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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 podocnemid 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 platyrhine 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

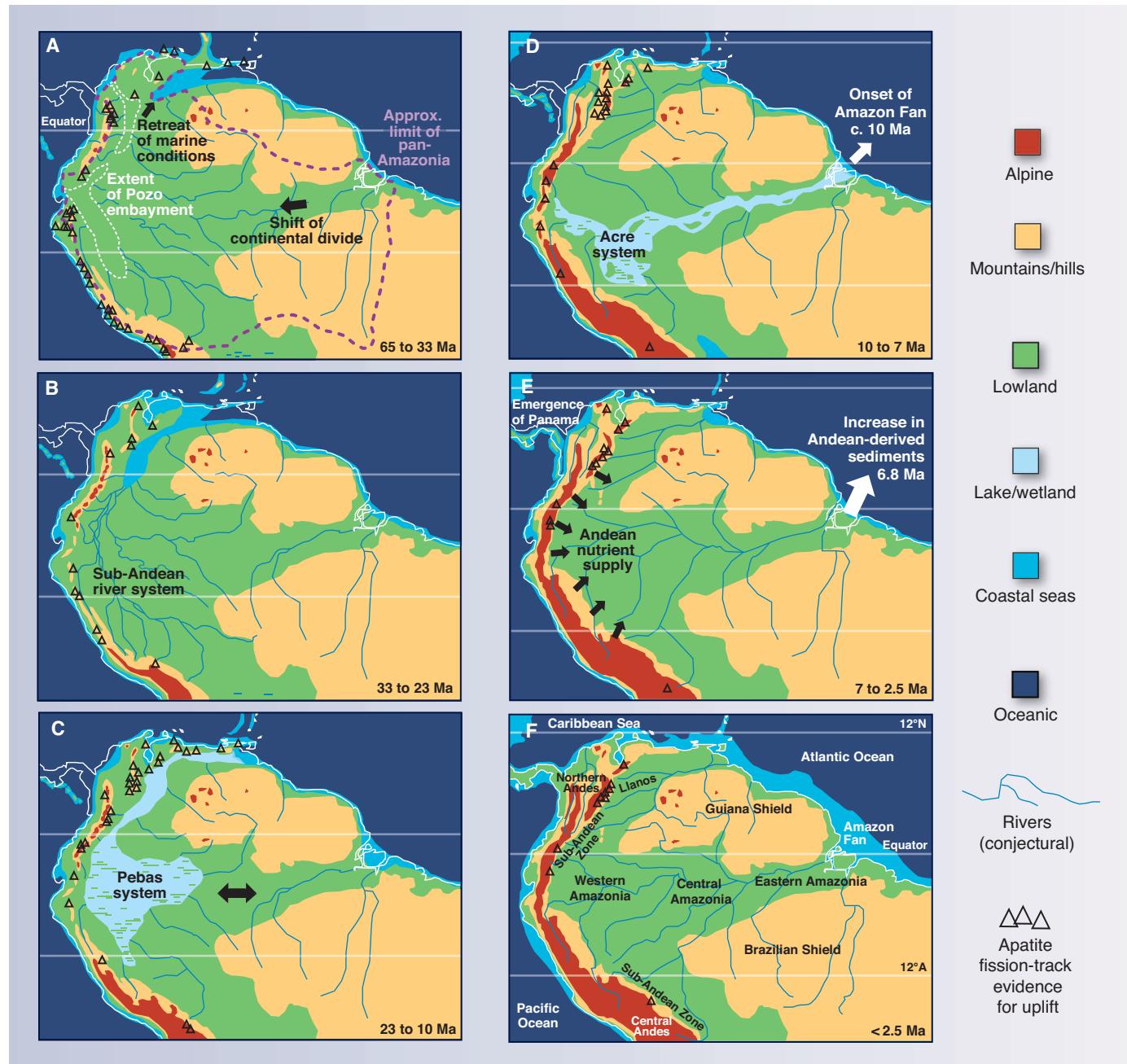


Fig. 1. Paleogeographic maps of the transition from “cratonic” (A and B) to “Andean”-dominated landscapes (C to F). (A) Amazonia once extended over most of northern South America. Breakup of the Pacific plates changed the geography and the Andes started uplifting. (B) The Andes continued to rise with 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.

