Amazonia Through Time: Andean Uplift, Climate Change, Landscape Evolution, and Biodiversity

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The Amazonian rainforest is arguably the most species-rich terrestrial ecosystem in the world, yet the timing of the origin and evolutionary causes of this diversity are a matter of debate. We review the geologic and phylogenetic evidence from Amazonia and compare it with uplift records from the Andes. This uplift and its effect on regional climate fundamentally changed the Amazonian landscape by reconfiguring drainage patterns and creating a vast influx of sediments into the basin. On this "Andean" substrate, a region-wide edaphic mosaic developed that became extremely rich in species, particularly in Western Amazonia. We show that Andean uplift was crucial for the evolution of Amazonian landscapes and ecosystems, and that current biodiversity patterns are rooted deep in the pre-Quaternary.

Pleistocene forest remnants ("refugia") were long held to be responsible for Amazonian diversity (*1*). In the 1990s the centers of diversity, postulated as prime evidence for the refuge theory, were shown to be sampling artifacts (*2*). Over time, the theory was abandoned and an older origin for the Amazonian diversity was proposed (*3*). Perhaps more important, regional diversification events, as inferred from the fossil record and molecular phylogenetic studies, mostly predate the Pleistocene (*4*, *5*). Although the mechanisms of diversification remain elusive and speciation may occur with barriers (*6*) and even without clear barriers (*7*), it is now generally acknowledged that the development of Amazonian biota has been a long and complex process (*3*, *8*).

At the global scale, the Neogene (the 20 million years that preceded the Pleistocene) was a defining period during which much of the present geography and biotic composition was formed (*9*). The process of species diversification is strongly linked to tectonism and climate, both in the terrestrial (*10*, *11*) and marine realms (*12*). The dynamic geologic history of South America should thus be very relevant for understanding the origins of the present diversity.

Recent advances in the fields of Andean and Amazonian geology and phylogenetics have proceeded in parallel. The geosciences community provided new data on mountain building in the Andes and on the timing and types of biotic and paleoenvironmental changes in lowland Amazonia. Climatologists modeled the atmospheric patterns that resulted from the formation of the Andean orographic barrier. At the same time, new molecular analyses based on DNA sequence variation of living organisms shed further light on the sequence and approximate timing of diversifications.

These new data made it clear that the Cenozoic uplift history of the Andes and its effect on regional climate (*13*, *14*) has had a large impact on the landscape evolution in entire northern South America, including Amazonia (*15*, *16*). Although links between the Andean orogeny and neotropical diversification have long been suggested (*17*), only recently have researchers started to explore dated phylogenetic trees [e.g., (*18*, *19*)], in combination with more realistic, complex geological scenarios (*8*, *20*).

Here, we review the timing and extent of mountain building in northern South America and compare it with geologic evidence from sedimentary basins in Amazonia. We explore the origins of Amazonian ecosystems and biodiversity with the use of a combination of geologic (including paleontologic) and ecologic data sets as well as dated molecular phylogenies. Through schematic representation of these findings, we summarize the geologic evolution of this area, outline the age structure of its biodiversity, and provide a guideline for future integrated geologic, biogeographic, and conservation studies.

Amazonia Prior to Andean Influence: An Ancient, River-Dominated Landscape

The area known today as Amazonia was once part of a much larger "pan-Amazonian" region, which, before the late Miocene [until 10 million years ago (Ma)], included the area of the present Amazon, Orinoco, and Magdalena drainage basins (Fig. 1A). At times this region extended to the south, into the northern Paraná region (*21*). We call this vast area pan-Amazonia because we know from the fossil record that a diverse fauna existed, elements of which are now restricted to Amazonia.

Most of Amazonia's geologic history was centered on the Amazon Craton, the hard rock core in the eastern part of South America, but this situation changed during the course of the Cenozoic. Following continental breakup (135 to 100 Ma), both the growing Atlantic Ocean and plate tectonic adjustments along the Pacific margin (*22*) caused deformation within the Amazon Craton, and later the formation of the Andes (figs. S1 to S4) (*23*). Archives of this regional history are stored within a series of north-south–trending foreland basins along the Andes, in the east-west–trending intracratonic basins, and in the Amazon submarine fan in the Atlantic (*24*–*26*).

