Since at least the Triassic (~252–201 Ma), the western margin of the South American continent has hosted a magmatic arc that resulted from eastward subduction of oceanic plates of the (paleo-)Pacific Ocean (Pepper et al. 2016). For most of its history, this arc consisted of isolated volcanic centers surrounded by large lakes and low and flat coastal plains (Quade et al. 2015). It was only in the Late Cretaceous (~100–66 Ma) that uplift along the Andean margin started (Horton 2018). Crustal shortening and surface uplift initiated in the Southern (Patagonian) Andes at ~100 Ma and in the Central Andes of Bolivia, Perú, and Ecuador at ~80–70 Ma. During the Late Cretaceous and early Paleogene, most of Colombia and western Venezuela were still covered by shallow seas (Sarmiento-Rojas 2019). Surface uplift in this northwestern corner was initiated after the leading edge of the Caribbean Plate collided with the Ecuadorian margin of South America at ~80 Ma (Montes et al. 2019).

At the start of the Neogene (~23 Ma), the Andes consisted of a more or less continuous mountain range, albeit significantly smaller in width and height compared to today (Boschman 2021). At this time, high (i.e., close to modern) elevations were present only in the Patagonian Andes (Colwyn et al. 2019) and in the Western Cordillera of the Central Andes (Quade et al. 2015, Sundell et al. 2019). The Eastern Cordillera and Altiplano region of the Central Andes (now higher than 4,000 m) stood at ~1,000–2,000 m (Leier et al. 2013, Garzzone et al. 2014,

Geodiversity:

constitutes the rock, mineral, fossil, landform, sediment, and soil composition of an area, but also the hydrology, topography and the natural processes that alter them

Sporomorph:

refers to pollen and spores, the reproductive material of plants, ferns, fungi, and moss

Speciation rate:

rate at which new species form (denoted as λ)

Oceanic spreading:

the formation of new oceanic crust at a mid-oceanic ridge

Magmatic arc:

a belt of volcanoes formed above a subducting oceanic tectonic plate

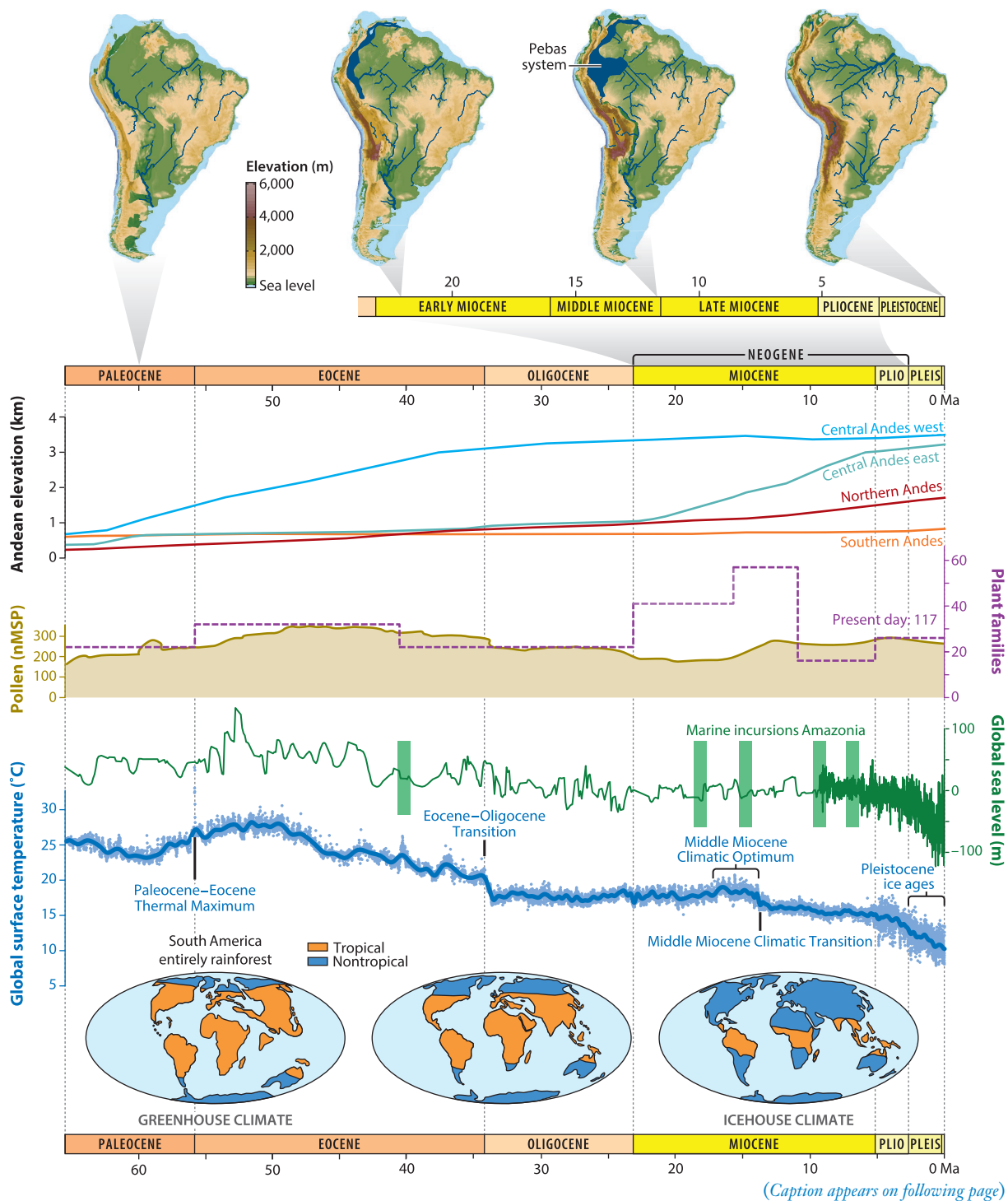


Figure 1 (Figure appears on preceding page)

Overview of Cenozoic geological, climatic, and biotic evolution. Andean uplift and river evolution maps (*top row*) from Boschman (2021) and Boschman et al. (2021); Andean uplift curves of the Northern (13°N–14°S), Central (14°S–34°S), and Southern (34°S–56°S) Andes based on Boschman (2021); pollen species curve from Jaramillo et al. (2006) and Hoorn et al. (2010); number of plant families present in the Amazon, based on overview in **Supplemental Tables 1.1–3** (this study); global sea-level curve from Miller et al. (2020); marine incursions in Amazonia (i.e., phases of flooding) from Bernal et al. (2019); global surface temperature curve based on oxygen isotope ratio data of benthic foraminifera shells from Westerhold et al. (2020), converted to surface temperature using the equations from Hansen et al. (2001). For details, see the **Supplemental Text** and global tropical/nontropical biome maps from Meseguer & Condamine (2020).

Fiorella et al. 2015, Sundell et al. 2019). Similarly, in the Northern Andes, the bulk of the surface uplift took place during the Neogene, meaning that at its start, elevations were still low (e.g., less than 2,000 m for the Eastern Cordillera) (Anderson et al. 2015, 2016) (**Figure 1**).

In the western Amazon, the area east of the rising Andes, late Paleogene–early Neogene surface uplift caused flexural subsidence, creating a mountain-parallel system of rivers and wetlands connecting with the Magdalena and Orinoco drainage systems, draining toward the Caribbean Sea in the north (Hoorn et al. 2010, Wesselingh & Hoorn 2011, Albert et al. 2018). During the mid-Miocene (~16–11.5 Ma), this wetland system (known as the Pebas system) expanded further east, beyond the region of flexure related to mountain building, with a maximum extent estimated to be ~1 million km² (Wesselingh et al. 2001). Recent geodynamic modeling studies showed that a component of this subsidence may have resulted from the dynamic topography associated with the migration of the South American continent over the subducted lithosphere of the Nazca Plate (Shephard et al. 2010).

Continued mountain building in the late Miocene uplifted the central and eastern ranges of the Central Andes (Altiplano and Eastern Cordillera), and eastern ranges of the Northern Andes (the Garzon Massif, Eastern Cordillera, and Merida Andes), thereby creating a separate drainage system in the Magdalena Valley (Anderson et al. 2015, 2016; Bermúdez et al. 2017; Albert et al. 2018) (**Figure 2**). Furthermore, the arrival of Andean sediments at the mouth of the Amazon River at ~10 Ma indicates that the modern continental-scale eastward-flowing Amazon River was established by then (Figueiredo et al. 2009, 2010; Hoorn et al. 2017). This river reorganization likely resulted from eastward tilting of the continent associated with dynamic topography (Shephard et al. 2010), thereby connecting the western and eastern Amazon basins, and separating the Orinoco drainage basin in the north. With the establishment of this transcontinental drainage network, the Pebas wetland environments disappeared and were replaced by a fluvial-dominated landscape, also known as the Acre phase (Hoorn et al. 2010). From the late Miocene until the Holocene (~11.5 Ma–10 ka), large sediment aprons or megafans occurred at the intersection of the Andes with the Amazon lowlands while filling the Subandean sedimentary basins with clastic sediments (Latrubesse et al. 2007, Wilkinson et al. 2010).