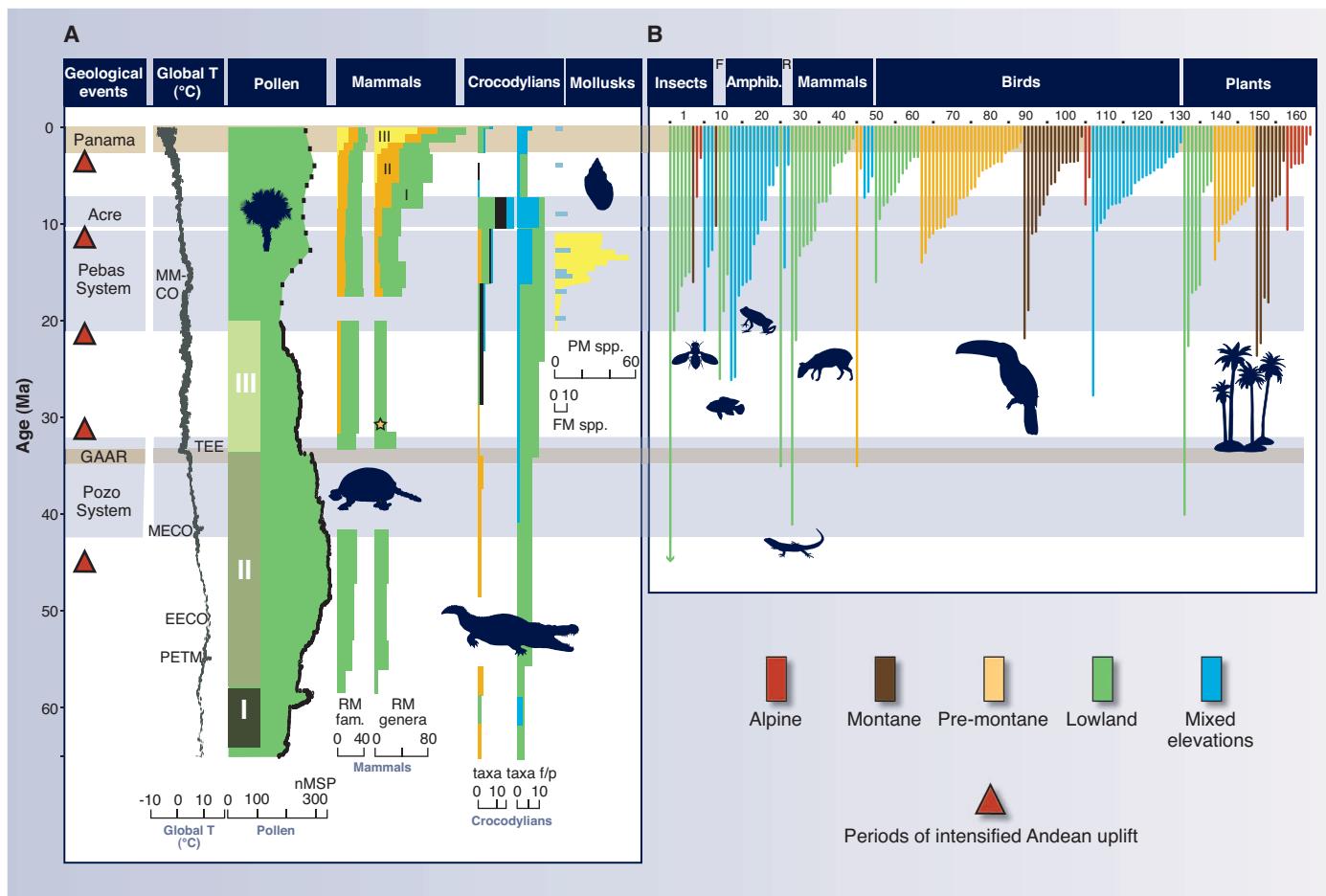


Fig. 2. Biotic changes in Amazonia through time (23). **(A)** The Cenozoic fossil record of the tropical lowlands reveals the timing of biotic turnover. Paleogene floral diversity (from pollen records) increased with high temperature, but in the Neogene it was unrelated and remained relatively high even 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

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 fluvio-tidal 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 di-

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 low-

lands (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).