Testimony to the post-breakup changes on the craton are alluvial and braided river deposits of Cretaceous age that accumulated in the east-west–stretching sedimentary basins. These drainage systems were captured in a "reversed" trunk river with westward flow (*27*), quite dissimilar from the present Amazon River. The drainage divide was initially situated in eastern Amazonia, but during Paleogene times (~65 to 23 Ma) it migrated westward (*25*, *28*), giving way to the precursor of the modern lower Amazon River (Fig. 1, A and B). Toward the end of the Paleogene, the continental divide was located in Central Amazonia and separated east- and west-flowing Amazonian rivers (*24*).

During the Paleogene, the western and northwestern parts of the pan-Amazonian lowlands were characterized by alternating fluvial conditions and marginal marine embayments (*26*). Fossils show that a diverse mammalian fauna including rodents, marsupials, ungulates, and xenarthrans existed in the central-western part of pan-Amazonia [e.g., (*29*)]. Paleogene fossils also reveal diversification of a variety of freshwater catfishes, characins, and cichlids now prominent in Amazonian waters

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(*21*, *30*). Typical South American mammals such as the xenarthrans (sloths, armadillos, and anteaters), as well as podocnemidid turtles and plant groups such as *Nothofagus*, *Araucaria*, *Gunnera*, and Winteraceae, may have colonized South America through the southern "Gondwanan" connection with Antarctica and Australia, which lasted until the Late Eocene (*31*–*33*). But the role of dispersal versus vicariance in shaping disjunct distributions in the southern hemisphere is intensely debated. Despite continental isolation to the north lasting until the Pliocene, waves of immigrants (e.g., bats and plant families such as Malpighiaceae, Fabaceae, Annonaceae, and Rubiaceae) arrived from the boreotropical regions while caviomorph rodents and platyrrhine primates possibly crossed the Atlantic from Africa (Fig. 2A).

Andean Uplift, a Major Driver for Change in the Amazonian Landscape and Biota

Uplift in the Central and Northern Andes was a partially synchronous process caused by plate tectonic readjustments [(*23*); see also references in (*16*)]. Plate subduction along the Pacific margin caused uplift in the Central Andes during the Paleogene [65 to 34 Ma; see references in (*14*, *16*)]. Posterior plate breakup in the Pacific (~23 Ma) and subsequent collision of the new plates with the South American and Caribbean plates resulted in intensified mountain building in the Northern Andes (figs. S1 to S4) (*16*). Mountain building first peaked in this region by the late Oligocene to early Miocene (~23 Ma), at an age