2.2. Neogene Climatic Changes and the Amazonian Landscape

During the Paleogene, a large portion of northern South America was covered by continuous tropical rainforests that are indicative of year-round warm and humid conditions (**Figure 1**). The Oligocene–Miocene transition (~34–23 Ma), however, was characterized by significant global cooling, which led to the onset of growth of the polar ice caps (Westerhold et al. 2020) (**Figure 1**). This transition also coincided with the beginning of the formation of the dry diagonal (**Figure 2**) that separated the Amazon from the Atlantic rainforest in eastern Brazil. The hypothesized ~30 Ma age of the dry diagonal is supported by phylogenetic data and biogeographical analyses (e.g., Lohmann et al. 2013, Thode et al. 2019).

Supplemental Material >

Flexural subsidence: the sinking of Earth's crust due to loading (by, e.g., a mountain range) nearby

Tropical rainforest: forest that occurs within 23.5° north or south of the equator in areas with no dry season and monthly precipitation of at least 60 mm



Figure 2

Main sedimentary basins in northern South America that are mentioned in the text. The dry diagonal is adapted from Morrone (2014).

After a period of relatively stable global climate during the early Miocene, temperatures peaked in the Middle Miocene Climatic Optimum (MMCO) (~16.9–14.7 Ma). But cooling reinitiated during the Middle Miocene Climatic Transition (MMCT) (~14.7–13.8 Ma) and persisted until the mid-Pliocene Warm Period (~3 Ma), with the Pleistocene glacial cycles initiating at ~2.6 Ma (Westerhold et al. 2020, Steinthorsdottir et al. 2021) (**Figure 1**). Paleosols in the Magdalena Valley (Colombia) are representative of this cooling trend, showing a switch from reducing to oxidizing conditions in the mid-Miocene (~13.1 Ma), at a time when the Magdalena region was still connected with the Amazon. This transition, from humid to arid climate, is thought to be related to a shift in the Intertropical Convergence Zone (Salazar-Jaramillo et al. 2022). Likewise, the La Guajira Desert (Caribbean coast) (**Figure 2**) once hosted a humid tropical rainforest that turned into a desert somewhere between the Miocene and Pliocene (17.3 and 3 Ma) (Jaramillo et al. 2020).

In the Amazon, the most complete Cenozoic sedimentary sequences are situated along the Brazilian equatorial coastline, where the Amazon River meets the Atlantic Ocean (**Figure 2**). This vast marine archive is more than 10 km thick and comprises sediments from the Cretaceous (<66 Ma) to the Pleistocene (<2.6 Ma) (Watts et al. 2009), with terrestrial sedimentation rates increasing at 10–8 Ma, 4.5 Ma, and particularly 2.6 Ma onward. Although the rise in sediment accumulation in the Atlantic Ocean has been linked with regional aridification and Andean uplift (Dobson et al. 2001; Harris & Mix 2002; Figueiredo et al. 2009, 2010), in the central

Amazon warm, humid, and seasonal climatic conditions prevailed. The latter is based on paleosol geochemistry data, which point at intense weathering and kaolinite replacement between 8 and 6 Ma (Guinoiseau et al. 2021) and goethite precipitation at ~3 Ma (Gautheron et al. 2022).

Taken together, these data suggest that the Amazon experienced extensive recycling (i.e., erosion and renewed deposition) of the landscape since the MMCT. These conditions must have severely affected the local floristic composition, the overall biodiversity, and the paleobiogeography that shaped the modern Neotropical flora. In the next section we evaluate the palynological record and assess how plants may have responded to these abiotic changes.

Palynology: the study of microscopic organic matter that is produced by plants (including pollen and spores) but also fungi, mosses, and algae

3. INSIGHTS INTO DEEP TIME AMAZONIAN FLORAS

The Neogene sediments in the western Amazon are about 900 m in thickness, but differences are observed among the sedimentary basins (Wesselingh 2006, Wanderley-Filho et al. 2010, Da Silva-Caminha et al. 2020). Despite the limited exposure and dense vegetation cover, the sedimentary history of the western Amazon is relatively well known thanks to a Brazilian coring project (Maia et al. 1977). Eighty-four cores were drilled in the Solimões Basin (**Figure 2**), representing the only continuous and high-quality sedimentary archive for this region to date. These cores, combined with outcrop data, provided a basis for multiple palynological and lithological studies that permitted relative age determination of the sediments, paleoecological and paleoenvironmental reconstructions (e.g., Hoorn 1993; Da Silva-Caminha et al. 2010; Jaramillo et al. 2010, 2017; d'Apolito 2016, Leite et al. 2017, 2021; Linhares et al. 2017, 2019; Leandro et al. 2019, 2022; d'Apolito et al. 2021) (**Supplemental Table 2**), provenance analyses (Andean or Amazon source), and absolute age determination of the sediments based on isotope data (Roddaz et al. 2005, Horbe et al. 2019, Kern et al. 2020). A schematic overview of the lithology, sediment ages, and phytogeographic and interpretation through time is presented in **Figure 3**.

Supplemental Material >

Palynology is an essential tool to estimate the relative age of sedimentary records (see the sidebar titled Biostratigraphy and Regional Vegetation Changes) and to study changes in floristic composition through time. In this review, we refer to three biostratigraphic schemes that are currently applied in northern South America (but see **Supplemental Table 3**), and we use these schemes as a timeline to mark important changes in the Amazonian Neogene flora. Some of the most characteristic pollen types and biostratigraphic markers of the Neogene of western Amazon are shown in **Figure 4**.

The first biostratigraphic scheme was developed in the Guyana Basin (Van der Hammen & Wymstra 1964, Wijmstra 1971) (**Figure 2**) and in the Amazon submarine fan (Regali 1971) (**Figure 2**). In turn, the second scheme was developed in the Venezuelan coastal basins (Germeraad et al. 1968, Lorente 1986, Muller et al. 1987) (**Figure 2**), and elaborated further on the first scheme; both schemes are age calibrated based on the international marine microplankton zonation. The third scheme was developed in the Llanos Basin (**Figure 2**; Subandean zone) and is age calibrated based on carbon isotopes, foraminifera, and magnetostratigraphy (Jaramillo et al. 2011). This biostratigraphic scheme is partially replicated in the Peruvian (Marañón) Subandean Basin (Parra et al. 2020) (**Figure 2**).

In the Amazon, the biostratigraphy shows conflicting patterns (see Latrubesse et al. 2007, d'Apolito 2016, Leite et al. 2021, Leandro et al. 2022) that can be explained by the multiple dispersal events that are reported for the Neotropics (Antonelli et al. 2018). While the Amazon is a source of biodiversity (Antonelli et al. 2018), the fossil record in northern South America shows that the region also received many species from other localities through dispersal events (e.g., Germeraad et al. 1968).