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-

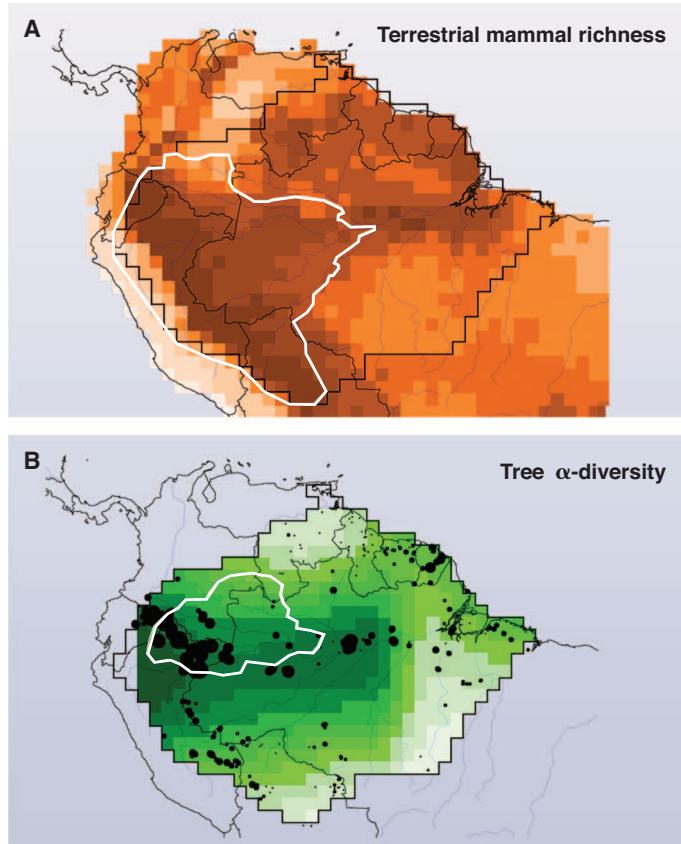


Fig. 3. Present Amazonian diversity patterns. See figs. S6 and S7 for depictions of the close relationship among Amazonian geology, soils, climate, and diversity. **(A)** Terrestrial mammal richness (range: lightest color, 2 to 10 species; darkest, 89 to 109 species) (69); white polygon denotes relatively 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).

versification 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

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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Materials and Methods

Figs. S1 to S8

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Supporting Online Material for

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

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Table S1

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METHODOLOGY

1) Andean Geology (Figures S1-5)

General explanation of apatite fission-track (AFT) thermochronology and its application in the reconstruction of mountain building in the Andes

Apatite fission-track (AFT) thermochronology is used to provide an overview on mountain building across the Andes (Fig. S1) and –in the context of this article– is used to compare geological development in lowland Amazonia with e.g. molecular phylogenetic data. AFT analysis is a thermochronologic method that yields the time when rock passed through the 2 to 5 km depth window or ~60°-110°C temperature window during exhumation (Fig S2), as a result of upper crustal tectonic and/or surface processes e.g. (S1, 2). Therefore, AFT analysis provides cooling ages and not rock formation ages in orogenic contexts. A more complete overview of the Andean evolution, based on comparison of different geological techniques (including zircon and U-Th/He thermochronology (AFT, ZFT) is currently in preparation (Bermúdez et al.).

To understand what AFT ages indicate, it is necessary to differentiate between three important concepts: surface uplift, rock uplift and exhumation (see Figure (S2) and ref (S3)):

1) *Surface uplift*, is the displacement of the Earth's surface with respect to the geoid. The geoid is defined as the “*equipotential surface which would coincide exactly with mean ocean surface of the Earth, if the oceans were in equilibrium, at rest, and extended through the continents*” (Wikipedia).

For example in Figure S2 the orange point at the surface changes its elevation from 0 meters to 2000 meters with respect to the geoid. This corresponds to a surface uplift of 2000 meters. Surface uplift is therefore closely related to the creation of topography. The difference in surface temperature at sea level and at 2000 m elevation is about 10°C, given a common mountain lapse rate of 5°C/km.

2) The displacement of rock with respect to the geoid is known as *rock uplift*. In the same figure (Fig. S2), the hexagon symbols correspond to the accessory mineral apatite inside the rock column that is displaced toward the surface because of erosion at the surface and/or tectonic processes such as normal faulting.

3) *Exhumation* or *denudation* is the difference between rock uplift and surface uplift. Exhumation is thus equal to erosional denudation -or mass removal- from outcropping rocks. Erosional denudation can only happen when a minimum amount of topography is created. Thus the onset of exhumation can be used as a proxy to assess the onset of the creation of topography during mountain building and initial uplift. AFT data in orogenic contexts therefore provides an idea on the timing of erosional denudation.