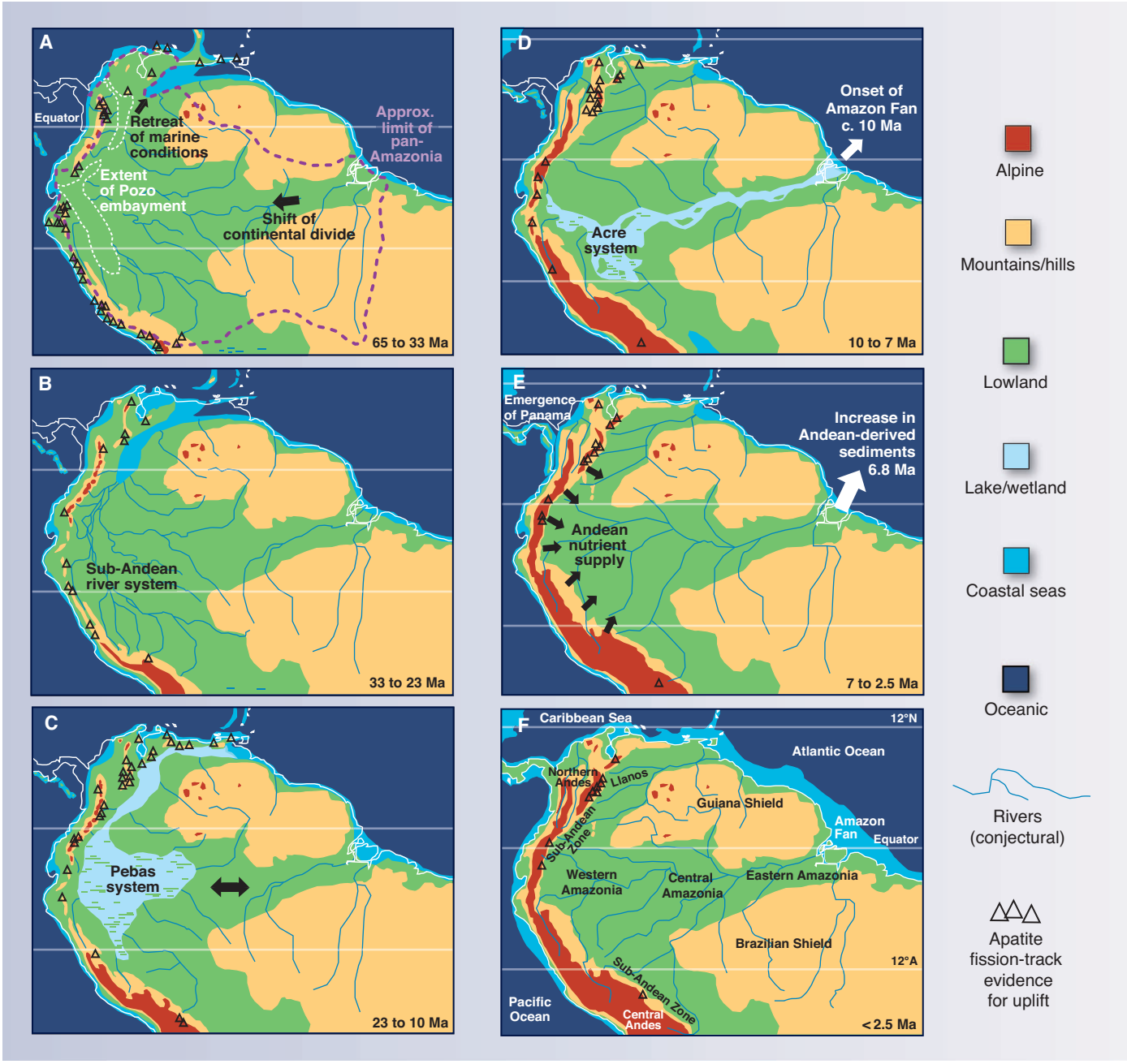


Fig. 1. Paleogeographic maps of the transition from "cratonic" (**A** and **B**) to "Andean"-dominated landscapes (**C** to **F**). (A) Amazonia once extended over most of northern South America. Breakup of the Pacific plates changed the geography and the Andes started uplifting. (B) The Andes continued to rise with the main drainage toward the northwest. (C) Mountain building in the Central and Northern Andes (~12 Ma) and wetland progradation into Western Amazonia. (D) Uplift of the Northern Andes restricted "pan-Amazonia" and facilitated allopatric speciation and extirpation [e.g., (*21*)]. (E) The megawetland disappeared and *terra firme* rainforests expanded; closing of Panama Isthmus and start of GABI. (F) Quaternary. Note that South America migrated northward during the course of the Paleogene.