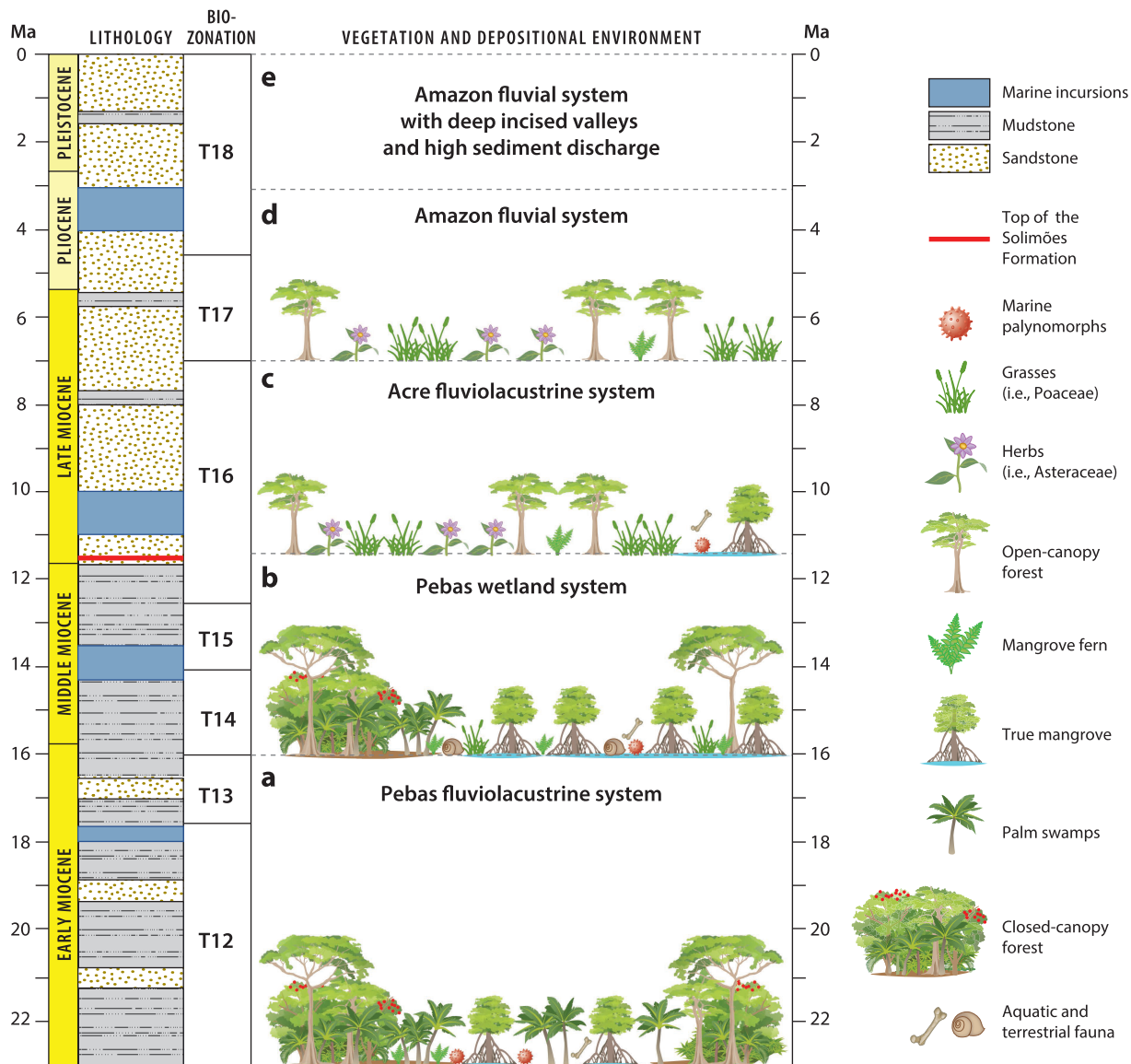


Figure 3

On the left is a summary of the lithological changes in the Solimões and Içá formations, with the top of the Solimões Formation marked by a red line (adapted from d'Apolito et al. 2021, Kern et al. 2020). Marine incursions are marked in blue (adapted from Jaramillo et al. 2017, Espinosa et al. 2021, Leandro et al. 2022). The biozonation is from Jaramillo et al. (2011). On the right are the phytogeographic (vegetation) and environmental changes through time.

4. THE AMAZONIAN FLORA: ORIGINS AND CHANGES ACROSS TIME AND SPACE

The typical closed-canopy tropical rainforest was first formed in the Paleocene (66–56 Ma) (Burnham & Johnson 2004, Carvalho et al. 2021). Fossil leaves, seeds, pollen, and spores suggest that this forest was highly diverse and already hosted an assemblage of characteristic tropical

BIOSTRATIGRAPHY AND REGIONAL VEGETATION CHANGES

In biostratigraphy, fossils are used to determine the relative age of sediments. The presence of diagnostic pollen and spore taxa with distinct morphology and wide distribution (Germeraad et al. 1968) also provides a timeline for geographic changes in plant distribution. In South America, the application of palynology as a biostratigraphic tool was established by the hydrocarbon industry (e.g., Van der Hammen & Wymstra 1964, Germeraad et al. 1968, Regali 1971, Lorente 1986, Jaramillo et al. 2011). Biostratigraphic schemes are based on speciation and extinction events that are reflected in the first and last appearances of pollen taxa, but they can also be based on taxonomic assemblages (Guex 1991) or on the graphic correlation of well and outcrop data (Shaw 1964, Edwards 1989, Jaramillo et al. 2011). Furthermore, the application of sequence biostratigraphy, a method commonly used in subsurface appraisal in the hydrocarbon industry, identifies palynological cycles (i.e., changes in vegetation and environment) driven by changes in global sea level and astronomical cyclicity (Rull 2002). This technique has proven useful in the Amazon, where changes in global sea level induced vegetation changes (Hoorn et al. 2022b).

rainforest families (Jaramillo et al. 2006, 2010; Carvalho et al. 2021) (**Supplemental Tables 1.1–3**). The presence of pollen such as *Nothofagidites huertasii* (aff. *Nothofagus*) and *Cyclusphaera scabrata* (aff. *Araucaria*), which are nowadays restricted to southern South America, indicates that these taxa had a much broader biogeographic range during the Paleogene. Their disappearance in the Neogene is likely associated with global climate change and the rise of the angiosperms (Peralta-Medina & Falcon-Lang 2012, Jaramillo et al. 2013, Condamine et al. 2020).

In the Paleogene (~66–23 Ma), deltaic to fluvial conditions extended deep into northern South America. However, toward the end of the Eocene (~56–34 Ma), marine influence gradually waned, coinciding with global cooling, sea level fall, and a decrease in terrestrial plant diversity (Jaramillo et al. 2006, de la Parra et al. 2021). In the Oligocene (~34–23 Ma), deltaic environments transitioned into fluvial drainages with episodic marine incursions and sediment supply from both the Guiana Shield and the emerging Andes (Torrado et al. 2020). The Paleogene deltaic and estuarine environments of northern South America were characterized by mangrove vegetation composed of Nypoidae palms (e.g., Rull 2002), *Zonocostites ramonae* (aff. *Rhizophora mangle*) (Germeraad et al. 1968), and *Lanagiopollis* (*Psilatricolporites*) *crassa* (aff. *Pelliciera rhizophorae*) (Wijmstra 1968). However, the expanses of mangrove vegetation decreased as the extent of coastal environments dwindled. Nevertheless, mangroves still episodically expanded into the Amazon during the Neogene. Nowadays, the descendants of *Zonocostites* and *Lanagiopollis* (respectively, *Rhizophora* and *Pelliciera*) occur along the modern Atlantic and Pacific coasts of Central and South America, while Nypoidae palms are restricted to Southeast Asia (Lim et al. 2022).

4.1. Early Miocene (23.03 to 15.97 Ma), a Fluvial Landscape with Sediment Sources in the Andes and Amazon

During the early Miocene, global temperatures were on the rise and trending toward the MMCO (Westerhold et al. 2020, Steinthorsdottir et al. 2021). The vast pan-Amazonian territory was reduced due to progressive uplift in the Central and Northern Andes, turning former fluvio-deltaic settings into mountains (Ochoa et al. 2012). A wetland was developing at the Andean foothills (Wesselingh et al. 2006, Hoorn et al. 2010), while most of the western Amazon was still drained by fluvial systems of cratonic origin. In the Amazon, the rich sporomorph composition suggests a vegetation succession that is rich in palms and ferns on the floodplains, and a species-rich forest on the terra firme (d'Apolito 2016, Salamanca Villegas et al. 2016, Jaramillo et al. 2017, Jorge et al. 2019, d'Apolito et al. 2021) (**Supplemental Table 1.4**).