Figure S1A corresponds to a dataset of 905 AFT ages across the Northern and Central Andes (see references). All these ages indicate the timing of tectonic events that produce surface uplift and exhumation in these sectors. Differences can be observed between the Northern and Central Andes. For the Northern Andes of Venezuela, Colombia, and Ecuador age versus elevation plots for each of the areas denoted in rectangles (Figure S3).

The differences could be related to a non-homogeneous distribution of the samples in the Andes, different degrees of incision on both areas, or an actual trend in the uplift history. It is worth noting that no clear trends in the uplift history have been reported in the Andes based on other geological data, therefore this interpretation should be viewed with caution. However, as seen in Figure S1B the peaks in the histogram coincide with the main tectonic events reported in the literature all along the Andes (S4).

The histogram shown in Figure S1B indicates the frequency of AFT ages determined in the Northern and Central Andes and is based on published AFT data. The AFT ages were discriminated using cluster analysis for the whole dataset. The histogram was made taking into account two facts: 1) areas with high sample densities (denoted as rectangles in Figure S1A) and 2) areas where vertical profiles were sampled in order to estimate age-elevation relationships at specific locations. Figure S1B shows in general terms the various stages of exhumation found throughout the Northern and Central Andes. Note that the faster topographic growth and deformation rates in the Andes reported in the literature (S4) correspond with the peaks in the histograms. Subsequently, in Figure S3 we show a comparison between the age-elevation relationships and histograms for each of the areas denoted in rectangles, this in order to discriminate differences in terms of exhumation rates. The main objective of Figure S1B, however, is to identify different phases of surface uplift and exhumation and relate these with the landscape evolution and biotic developments in lowland Amazonia.

Data collection and methods concerning the apatite fission track ages represented in the interpolation map and the age/elevation relationship for different sectors of the Central and Northern Andes.

Apatite fission-track data were compiled from studies all across the Northern and Central Andes, Amazonas Basin, Caribbean Mountains, Trinidad, Tobago and Dutch Antilles (S5-39). The database consists of 905 AFT ages, with 592 ages from the Andes. Sample locations, AFT ages and a 250 m resolution Digital Elevation Model (DEM) (SRTM, NASA) were used in ArcGIS™ to generate Figure S1A. We used the method of natural neighbour interpolation (S40), only for samples from the Andes, in order to determine patterns of regional exhumation. This map should be considered as a first-order approximation. The interpretation, however, is focused on areas with high sample densities (denoted as rectangles in Figure S1A). The data inside these rectangles were used for generating age-elevation relationships (Figure S3 and S4). From the age elevation profiles different exhumation and deformation events can be inferred in different areas of the Andes. Those events cover the entire range of deformation events (S4), but their areal extension does not necessarily mean they were exclusive of that precise part of the Andes. However, the plots do reinforce the idea of an ubiquitous more important Late Miocene-Pliocene deformation event with associated higher exhumation rates (steeper slopes in the plots). The lesser representation of those late Miocene higher exhumation rates in the Ecuadorian and Peruvian Andes appear to be biased by the presence of more samples to the west, where deformation in the Andes is expected to be older.

In Figure S1B, we show a histogram and Probability Density Function (PDF) for the entire AFT age database of the Andes. We used cluster analysis (k-means algorithm of ref (S41); and MClust of ref (S42, 43)) in order to determine major exhumation events. For this, the number of components (age populations) was selected using the BIC (Bayes Information Criteria, (S44)).

2) Paleontological section (Figure 2A)

The diversity data depicted in Figure 2A are derived from various published sources (see caption), but also include some additional data that are outlined here.

Pollen

The Paleogene-early Miocene pollen data and methodology for computing diversity counts have been published in ref (S45). Additional samples spanning the Neogene have been incorporated (S46). They have been processed in the same way as those in ref (S45).

Roman numbers I-III in figure 2A denote three successive pollen floras (and by implication different rainforest types) during the Paleogene.

Crocodilians

The Neogene crocodilian occurrences as well as the caimanine cladogram have been published in ref (S47). Additional data used to construct the occurrences of tropical South American

crocodilian records are given below. these include Paleogene southern South American taxa but not the marine crocodyliforms Dyrosauridae (Cretaceous-Eocene).

Paleogene crocodilian occurrences.