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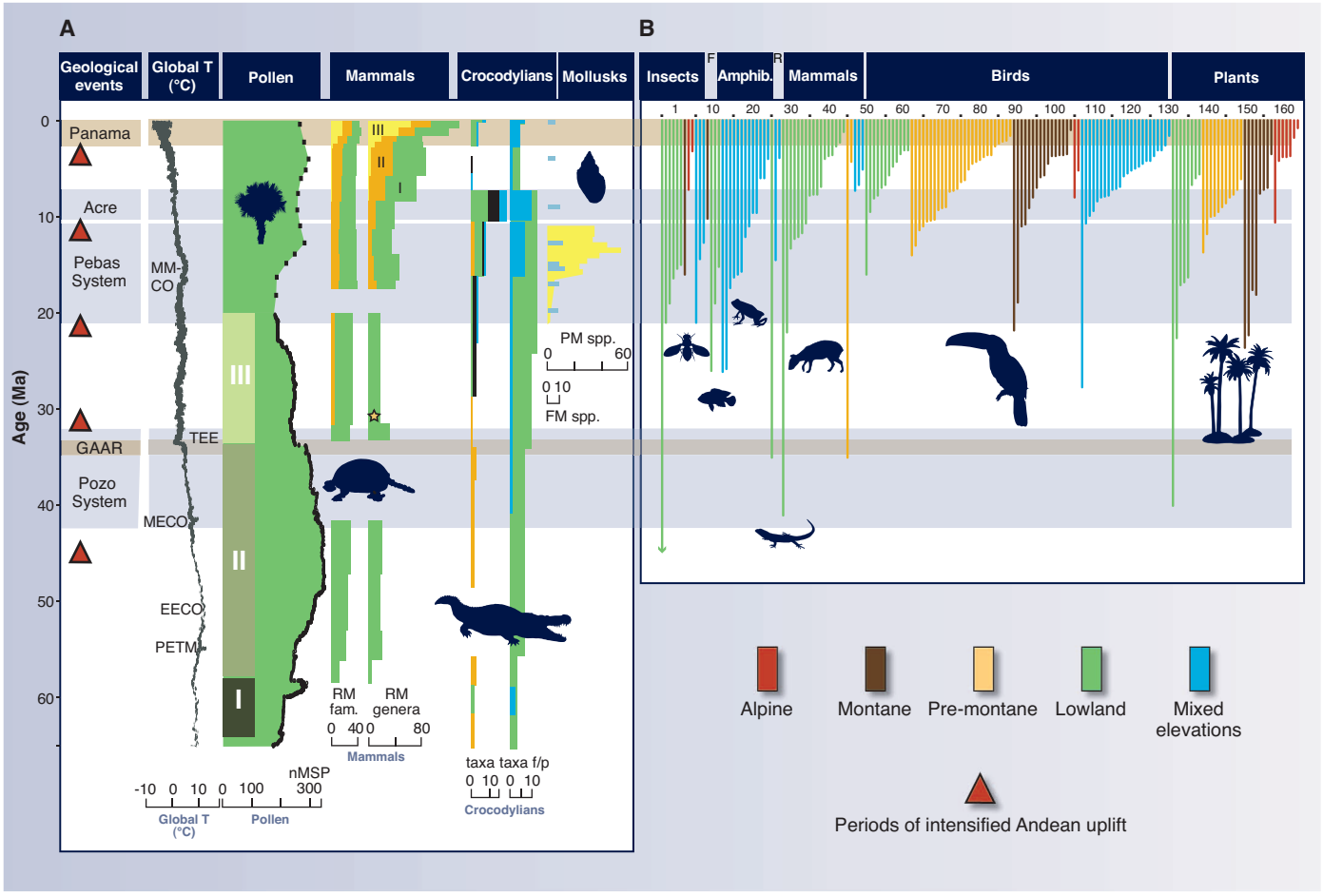


Fig. 2. Biotic changes in Amazonia through time (*23*). (**A**) The Cenozoic fossil record of the tropical lowlands reveals the timing of biotic turnover. Paleogene floral diversity (from pollen records) increased with high temperature, but in the Neogene it was unrelated and remained relatively high even under cooler conditions. Mollusks and crocodiles diversified with the onset of the Miocene megawetlands and declined with its demise. The fossil record, as is shown for the caimanine crocodiles (blue in the right column), is nonetheless incomplete when compared to minimum expected numbers of species (green in the right column) derived from phylogenetic reconstructions (*23*). Late Neogene mammal diversification was particularly strong among North American derived taxa. MMCO, Middle Miocene Climate Optimum; PETM, Paleocene-Eocene Thermal Maximum; MECO, Middle Eocene Climate Optimum; EECO, Early Eocene Climate Optimum; TEE, Terminal Eocene Event; GAAR, Greater Antilles-Aves Ridge; nMSP, number of pollen morphospecies; RM, running mean; f/p, from the fossil record or as based on caimanine phylogeny; FM, fluvial mollusk; PM, Pebasian endemic mollusk species. Crocodylians: Left column, number of species from fossil record; right column, number of caimanine species from fossil record versus number of lineages (orange, non-eusuchian crocodyliforms; green, Caimaninae; black, Gavialoidea; blue, Crocodylidae). Global temperature curve is based on (*68*). Abbreviations are further explained in (*23*). (**B**) Diversification of modern lineages revealed from molecular phylogenies. The lines illustrate the approximate timing of diversification for genera of animals and plants in northern South America, in relation to the elevation zone they inhabit (lowland, 0 to 500 m; premontane, 500 to 1500 m; montane, 1500 to 3000 m; alpine, 3000 to 4800 m). Nearly all living genera in northern South America have a pre-Quaternary origin, but ages of taxa differ between major elevation zones. Several highland genera are fairly young; lowland genera are a mixture of young and old lineages. Numbers above individual lines refer to table S1, where additional details are given.