Supplemental Material >

Terra firme:
non-flooded Amazon
rainforests

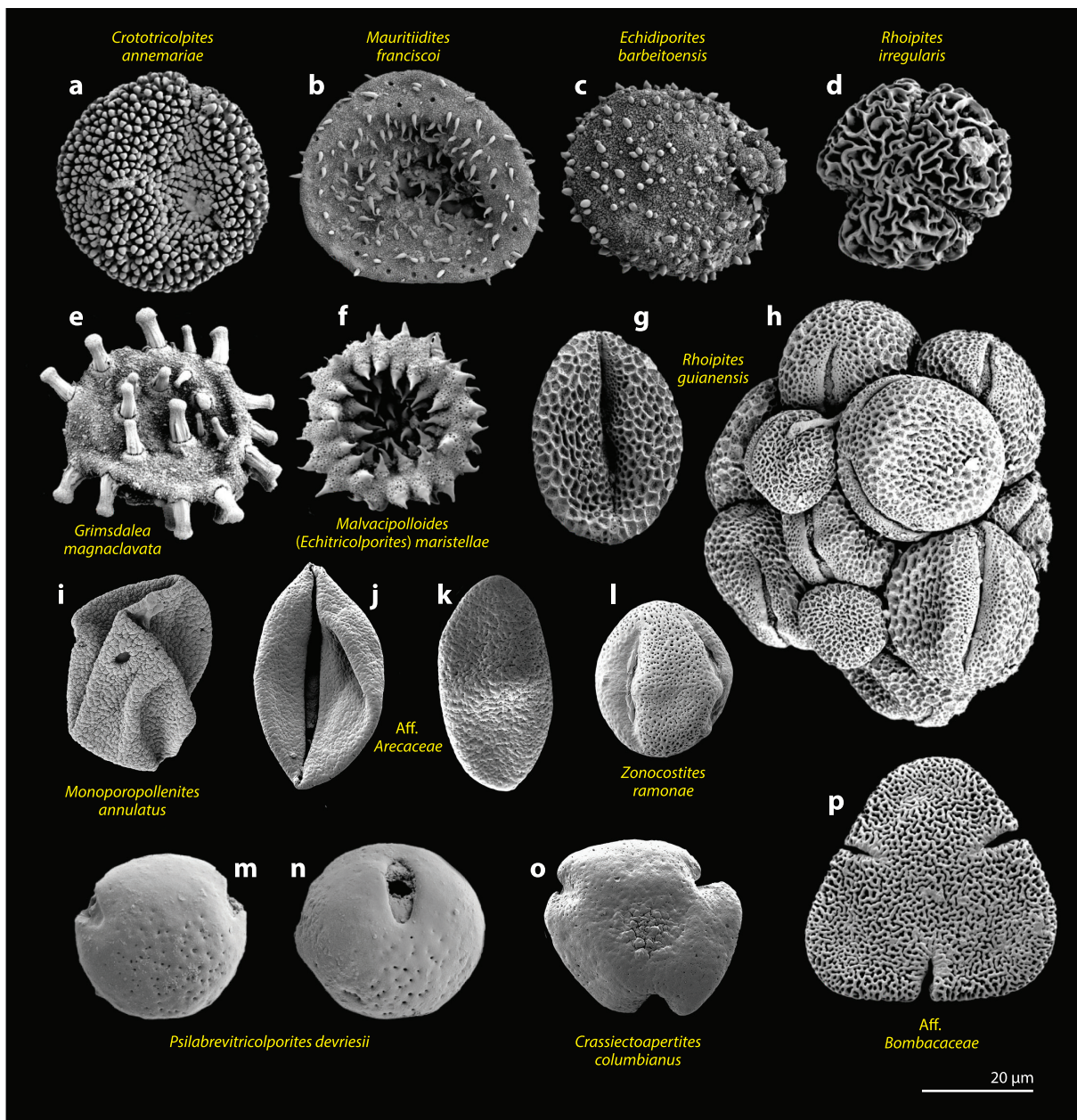


Figure 4

Characteristic pollen types from Neogene sediments in the Amazon. Photographs in panels *a*, *d*, *j*, *o*, and *p* by Hannah Banks and Carina Hoorn at Royal Botanic Gardens, Kew. Photographs in panels *b*, *c*, and *e* from Bogotá-Angel et al. (2021). Photographs in panels *f–h* from Hoorn et al. (2019). Photograph in panel *i* from C. Wei (manuscript in preparation). Photographs in panels *k–n* from Sciumbata et al. (2021). Plate credits courtesy of Caixia Wei.

Global sea level was on the rise (Miller et al. 2020), and mangroves thrived along the Venezuelan (Lorente 1986) and eastern Amazonian coastline (Van der Hammen & Wymstra 1964, Wymstra 1971, Aguilera et al. 2013). The western Amazon remained connected to the Caribbean, enabling the coastal taxa to bridge about 2,000 km and reach the Amazon heartland (Hoorn 1993, d'Apolito 2016, Salamanca Villegas et al. 2016, Jaramillo et al. 2017, d'Apolito et al. 2021). This meant that a plethora of marine organisms, such as the dolphins and fishes, but also coastal plants and their associates, were able to disperse and settle in the western Amazon (Bernal et al. 2019, Sciumbata et al. 2021).

At the height of the marine incursions, dinoflagellate cysts (marine algae) and marine protozoans such as microforaminifera colonized the (oligohaline) fluvio-estuarine environments, followed by mangroves such as *Verrutricolporites rotundiporus* (aff. *Crenea*, Lythraceae), *Zonocostites ramonae* (aff. *Rbizophora*), *Lanagiopollis crassa* (aff. *Pelliciera*), and the mangrove fern *Deltoidospora adriennis* (aff. *Acrostichum*) (Hoorn 1993; Boonstra et al. 2015; d'Apolito 2016; Jaramillo et al. 2017; Linhares et al. 2017, 2019; d'Apolito et al. 2021; Espinosa et al. 2021; Leandro et al. 2022). The nearest living relatives of these species are nowadays common on the coastal mudflats of Colombia and Brazil (Germeraad et al. 1968). Upstream in the estuaries and river, where salinity was diluted by freshwater, the mangroves were fringed by palm swamps formed of *Mauritiidites franciscoi* (aff. *Mauritiinae*), *Ranunculacidites operculatus* (aff. *Alchornea*), *Psilamonocolpites amazonicus*, and *Psilamonocolpites nanus* (aff. *Euterpe*) (Salamanca Villegas et al. 2016).

Closer to the Andes, mangrove-dominated assemblages were less prominent, and in the biostratigraphic schemes *Lanagiopollis crassa* and *Verrutricolporites rotundiporus* (biostratigraphic markers in the Atlantic coastal basins) are replaced by species such as *Horniella lunarensis* and *Corsinipollenites oculustinctus* (Onagraceae, i.e., aff. *Ludwigia* or *Jussiaea*) (Jaramillo et al. 2010). The latter is nowadays common in freshwater swamps, suggesting the marine influence did not reach the area at this time. Overall, the early Miocene pollen assemblages are very species-rich, pointing to the existence of a very diverse terra firme forest (Salamanca Villegas et al. 2016, d'Apolito 2016, Jaramillo et al. 2017, Jorge et al. 2019, d'Apolito et al. 2021).

Under freshwater conditions, the Amazonian floodplain swamps and oxbow lakes remained densely populated by palms such as *Mauritiidites franciscoi* (aff. *Mauritiinae*), *Psilamonocolpites amazonicus*, and *P. nanus* (aff. *Euterpe*), as well as ferns such as *Verrucatosporites usmensis* (aff. *Stenochlaena*) and *Polypodiaceisporites tibui* (Polypodiaceae) (Salamanca Villegas et al. 2016). Other species typical of the early Miocene floodplains are *Rhoipites* (*Retitricolporites*) *guianensis* (aff. *Grewioideae*), *Striatopollis catatumbus* (Fabaceae, Caesalpinioideae), *Retitrescolpites irregularis* (*Amanoa*), *Ranunculacidites operculatus* (*Alchornea*), *Psiladiopites minimus* (Moraceae), and *Malvacipolloides* (*Echitricolporites*) *maristellae* (aff. *Abutilinae* and *Malvinae*) (Van der Hammen & Wymstra 1964, Wymstra 1971, Jaramillo et al. 2010, Salamanca Villegas et al. 2016, Hoorn et al. 2019, Leandro et al. 2019).

The end of the early Miocene is marked by the arrival of *Malvacipolloides maristellae* (aff. *Malveae*, subtribes *Abutilinae* and *Malvinae*) (Muller et al. 1987, Jaramillo et al. 2011). This important biostratigraphic marker is of Central and North American origin (Hoorn et al. 2019, Espinosa et al. 2020). The north-south migration of *M. maristellae* (and other plants) preceded the closure of the Central American Seaway (15 Ma) (Montes et al. 2015); however, monkeys and many other organisms were also able to cross the narrowing sea (Bloch et al. 2016). The rise of *M. maristellae* in the fossil record suggests it thrived in the fluvial environments, but increasing salinity and expanding wetland conditions are thought to have caused their rapid extinction (Hoorn et al. 2019, Espinosa et al. 2020). Much later, in the Quaternary, a new immigration wave of the *Abutilinae*-*Malvinae* took place, followed by rapid diversification and colonization of the Andean slopes (Hoorn et al. 2019).

The transition into the middle Miocene is marked by the appearance of *Psiladiporites minimus*, a species that is morphologically similar to the pollen of *Ficus*, *Artocarpus*, and *Sorocea* (aff. Moraceae) (Van der Hammen & Wymstra 1964, Germeraad et al. 1968, Wijmstra 1971, Lorente 1986, Muller et al. 1987, Hoorn 1993, Leite 1997, Jaramillo et al. 2010). *Psiladiporites minimus* is often associated with *Crototricolpites annemariae* (aff. *Croton*) (Hoorn 1993; Linhares et al. 2017, 2019), *Proxapertites tertiaria* (aff. *Crematosperma*), and *Retimonocolpites absyae* (aff. *Viola*) (Hoorn 1993) and has been found exclusively in the biostratigraphic schemes of the Atlantic coastal basins and western Amazon, but not in the Subandean basins. However, the Miocene expansion of this taxon coincides with age estimates from molecular studies for the onset of Neotropical figs (*Ficus*, Moraceae) (Machado et al. 2018). Nowadays the Moraceae are widely distributed across the Amazon and commonly observed in the palynological records from Holocene river floodplains (de Assis et al. 2017).