Early Paleocene (Danian), El Molino Formation (upper part), Bolivia, and Yacoraite Formation (upper part), Argentina: *Dolichochampsia minima* (non-eusuchian crocodyliform) (S48).

Early Paleocene (Danian), Santa Lucia Formation, Bolivia: *Zulmasuchus querejazui* (= *Sebecus querejazus*) (Sebecidae, non-eusuchian crocodyliform) (S49).

Late Paleocene (Thanetian or Riochican), Maiz Gordo Formation, Argentina: *Bretesuchus bonapartei* (Sebecidae, non-eusuchian crocodyliform) (S50).

Late Paleocene (Thanetian or Itaboraian), unnamed beds, Itaborai Basin, Brazil: three yet undescribed sebecid species (Sebecidae, non-eusuchian crocodyliforms) (S50) and unpublished material.

Middle-Late Eocene, Lumbra Formation (“Casamayoran”), Argentina: *Ayllusuchus fernandezi* (Sebecidae, non-eusuchian crocodyliform) (S51).

Middle-Late Eocene, Divisadero Formation, Argentina: *Ilchunaia parca* (Sebecidae, non-eusuchian crocodyliform) (S52).

Late Oligocene (Chattian or Deseadean), Tremembé Formation, Brazil: *Caiman tremembensis* (Caimaninae). (S53).

Southern records (two Paleocene and two Eocene records from Chubut Province (Argentina)):

Early Paleocene (early Selandian or Peligrense), Salamanca Formation: *Necrosuchus ionensis* and *Eocaiman palaeocenicus* (basal Caimaninae) (S54, 55).

Late Eocene (early Priabonian or Barrancan), upper Sarmiento (“Casamayor”) Formation:

Eocaiman cavernensis (basal Caimaninae) (S56).

Middle to Upper Eocene (Vacan), lower Sarmiento (“Casamayor”) Formation: *Sebecus icaeorhinus* (Sebecidae, non-eusuchia crocodyliform) (S54).

Mollusks

The Miocene Pebasian diversity curve was derived from a rarefaction analyses of distribution data explained in ref (S57). The freshwater mollusk faunas comprise raw species numbers for three mid-large size shelled groups with a good fossil record that are usually associated with fluvial and lacustrine environments, viz. pearly freshwater mussels (Hyriidae and Mycetopodidae), apple snails (Ampullariidae) and freshwater cerithoideans (Pachychylidae and Thiaridae) (S58). Only fossil faunas that have been studied by the authors or that have received treatment in several papers are included. All faunas lived in freshwater environments, fed by Andean derived waters.

Freshwater mollusk species numbers in Neogene northwest South American deposits. Age of Pebas zones in ref (S59).

Pacaya-Samiria fauna (Recent, Marañon Basin, Peru, fluvio-lacustrine ref (S60): Cerithoidea (Pachychilidae + Thiaridae) 0; Ampullariidae 1, Unionoidea (Hyriidae + Mycetopodidae) 4.

La Llanera fauna (Pliocene, Las Piedras Formation, East Venezuela Basin, Venezuela, fluvio-lacustrine, refs (S61): Cerithoidea 0; Ampullariidae 1, Unionoidea 4.

Acre fauna (Late Miocene, Solimões Formation, Acre-Madre de Dios Basin, Brazil, fluvio-lacustrine, ref (S62): Cerithoidea 1; Ampullariidae 1, Unionoidea 7.

Pebas-3 fauna (*Grimsdalea* zone) (late Middle – early late Miocene, Pebas Formation, Solimões Basin, Peru-Colombia, fluvial to long-lived lake) ref (S59): Cerithoidea 6; Ampullariidae 1, Unionoidea 4.

Pebas-2 fauna (*Crassoretitriletes* zone) (middle Miocene, Pebas Formation, Solimões Basin, Peru, fluvial to long-lived lake, ref (S59): Cerithoidea 4; Ampullariidae 1, Unionoidea 3.

Loyola fauna (middle Miocene, Loyola Formation, Cuenca Basin, Ecuador, fluvio-lacustrine, refs (S62, 63): Cerithoidea 4; Ampullariidae 1, Unionoidea 7.

Pebas-1 fauna (*Retitricolporites* zone) (late Early – early Middle Miocene, Pebas Formation, Solimões Basin, Peru and Putumayo Basin, Colombia, fluvial to long-lived lake) ref (S58): Cerithoidea 5; Ampullariidae 1, Unionoidea 2.