that coincides with the diversification of the first modern montane plant and animal genera (Fig. 2B). However, the most intense peaks of Andean mountain building followed during the late middle Miocene (~12 Ma, Fig. 1C) and early Pliocene (~4.5 Ma, Fig. 1E and figs. S3 to S5) (*16*). Plate reorganization ultimately resulted in closing of the Panama Isthmus during the Pliocene (at ~3.5 Ma) (*34*) and led to the Great American Biotic Interchange (see below).

Mountain building in the Andes generated tectonic load and renewed accommodation space in the adjacent foreland basins. As mountain building progressed and a critical elevation (~2000 m; figs. S3 to S5) was surpassed, rainfall increased along the eastern flank. This coupling of tectonic and climatic processes resulted in further uplift, erosion, and water and sediment supply (*13*, *14*, *35*) and is in accordance with changes in the depositional record of the Andean foreland and Amazonia (fig. S5). However, the Andean sediment flux that engulfed lowland Amazonia (*36*) was not continuous; intramontane basins and perimontane basins may have captured influx for periods of millions of years, resulting in pulses of deposition eastward.

Parallel to intensified uplift in the Andes, a large wetland of shallow lakes and swamps developed in Western Amazonia (Fig. 1C) (*37*). These new aquatic environments of the "Pebas" system were colonized by rapidly radiating endemic invertebrate faunas composed of mollusks and ostracods (*38*). This was also the stage for a diverse reptile fauna including gharials, caimans, and turtles (Fig. 2A). One of the most remarkable representatives of this now-extinct fauna was *Purussaurus,* the largest known caiman, which reached ~12 m in length (*39*).

The wetland fragmented the preexisting rainforests, yet a diverse forest that already bore resemblance to the modern forest (in terms of plant family composition) remained at the margins of this new aquatic system (*15*, *40*). Although lower than in the Paleogene, plant diversity (as indicated by pollen types) peaked at 13 Ma, near the end of

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the Middle Miocene Climatic Optimum (Fig. 2A). Geochemical evidence from mollusk shells further indicates that a modern type of monsoonal climate was already present and provided a seasonal water influx into the wetland system (*41*). Terrestrial taxa such as xenarthrans, *Gonatodes* geckos, and leaf beetles, as well as cichlid fish in the aquatic environments, lived and diversified in the wetlands (Fig. 2B and table S1).

Taxa of marine ancestry in the Miocene (*42*) or earlier (*43*), such as potamotrygonid stingrays, thrived in the Amazonian freshwater wetlands. Periods with somewhat elevated salinities are also indicated by benthic foraminifera, barnacles, (marginal) marine mollusks, and the geochemical signature in the mollusk shells (*44*). These marine invertebrates, however, were Neogene arrivals and disappeared with the withdrawal of marginal marine conditions. Other indicators of marine influence in the wetlands were dinoflagellates, pollen from mangrove trees, and marine ichnofossils. Biogeographic reconstructions based on phylogenies also fit this scenario (*8*, *20*, *42*). Despite such evidence, the extent of marine influence in Amazonia is still debated (*45*).

By the end of the middle Miocene (~12 Ma), faster and more widespread Andean mountain building prompted peak topographic growth. This created deep canyon incision and erosion in the Central and Northern Andes, especially in the Eastern Cordilleras and in the Venezuelan Andes (figs. S1 to S4) (*16*, *46*), where alluvial megafans developed (*47*, *48*). It also coincided with raised sedimentation rates in the Andean foreland basins that eventually became overfilled. At ~10 Ma, coinciding with global sea level drop and climate cooling, Andean sediments reached the Atlantic coast through the Amazon drainage system, and the Amazon River became fully established at ~7 Ma (*24*, *49*).