4.2. Middle Miocene (15.97 to 11.63 Ma), the Andes as a Major Sediment Source and Biodiversity Driver in the Pebas Wetland System

Between the early to middle Miocene (~16.9–14.7 Ma; MMCO), global temperatures soared, and global sea level peaked to ~75 m above present, leading to pronounced marine incursions into the Amazon (Hoorn 1993, Jaramillo et al. 2017, Hoorn et al. 2022b). Meanwhile, in the Central and Northern Andes (see Section 2.1), rapid uplift generated a high topography that acted as an orographic barrier and affected both regional climate and paleoenvironments (Hoorn et al. 2010). In combination with dynamic topography, depositional conditions in the western Amazon changed from a predominantly fluvial to a wetland environment (Hoorn et al. 2010, Bicudo et al. 2019).

The Pebas system received sediment input from the Andes due to accelerated mountain uplift. In consequence, a myriad of Andean taxa are found in the sporomorph records, which are indicative of high montane forests and proto-paramo (i.e., Andean alpine meadows), suggesting that elevations ranged from 1,500 to 3,500 m in the mid-Miocene (Hoorn et al. 2022b) (**Supplemental Table 1.5**). The Pebas system was intermittently connected to the Caribbean and was driven by astronomical cycles that controlled flooding, sedimentation, and vegetation (Wesselingh 2006, Vonhof & Kaandorp 2010, Hoorn et al. 2022b). Shallow lakes and swamps were surrounded by diverse lowland forests (Hoorn 1993, Jaramillo et al. 2010, Hoorn et al. 2022b) (**Supplemental Table 1.1**). Moreover, fossil wood data sampled along the Amazon River near Iquitos showed that the local forest was composed of typical terra firme forests that grew in the proximity of a delta (Pons & Franceschi 2007) (**Supplemental Table 1.5**). Gomes et al. (2021) further suggest that this middle Miocene flora was more homogeneous and more species-rich than the modern lowland forest of the varzea and floodplain lakes of the Amazon River.

During the peak of the global high sea level stand (~16.9–14.7 Ma; MMCO), the lake shores in the Pebas system were fringed by mangroves such as *Zonocostites ramonae* (Rhizophoraceae) and the back-mangrove fern *Deltoidospora adriennis* (aff. *Acrostichum aureum*). At the time, the coastline of the eastern Amazon also expanded land inward, as shown by typical shallow marine carbonate deposits (Pirabas Formation), which contain remains of coastal fauna and mangroves (Aguilera et al. 2013).

In the western Amazon, internal linings of foraminifera (single-celled protozoans) and dinoflagellate cysts (single-celled algae) point at oligohaline conditions (Hoorn 1993; Boonstra et al. 2015; Antoine et al. 2016; d'Apolito 2016; Leite et al. 2017, 2021; Linhares et al. 2017, 2019; Leandro et al. 2019, 2022; d'Apolito et al. 2021; Hoorn et al. 2022b). As sea level lowered, a succession of Mauritiinae and *Euterpe*-like palms colonized the swampy lakeshores. Further

lowering of the sea level prompted grasses and ferns, such as *Verrucatosporites usmensis* (aff. *Stenochlaena*, Blechnaceae) and Polypodiaceae (Hoorn 1993, Hoorn et al. 2022b), to colonize the lake shores. One of the most iconic species of the Pebas system is *Grimsdalea magnaclavata*, a Mauritiinae-type palm (Pocknall & Jarzen 2012, Bogotá-Angel et al. 2021) that thrived during the oligohaline wetland conditions. Although this species was relatively rare in the Venezuelan coastal basins (Lorente 1986), it was very common in Trinidad during the Pliocene (Pocknall 2020).

Ferns and algae typical of high-nutrient (eutrophic) aquatic systems, such as *Azolla* (Salvininiaceae) and *Pediastrum*, respectively, were common in the Pebas system (Sá et al. 2020, Hoorn et al. 2022b). But algae such as *Botryococcus*, typical of low-nutrient aquatic (oligotrophic) systems, were also found, indicating that wetland conditions fluctuated depending on nutrient input, something also observed in modern shallow lakes (Sá et al. 2020). Notably, *Botryococcus* and *Pediastrum* are much less abundant in the Pebas system than in other equivalent freshwater depositional systems, supporting the hypothesis that this Miocene wetland was characterized by unique geochemical conditions (Hoorn et al. 2022b).

The tree climbing fern *Crassoretitriletes vanraadschooveni* (Germeraad et al. 1968) and the palm *Grimsdalea magnaclavata* are the most important biostratigraphic markers of the middle Miocene in northern South America. *Crassoretitriletes vanraadschooveni* (family Schizaceae) is closely related to *Lygodium mycrophyllosum*, a taxon that originated during the Eocene in Australia and Antarctica (Rozefelds et al. 2017). Its arrival in South America is dated as 14.2 to 11.6 Ma, and it was observed in almost all of the sedimentary basins in northern South America (Regali 1971, Wijmstra 1971, Lorente 1986, Muller et al. 1987, Jaramillo et al. 2011, Parra et al. 2020). Instead, *G. magnaclavata* shows two dispersal phases: a phase between 16.1 to 14.2 Ma, prior to the arrival of *C. vanraadschooveni*, which was observed in the Subandean basins (Jaramillo et al. 2011) and the western Amazon (d'Apolito 2016, Espinosa et al. 2021), and a phase from 11.9 to 9.7 Ma, after the appearance of *C. vanraadschooveni*, observed in the Venezuelan coastal basins (Germeraad et al. 1968, Lorente 1986, Muller et al. 1987), the Amazon submarine fan (Regali 1971), and western Amazon (Hoorn 1993; Leite et al. 2017, 2021; Linhares et al. 2017, 2019; Leandro et al. 2019, 2022).

Toward the end of the middle Miocene, from 14.7 to 13.8 Ma (MMCT), a global cooling trend was initiated and global sea level started to drop (Miller et al. 2020, Westerhold et al. 2020, Steinthorsdottir et al. 2021). In the central Amazon, the mid-Miocene to Pliocene transition is represented by lacustrine to fluvial conditions and a change in forest composition (Dino et al. 2012, Guimarães et al. 2015, Soares et al. 2015).

4.3. Late Miocene to Pliocene (11.63 to 2.6 Ma), Transition to the Amazon River System

During this time, global climate cooling accelerated, and the global sea level dropped further. This trend reversed during the Pliocene with the onset of a new climatic optimum from 3.2 to 2.5 Ma (Miller et al. 2020, Westerhold et al. 2020). In the Eastern Cordillera (Northern and Central Andes), mountain uplift accelerated (see Boschman 2021), while subsidence in both the Subandean and Amazon sedimentary basins increased (Roddaz et al. 2010). These geological events, and the eastward shift of the center of subsidence due to the changes in dynamic topography (Shephard et al. 2010), led to changes from lacustrine (Pebas phase) to fluvial (Acre phase) deposition in the western Amazon (Latrubesse et al. 2007, 2010; Hoorn et al. 2010; Da Silva & de Souza 2015; see also overview in Espinosa et al. 2021), and the trans-continentalization of the Amazon River (Figueiredo et al. 2009, 2010; Hoorn et al. 2017; Albert et al. 2018).

Data from outcrops of late Miocene to Pleistocene sediments suggest that tropical forests were less diverse at that time (**Figure 3; Supplemental Tables 1.1 and 1.6**) (Da Silva-Caminha et al. 2010, Latrubesse et al. 2010, Nogueira et al. 2013, Guimarães et al. 2015, Da Silva & de Souza

Supplemental Material >

2015). Moreover, in 2008, the construction of a bridge near Manaus (**Figure 2**) facilitated a series of sediment cores that provided exciting new insights into the late Neogene floristic history of the Amazon. Samples from these cores were dated as late Pliocene to early Pleistocene and contained pollen from taxa typical of fluvial floodplain environments (Soares et al. 2017, d'Apolito et al. 2018). This palynological assemblage also included cold-adapted taxa such as *Podocarpus*, *Hedyosmum*, *Ilex*, *Myrsine*, and *Alnus*, and an abundance of herbs (*Asteraceae* and *Poaceae*). This suggests that the Amazon forest was transformed into an open-canopy forest, following the effects of the glacial-interglacial cycles (Rodríguez-Zorro et al. 2022). The abundance of herbs, such as *Asteraceae* and *Poaceae*, was also common in these environments and points at an open-canopy type of forest.

At a global level, the late Neogene coincides with the dispersal and expansion of herbaceous plants. Phylogenetic studies suggest that the *Asteraceae* originated in southern South America during the Cretaceous and reached northern South America by the early Miocene (Mandel et al. 2019). The fossil record further indicates that this dispersal happened in three phases: At 17.4 Ma *Echitricolporites spinosus* (*Asteroideae* or *Tubuliflorae*) arrived in northern South America, followed by the arrival of *Fenestrites* (*Cichoreacidites*) *longispinosus* (*Cichorioideae* or *Liguliflorae*) at 12.7 Ma, and *Echitricolporites mcneilly* (*Cichorioideae* or *Liguliflorae*) at 4.8 Ma (Jaramillo et al. 2011). However, in the Venezuelan coastal basins, *E. spinosus* only arrived at 10.6 Ma, while *F. longispinosus* and *E. mcneilly* arrived at 8.4 Ma and 3.8 Ma, respectively (Lorente 1986). *Poaceae* (the grasses) were already common in the middle Miocene but became much more abundant during the late Miocene and Pliocene. Nevertheless, it is plausible that part of the grass fossils that are found in the Amazon were transported through fluvial transport from the high Andes (Kirschner & Hoorn 2019).