La Cira/ Santa Teresa fauna (early Miocene, Santa Teresa Formation and Colorado series, Magdalena Basin, Colombia, fluvial to lacustrine, refs 6, 11): Cerithoidea 3; Ampullariidae 0, Unionoidea 4.

Mammals – from ref (S64)

South American mammal data from Marshall & Cifelli (1990; ref (S64) (I) groups derived from taxa present in South America during the onset of the Cenozoic, (II) platyrhine monkeys and caviomorph rodents first appearing in the fossil record during the Oligocene, (III) North American immigrants and their descendants. RM fam = running means for families from (S64). Since the latter publication major new faunas have been published (e.g. (S65-67)) and updated analyses are wanted.

3) Molecular section (Table S1)

We attempted to select genera (or equivalent clades) that *i*) were mainly distributed in northern South America (tropical Andes, Amazonia and the Guiana Shield); *ii*) had a reasonable taxon sampling to allow reliable estimation of crown ages; in cases with poor taxon sampling, we kept only studies designed to cover the morphologic and geographic range of the taxon in order to ensure a non-random, over dispersed sampling that is likely to approximate the age of the crown node of the group;; *iii*) were directly or indirectly dated by calibration with fossils or known rates of nucleotide substitution (but not geologic events such as the closure of the Panama Isthmus or the Andean uplift). Elevation and distribution ranges were taken from the original publications, personal communications with the authors and other sources. We stress, however, that *i*) this is a comprehensive but not complete list; and *ii*) there is variation in the confidence of age estimates depending on several factors (e.g. dating method used, taxon sampling, phylogenetic uncertainty, and calibration issues). This survey synthesizes a great deal of present knowledge, but we recommend examining the cited references for further information on particular clades.

Elevation zones in which the clades listed mainly occur, although single species in larger genera may be exceptions: **lowland** (0-500 m), including lowland rainforest in Amazonia and the Chocó in western Colombia and Ecuador; **pre-montane** (500-1,500 m), including rainforest in the flanking lowland and pre-montane areas along the eastern side of the Andes; **montane** (1,500-3,000 m), including mid-elevation montane forests (e.g., cloud and elfin forests); **alpine** (3,000-4,800 m), including alpine-altitude grasslands (páramo); **mixed** category includes lineages which show a mixed preference between lowland, pre-montane and montane.

4) Edaphic section (Figure S6C)

In the humid Tropics, main soil forming processes are weathering and leaching of all soluble compounds, whether present in the parent material or released upon weathering (S68). Main compounds that accumulate include residual quartz, and newly formed kaolinite (clay mineral) and sesquioxides, which comprise secondary minerals such as gibbsite and hematite. Over time, soils in fresh sediment or rock develop towards Ferralsols (high in Fe or Al) or Podzols (high in quartz), depending on the composition of the parent material (highly siliceous or not). While developing, the content of weatherable minerals and related nutrient status of the soils declines to ultimately very low levels. In Ferralsols, phosphorus deficiency often becomes extreme, due to its fixation by sesquioxides. In late stages of soil development, atmospheric inputs and cycling by the vegetation largely control contents of basic cations (S69).

Time spans required for Ferralsols or Podzols to develop largely depend on parent material composition and its related resistance against weathering (e.g. (S70)). They are in the order of several hundred thousand years, implying that Ferralsols and Podzols are already found on Middle Pleistocene terraces. Stages in soil development have been described as characteristic soil successions, such as those for the Colombian Amazon by ref (S71). They range from Fluvisols and Regosols, through Luvisols, Acrisols and Arenosols, to Ferralsols and Podzols. It should be emphasized, however, that saprolite depth in soils of such Pleistocene age is limited to several meters only, since saprolite develops at a much slower pace. For the often extremely deep and highly weathered saprolite of the craton (more than 100 meters) much longer periods of time were required, which are at the scale of tenths of millions of years. Thus, in more recent

soils slight erosion is sufficient to expose fresh or slightly weathered material, whereas deep saprolite requires serious denudation and dissection for such material to be exposed.

The map in Figure S6C was produced using FAO/IIASA/ISRIC/ISSCAS/JRC, *Harmonized World Soil Database (version 1.1)* (S72). Based on the extent, nature and pattern of soil formation (successional stages) and the thickness of the saprolite, which relates to the longer-term geological history, a number of edaphic macro-units were defined (See also ref 73).