Meanwhile, the Western Amazonian wetland changed from a lacustrine to a fluvial or fluviotidal system (Fig. 1D) (*37*, *45*, *50*), which resembled the present-day Pantanal in southern Amazonia (*45*). This so-called "Acre" system harbored a very rich aquatic vertebrate fauna that included mega-sized gharials, caimanines, and side-neck turtles (*39*), which eventually declined with the disappearance of megawetlands in Western Amazonia at ~7 Ma (Fig. 2A) (*21*, *38*, *39*). Most of the endemic mollusk fauna was unable to adapt to the initial fluvial conditions and was strongly reduced around 10 Ma (*38*). The floodplains of this system were dominated by grasses (*51*) and were inhabited by a more diverse xenarthran fauna than at present (*52*).

Preliminary palynological evidence indicates a ~10 to 15% increase of plant diversity between ~7 and 5 Ma, shortly after the wetlands were replaced by forested habitats (Fig. 2A). Molecular studies of tree genera such as *Guatteria* (Annonaceae, ~250 species) and *Inga* (Fabaceae, ~300 species) show a similar trend of rapid diversification following the demise of Amazonian wetlands (*53*, *54*). This suggests that the establishment of terrestrial conditions in Western Amazonia may have been an important prerequisite for the diversification of the current biota of this region. However, the actual triggers of speciation in these and other cases may have been much more complex, involving factors such as soil adaptation and plant-herbivore interactions (*55*).

Western Amazonia from then on bore the key geographic features of the landscape as we know it today (Fig. 1, E and F). It had changed from a drowning, negative relief into a positive relief incised by an increasingly entrenched river system with high sediment load. By the late Miocene, good swimmers such as proboscideans had crossed the relatively small seaway that remained between Central and South America and were at the forefront of a major immigration wave (*56*, *57*).

The final scenes of this history are characterized by further Andean uplift (Fig. 1F), closure of the Panama Isthmus (~3.5 Ma), the Quaternary ice ages (2.5 to 0.01 Ma), and restriction of megafans in the foreland basin zone. This, together with neotectonic processes in Amazonian lowlands (*28*), caused uplift of the Neogene deposits, development of widespread river terrace systems, and readjustments of river patterns, and led to the mosaic-type landscape of the present (*58*). The accelerated uplift phases during the last 10 Ma fostered spectacular radiations of highland plants such as lupines (*59*), as well as tanagers, bumblebees, and some rodents (Fig. 2B and table S1). This was also a time of extensive migration, when both Amazonia and the new montane habitats in the Andes were colonized by taxa of North American descent during the Great American Biotic Interchange (GABI) (*56*).

The GABI caused decline in the number of endemic South American mammal families during the Pliocene and especially the Quaternary. However, the overall generic diversity of South American mammal taxa remained stable, and the total number of genera increased by the strong diversification of taxa derived from North American immigrants (*56*) (Fig. 2A). Molecular studies suggest that many bird lineages also took part in the GABI (*60*, *61*). By contrast, plants have been more capable of overseas dispersal, and many lineages crossed the Panama Isthmus before its final closure (*62*), whereas others probably reached South America directly from Africa (*63*). These results, based on molecular and fossil studies, suggest that immigrants from other landmasses have played an important role in the historic assembly of the Amazonian biota (*64*).