An important biostratigraphic marker for this time frame is the fern *Cyatheidites annulatus* (Jaramillo et al. 2011), an immigrant from southern South America, that arrived in northern South America between 7.1 and 4.8 Ma (Jaramillo et al. 2011). Other remarkable arrivals in this period are *Ctenolophonidites suigeneris* (*Ctenolophonaceae*) (5.5 Ma) (Parra et al. 2020) and *Bombacacidites baculatus* (4.8 Ma; *Malvaceae*) (Jaramillo et al. 2011).

When looking at the Neogene as a whole, the Amazonian floristic diversity was shown to include 23 families in the early Paleogene and 32 families in the late Paleogene (Burnham & Johnson 2004, Ochoa et al. 2012, Carvalho et al. 2021). This diversity rose to 48 families in the early Miocene (Salamanca Villegas et al. 2016) and peaked at 79 families in the middle Miocene (Hoorn et al. 2022b). Between 18.8 and 10.7 Ma, 67 families were identified (d'Apolito et al. 2021). Notably, plant family diversity dropped in the late Miocene to 25 families (Latrubesse et al. 2007, 2010) or 20 families (Nogueira et al. 2013), but rose again to 25–30 families in the Plio–Pleistocene (d'Apolito et al. 2018, Carvalho et al. 2021). Today, at least 117 families are known to occur in the Amazon rainforest (ter Steege et al. 2013), suggesting a huge rise in diversity from Pleistocene to Quaternary. It should be highlighted that, of these 117 families, 24 account for 75% of the overall modern diversity (Carvalho et al. 2021).

5. PHYLOGENETIC PERSPECTIVES OF THE AMAZON FLORA UNDER ENVIRONMENTAL CHANGE

Despite the extensive information on floristic changes through time based on fossil pollen data summarized above, correlating such changes to environmental and landscape changes remains challenging. Many studies have proposed that long-term climatic and geological changes have played crucial roles for species diversification (e.g., Jaramillo et al. 2006, Antonelli et al. 2009, Hoorn et al. 2010). Yet, these studies are mostly based on descriptive comparisons and correlations between dated speciation or extinction events and paleoenvironmental events. As

PHYLOGENIES AND DIVERSIFICATION THROUGH GEOLOGICAL TIME

Phylogenies are branching diagrams representing the evolutionary relationships among species. They are based on DNA and/or morphological data from extant species but sometimes contain fossil species. When time-calibrated (with fossils, molecular clock rates, and/or other methods), phylogenies provide information on the timing of diversification events and diversification rates through geological time. With birth-death models, speciation and extinction rates can be extracted from a phylogeny. In such models, clades are assumed to evolve under a stochastic process, where both speciation and extinction follow a Poisson process, meaning that the expected waiting time to an event follows an exponential distribution (Nee 2006). Originally, speciation and extinction were assumed to be constant or modeled to either increase or decrease with time (Morlon 2014). However, estimating diversification rates from phylogenies of extant taxa is challenging. Indeed, numerous studies have highlighted different caveats pertaining to model limitations or the lack of fossil data (Kubo & Iwasa 1995, Quental & Marshall 2010, Burin et al. 2019). For instance, detecting whether rates vary through time has been questioned due to difficulties in deciphering whether speciation only or extinction only or both are responsible for rate variation (Liow et al. 2010, Burin et al. 2019). Another issue in birth-death models lies in estimates of extinction rates that do not match those in the fossil record (Quental & Marshall 2010, Rabosky 2010), which is due to recent clades diversifying quickly and masking the signal of extinction in other parts of the phylogeny (Morlon et al. 2011). Here we used the environment-dependent birth-death approach, an extension of Morlon et al. (2011)'s model, where speciation and extinction can also depend on external environmental variables (Condamine et al. 2013, 2019), such as temperature variation through time (see the **Supplemental Text**). By correlating speciation and extinction with environmental variables, this approach provides insights into the underlying processes and deep time events shaping biodiversity. Despite the aforementioned limits, these phylogenetic models uncover, for example, the drivers of conifer decline since the Late Cretaceous with extinction rates in agreement with those of the fossil record (Condamine et al. 2020).

a result, they are generally not appropriate when studying long-term environmental changes, such as the late Miocene cooling (~12–5 Ma) or Andean uplift. Furthermore, geological change is often intrinsically related to climate change, complicating precise linking between isolated environmental changes to single diversification events. For example, the uplift of the Andes has affected climate in the eastern Pacific Ocean and the South American continent (Sepulchre et al. 2010, Armijo et al. 2015).

Recent developments in phylogenetic modeling provide an opportunity to quantitatively explore factors that are potentially linked to speciation and/or extinction of lineages throughout geological and evolutionary time, addressing questions about the mechanisms that shape biodiversity patterns and the relationship between diversification and environmental change (Condamine et al. 2013, 2019) (see the sidebar titled *Phylogenies and Diversification Through Geological Time*). For South American plants, phylogenies have been used to estimate diversification in light of environmental changes, especially for Andean clades (e.g., Hughes & Eastwood 2006, Luebert & Weigend 2014, Lagomarsino et al. 2016, Pérez-Escobar et al. 2017). For example, speciation of Neotropical bellflowers (centropogonids) increases with changes in Andean elevation through time (Lagomarsino et al. 2016). Likewise, the two largest Andean orchid clades, Cymbidieae and Pleurothallidinae, colonized the Andes from lowland Amazonian rainforests in the early Miocene, which was followed by increased diversification in the Andes in the middle Miocene, indicating slower diversification in Amazonia (Pérez-Escobar et al. 2017).

Paradoxically, studies of in situ Amazonian plant diversification remain relatively rare compared to studies of Andean plants. We attribute this lack of knowledge to three possible reasons. First, it is difficult to sample the outstanding Amazonian species diversity across such a vast area

Supplemental Material >

Meta-analysis:

research process used to synthesize the findings of independent studies using statistical methods to extract a general trend

Diversification rate:

the difference between speciation and extinction rates (denoted as r , $r = \lambda - \mu$)

(ter Steege et al. 2013, Ulloa Ulloa et al. 2017), leading to undersampled phylogenies for Amazonian species-rich groups such as the iconic *Inga* [Fabaceae, ~400 species described, but only 126 species included in the latest dated phylogeny (Dexter et al. 2017)] and *Guatteria* [Annonaceae, ~180 species described, but only 75 species included in the latest dated phylogeny (Xue et al. 2020)]. Because taxon sampling is not random, diversification inferences based on incomplete sampling are usually biased. Second, many plant clades are not endemic to the Amazon but include many species in adjacent areas (e.g., Pérez-Escobar et al. 2017, Schley et al. 2018, Cabral et al. 2021, Calió et al. 2022), resulting in nonmonophyletic Amazonian groups and complicating in situ diversification studies. Supporting this idea, a biogeographic meta-analysis showed that Amazonia acted as a source of diversity for all adjacent regions through dispersal events out of Amazonia, especially in the past 10 Ma toward the Andes, Central America, and the Atlantic Forest (Antonelli et al. 2018). Third, speciation mechanisms are more intuitive in mountains than in lowland rainforests due to allopatric distributions, the evolution of adaptive traits, elevational gradients, and climate heterogeneity (Rahbek et al. 2019), which has contributed to a higher number of research projects in the Andes than lowland Amazonia (e.g., Hughes & Eastwood 2006, Madriñán et al. 2013, Luebert & Weigend 2014, Pérez-Escobar et al. 2022).

For these reasons, the patterns and processes of plant diversification in Amazonia remain largely unknown, especially when compared to animals (e.g., Hutter et al. 2017, Harvey et al. 2020). However, one meta-analysis of Neotropical clades suggests that the diversification of plants does not match that of animals (Meseguer et al. 2022). In plants, diversification rates are mostly constant through time or tend to increase toward the present, while diversification tends to decrease over time in animals (Meseguer et al. 2022). The observed increases in plant diversification might be attributed to climate cooling, with speciation increasing under cooler climates (Meseguer et al. 2022); the opposite pattern is found in animals globally (Condamine et al. 2019). However, the plant data sets available to date for the Amazon-Andean region seem to be dominated by clades that are rich in the Andes, limiting our understanding of diversification patterns in the Amazon. Recent taxon-specific diversification studies of some members of the Amazonian flora showed Miocene upshifts of speciation, namely, the Calophylleae, a clade that originated in the Amazon at ~17.1 Ma [11.8–23.5 Ma (Cabral et al. 2021)], and the *Eschweilera parvifolia* group (Lecythidaceae), a clade with an Amazon origin at ~13.6 Ma [10.2–17.1 Ma (Vargas & Dick 2020)]. Both Neotropical groups showed increasing diversification rates in the Amazon toward the present, providing additional evidence for the patterns recovered earlier (Meseguer et al. 2022).