- 1, Extremely old and nutrient poor soils with dominantly very thick saprolite (Ferralsols and Podzols), developed since Early Cretaceous under continuously humid tropical conditions and typical for the Amazon Craton and Paleozoic formations.
- 2, Extremely nutrient poor soils (mostly Podzols) in complex of highly weathered deposits derived from the Amazon Craton (mostly reworked saprolite), or in localized outcrops of Craton and associated Paleozoic formations. Outcrops of fresh rocks other than extremely resistant highly siliceous rocks (quartzites) are rare.
- 3, Various soils (Ferralsols/Podzols through Acrisols to Fluvisols), reflecting a wide range in age (Neogene to recent), weathering, and nutrient status. The landscape is a large-scale mosaic of dissected Cenozoic and Quaternary alluvial deposits (floodplains, terraces and fans) with mostly thin saprolite.
- 3b, as unit 3, but strongly dissected with relatively small-scale mosaic, probably resulting from glacio-eustatic incision of the Amazon River system.
- 4, ‘Old’ (Early Neogene?) and nutrient poor soils (Ferralsols) in slightly dissected Cenozoic formations (and minor Quaternary alluvial deposits) with moderately thick saprolite mostly.

5, Recent soils (mostly Gleysols) in poorly drained Late Quaternary deposits with initial weathering only.

6, Andean soils, mostly poorly to moderately developed in highly variable substrates, with slight weathering only due to more or less continuous denudation and/or deposition of pyroclastics.