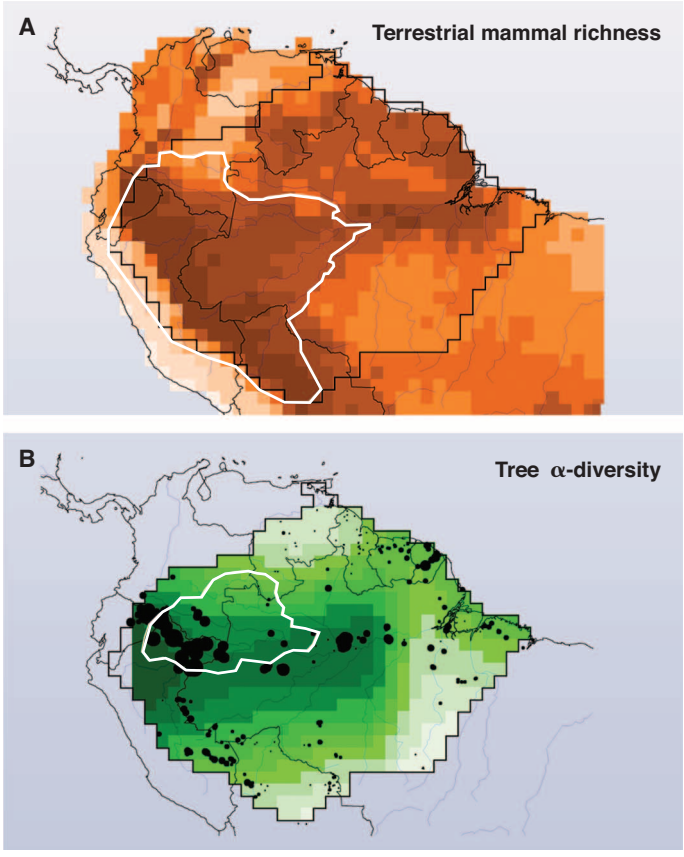


Fig. 3. Present Amazonian diversity patterns. See figs. S6 and S7 for depictions of the close relationship among Amazonian geology, soils, climate, and diversity. (**A**) Terrestrial mammal richness (range: lightest color, 2 to 10 species; darkest, 89 to 109 species) (*69*); white polygon denotes relatively rich soils (fig. S6C). (**B**) Tree α-diversity (*66*). Black dots: local tree α-diversity on 1-ha plots (n = 752); Fisher's α ranges from 3.6 to 300; green shades: loess spatial interpolation of 1-ha values (6 to 117); white polygon: area of least severe water shortage (see fig. S6D).

Can Geologic History Help Us Understand Present Biodiversity in Amazonia?

A comparison of present biodiversity patterns with geologic and edaphic units shows that the highest concentrations of terrestrial mammal and amphibian richness are found on Western Amazonian soils that developed on the Neogene (Andean) sediments (Fig. 3A and figs. S6 and S7). These soils show much higher variation in levels of nutrients and are in stark contrast to generally nutrient-poor soils on the craton in Eastern Amazonia (*65*). Forest productivity and forest dy-

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namics are also higher on these soils (fig. S8), which suggests that bedrock composition, diversity, and ecosystem productivity are interrelated (*66*).

Water geochemistry, sediment composition, and fertility of floodplains further confirm the disproportionate richness in nutrients of the Andean system versus the relative nutrient poverty in the "cratonic" aquatic system (*67*). It seems paradoxical that the old Amazon Craton, which had the opportunity to accumulate taxa for a much longer period than the young areas in Western Amazonia, has fewer species, genera, and families.

Nutrients and habitat heterogeneity are paramount in Amazonian diversity, but they are not the only ingredient. Tree α-diversity (i.e., the diversity measured on 1-ha plots) peaks in the wetter, less seasonal part of Western Amazonia (Fig. 3B), which suggests a role for climate in sustaining (and perhaps also driving) diversity (*66*). By contrast, the highest levels of mammal diversity appear little affected by rainfall seasonality, from aseasonal Ecuador down to highly seasonal Bolivia (Fig. 3A and fig. S6D); this suggests that additional factors such as productivity need to be considered.

Although the transition from a "cratonic" to an "Andean"-dominated system was a fundamental change in the evolution of Amazonian landscapes and species composition, all data suggest that this switch was a complex, stepwise process. Species accumulation was driven by more than one single, overarching mechanism, and Amazonian biodiversity was certainly not a by-product of just Pleistocene ice ages, but resulted from a much more extended period of evolution. However, after the draining of the wetlands (late Miocene), diversification in Western Amazonia must have been particularly rapid, as the diversity of this area greatly outnumbers the diversity in the cratonic areas.

Many outstanding research questions concerning Amazonia remain. Understanding the mechanisms that underlie the assembly and evolution of Amazonian biodiversity continues to be a major challenge that will require hitherto unrealized interdisciplinary scientific collaboration. Evolutionary studies linked to molecular phylogenies and fossil assemblages should focus on Neogene records and on species-rich but poorly sampled areas. Future research should be concentrated on the interface between the Cenozoic and cratonic areas, and on the transition zone between the Andes and Western (lowland) Amazonia (fig. S6). This area, together with the southern fringe of Amazonia, has become rapidly occupied by humans but nonetheless remains scientifically poorly known.

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