Through a literature review, we identified eight well-sampled, time-calibrated molecular phylogenies for which most of the extant species diversity is Amazonian [the so-called Amazon-centered clades sensu (Gentry 1982)]: (a) the *Andira* clade (~15.2 Ma; Fabaceae), including trees from *Andira* and *Hymenolobium*, two genera that are predominantly Amazonian in distribution, with a few recent species in the Cerrado (Simon et al. 2009); (b) *Anemopaegma* (~31.3 Ma; Bignoniaceae), mostly including lianas from the Amazon, with some species in the Cerrado (Calío et al. 2022); (c) the *Bactris* clade (~27.5 Ma; Arecaceae), containing spiny palms in *Astrocaryum* and *Bactris*, two genera centered in lowland Amazonian forests, with some species in Central America (Cássia-Silva et al. 2022); (d) the *Brownea* clade (~30.3 Ma; Fabaceae), including several iconic genera from lowland Amazon (e.g., *Brownea*, *Macrolobium*) (Schley et al. 2018); (e) the Chrysobalanaceae (~33 Ma; 80% of the family diversity is Neotropical), a clade mostly composed of Amazonian trees (Chave et al. 2020) and constituting one of the most common Amazonian plant families in the region, ranking seventh in tree dominance behind Fabaceae, Lecythidaceae, Sapotaceae, Malvaceae, Moraceae, and Burseraceae (ter Steege et al. 2013); (f) the *Eschweilera* section *Parvifolia* clade (~13.6 Ma; Lecythidaceae), composed of common Amazonian trees (Vargas & Dick 2020), representing a key component of the Amazonian flora (ter Steege et al. 2013);

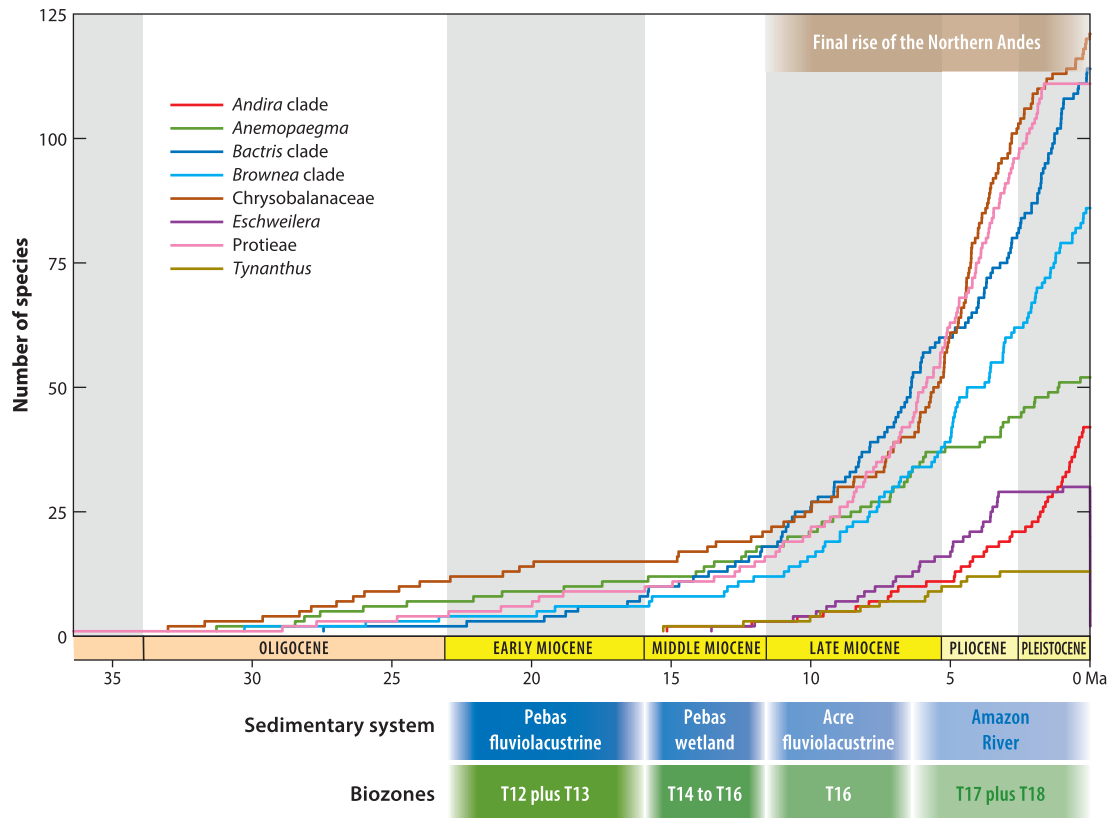


Figure 5

Lineage-through-time plots for a representative sample of time-calibrated phylogenies of Amazonian angiosperm clades. Shaded boxes represent the duration of sedimentary systems [lithological (following d’Apolito et al. 2021 and Kern et al. 2020)] and biozones in the Neogene (following Jaramillo et al. 2011) as described in **Figure 3**, proposed to have fostered the dispersal and radiation of Amazonian organisms.

(g) the subfamily Protieae (~24.8 Ma; Burseraceae), mostly composed of Amazonian trees and shrubs in the genus *Protium* (Fine et al. 2014); and (h) *Tynanthus* (~15.3 Ma; Bignoniaceae), composed of lianas from the Amazon and the Brazilian Atlantic Forest (De Medeiros & Lohmann 2015).

Lineages-through-time plots reconstructed using these eight time-calibrated phylogenies (**Figure 5**) indicate that five clades originated in the Oligocene and diversified slowly until the Neogene. The three other clades originated in the middle Miocene. In the Neogene, the early Miocene (fluvial system) seems to have fostered the radiation of notable clades, while the middle Miocene (Pebas wetland system) seems to represent a transition period with reduced diversification. In turn, the late Miocene (Acre system) represents the most important diversification period, showing rapid lineage accumulation for all clades (**Figure 5**). The Pliocene and Pleistocene (Amazon system) show some slowdowns of species accumulation, which might be an artifact of phylogenetic sampling. Together, these phylogenies suggest that the late Miocene, a time of large landscape reconfigurations with the final rise of the Northern Andes and the eastward shifts of the drainage systems (from the Acre to Amazon system), has drastically altered the evolutionary history of the Amazon flora.

Extinction rate: the rate at which species go extinct (denoted as μ)

Birth-death model: diversification is modeled as a two-rate process where species either give rise to new species (speciation, or birth) or go extinct (extinction, or death)

Supplemental Material >

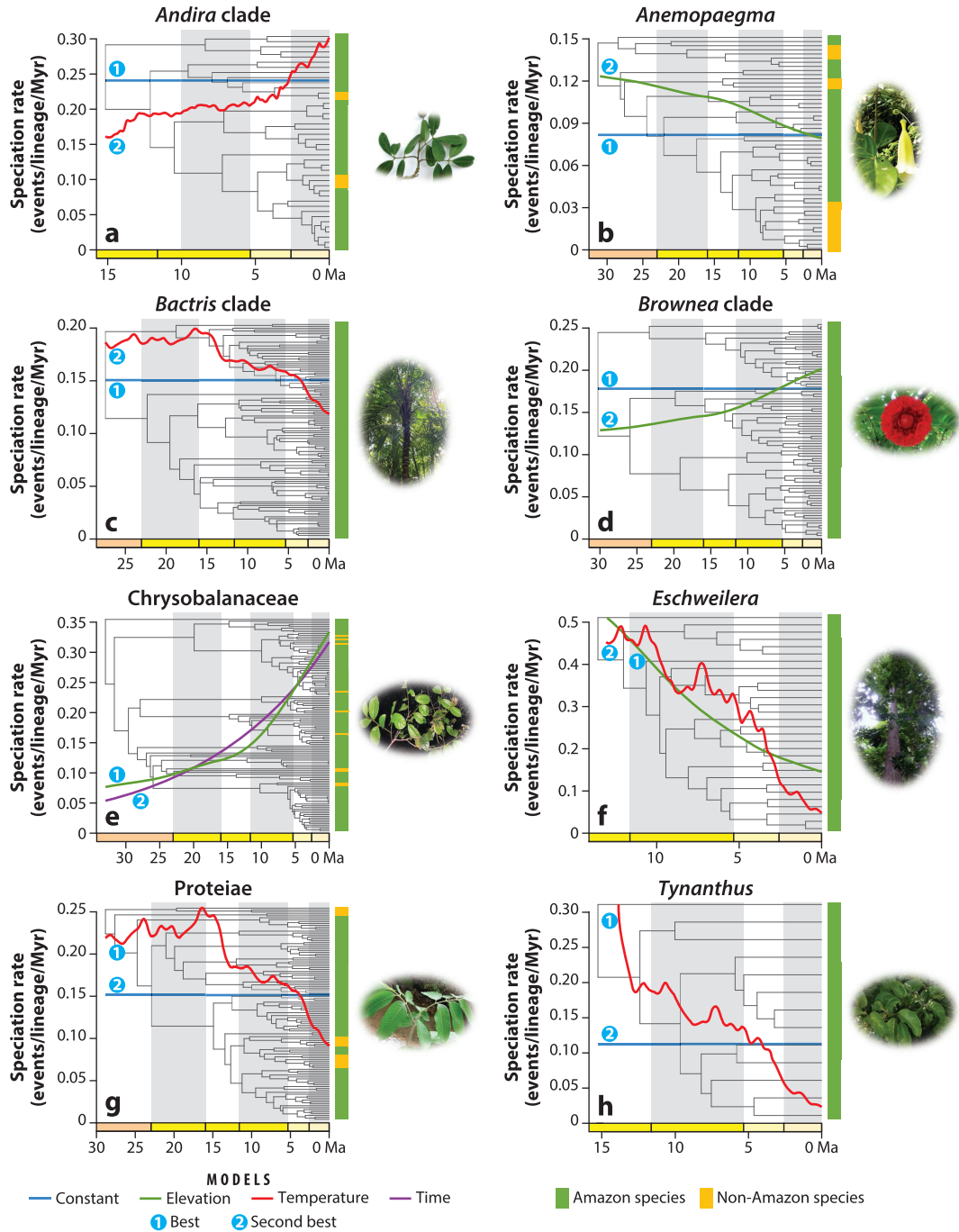
Given the evidence from fossil pollen data available, we expect phylogenetic data to recover similar changes in speciation rates. More specifically, we expect a decrease in diversification rates in the late Miocene, potentially related to the late Neogene global cooling. To test this hypothesis, we used a statistical framework to estimate rates of diversification from time-calibrated phylogenies incorporating models assuming that speciation and/or extinction rates are constant or dependent on time (i.e., classic birth-death model), or dependent on an external environmental variable that varies through time [i.e., environment-dependent birth-death model (Condamine et al. 2019)]. Similarly to Boschman & Condamine (2022), we evaluated fourteen diversification scenarios for each of the eight selected phylogenies by considering four types of models with diversification rates that are constant (two models), time-varying (four models), temperature-dependent (four models), and elevation-dependent (four models). The detailed methodology is presented in the **Supplemental Text**.

For the eight clades selected, we found that the constant-speciation model (**Figure 6, Supplemental Table 4**) was supported for the diversification of four clades, namely: *Andira* (second-best model is a temperature-dependent model, **Figure 6a**), *Anemopaegma* (second-best model is an elevation-dependent model, **Figure 6b**), *Bactris* (second-best model is a temperature-dependent model, **Figure 6c**), and *Brownea* (second-best model is an elevation-dependent model, **Figure 6d**). The remaining four clades showed statistical support for an environment-dependent model of diversification with either an elevation-dependent model for Chrysobalanaceae (second-best model is a time-dependent model, **Figure 6e**) or a temperature-dependent model for *Eschweilera* (second-best model is an elevation-dependent model, **Figure 6f**), Protieae (second-best model is a constant-rate model, **Figure 6g**), and *Tynanthus* (second-best model is a constant-rate model, **Figure 6b**). Interestingly, among the environment-dependent models (best explaining or second-best explaining), speciation rates increase for *Andira* (negatively correlated with temperature), and *Brownea* and Chrysobalanaceae (positively correlated with elevation), but decrease for *Anemopaegma* (negatively correlated with elevation) and *Bactris*, *Eschweilera*, Protieae, and *Tynanthus* (positively correlated with temperature) through time. These findings indicate that responses to environmental changes are highly clade specific.

For *Eschweilera*, Protieae, and *Tynanthus*, the temperature-dependent model estimated a positive correlation between speciation rates and global temperatures ($\alpha = 0.3926, 0.1233$, and 0.3666 , respectively) (**Supplemental Table 4**), which translates into faster speciation during warmer periods and vice-versa. These results support the hypothesis that the late Miocene cooling drove the lower speciation rate in these Amazonian plant clades. For the other five clades, the temperature-dependent model was not selected as the best fit. However, a positive correlation between speciation rates and global temperatures was recovered for *Anemopaegma* and the *Bactris* clade (**Supplemental Table 4**).

The elevation-dependent model estimated a positive correlation between speciation rates and Andean elevation for Chrysobalanaceae ($\alpha = 0.0019$) (**Supplemental Table 4**). This implies that this Amazon clade diversified faster in the later stages of the Andean orogeny, similar to Neotropical bellflowers (Lagomarsino et al. 2016) and orchids (Pérez-Escobar et al. 2017). Five out of the seven remaining clades showed a negative correlation between speciation rates and Andean elevation, suggesting higher speciation rates during an earlier phase of mountain building, a result that is in line with recent results on Neotropical frogs and squamates (Boschman & Condamine 2022).

The role of extinction cannot be ignored, as this evolutionary process represents a component of the net diversification rate shaping diversity dynamics (Morlon 2014). However, extinction rates can be difficult to estimate with phylogenies alone (Rabosky 2010; but see Morlon et al. 2011). The best-fit models did not identify nonzero extinction rates for the eight angiosperm



(Caption appears on following page)

Figure 6 (Figure appears on preceding page)

Diversification patterns of selected Amazonian clades. For each clade, the time-calibrated phylogeny is shown with the side bar depicting Amazonian and non-A Amazonian species. Speciation rates for each clade are shown as estimated with the best (●) and second-best (●) models of diversification (for details, see **Supplemental Table 4**). Clades are as follows: (a) *Andira* clade (Simon et al. 2009); (b) *Anemopaegma* (Calió et al. 2022); (c) *Bactris* clade (Cássia-Silva et al. 2022); (d) *Brownea* clade (Schley et al. 2018); (e) Chrysobalanaceae (Chave et al. 2020); (f) *Eschweilera* section *Parvifolia* clade (Vargas & Dick 2020); (g) Protieae (Fine et al. 2014); and (h) *Tynanthus* (De Medeiros & Lohmann 2015).

Supplemental Material >

clades. This result can be explained by the fact that Amazonia acts as a museum of diversity, buffering against species' extinction. It is also likely that these clades had not yet experienced extinction because of their young origins when compared to other clades. In particular, Neotropical gymnosperm clades are largely absent from the Amazon and mostly occur in the Andes, Atlantic Forest, Central America, or the Caribbean islands as observed for *Araucaria*, *Podocarpus*, or *Zamia*. There are only 34 conifer species over the entire South America, none of which are endemic to the Amazon (Farjon & Filer 2013). However, fossil evidence suggests that gymnosperms were present in the Amazon (Peralta-Medina & Falcon-Lang 2012), where they occurred in Cretaceous open-canopy forests (Carvalho et al. 2021), but went extinct locally in the Cenozoic, potentially due to biotic interactions with angiosperms through competition (Condamine et al. 2020) and the shift to closed-canopy forests.

6. EVOLUTION OF THE AMAZON FLORA IN A CHANGING CLIMATE AND LANDSCAPE: SUMMARY POINTS

1. Geological data indicate large changes in the configuration of the Amazon drainage basin during the Neogene, caused by the rising Andes in the west and a wetland system transitioning into the modern transcontinental Amazon River.
2. Cooling and aridification in combination with an increase in sediment discharge influenced floristic composition and phytogeography.
3. Fossil pollen suggests an overall decrease in diversity, with a change from fluvial and open aquatic environments fringed by closed-canopy forests (early to middle Miocene) toward fluvial floodplains with open-canopy forests and an expansion of herbaceous vegetation (late Miocene to Pliocene), a transition that parallels the geo-climatic history.
4. Given the incredibly high species richness of Amazonia and the recent efforts to study the Amazon flora, the number of well-sampled time-calibrated plant phylogenies available to date is surprisingly low, calling for more detailed phylogenetic studies of Amazonian plant clades.
5. The analysis of eight Amazonian plant phylogenies suggests a mixed diversification scenario, with constant speciation rates for most groups, and clade-dependent diversification to past environmental changes.
6. Clade-specific responses to environmental changes show the need to emphasize system complexity rather than to generalize: Amazonia is both a refuge and a cradle for generating biodiversity.
7. Our findings have implications for present-day biodiversity because major losses of the Amazon, a major biodiversity engine, will impact other parts of the globe by suppressing a primary source of evolutionary novelty.
8. The Amazon is highly threatened by human activities, which directly impacts other tropical biotas and leads to profound long-term evolutionary consequences for biotas located in adjacent regions.

DISCLOSURE STATEMENT

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