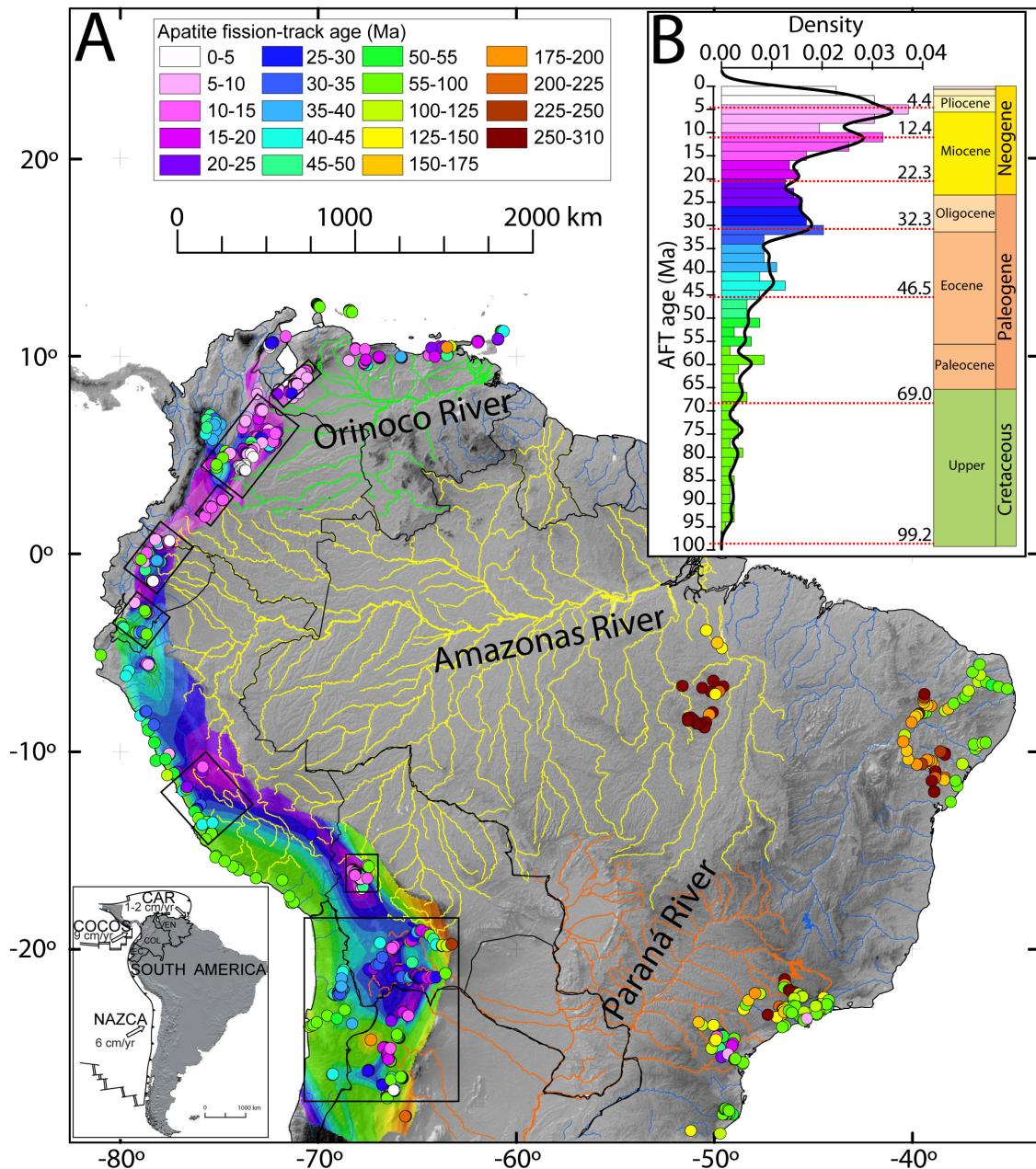
FIGURES S1-S7


Figure S1. A) Mountain building in the Northern and the Central Andes of South America based on apatite fission-track (AFT) data. Apatite fission-track (AFT) and interpolated AFT ages map across the Andes and lowland Amazonia (see supplementary data for references).

These ages indicate the time when rock passed through the 2 to 5 km depth window or $\sim 60^\circ$ - 110°C (Fig S2) as a result of tectonic and/or surface processes. AFT ages can be used as a proxy for the age of surface uplift and for estimating denudation rates. **B) Histogram and Probability Density Function (PDF) for the whole dataset of the Andes**, red lines correspond to populations of AFT ages, which were determined using cluster analysis. These populations provide an indication of the different exhumation phases across the Northern and Central Andes.

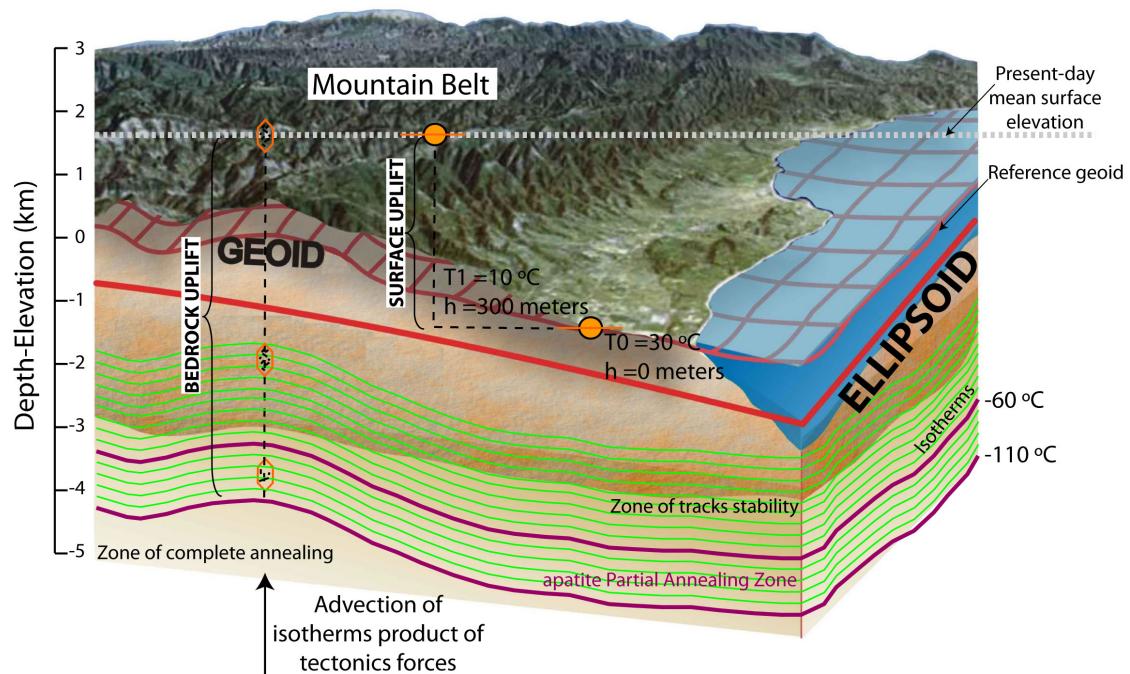


Figure S2. Underlying concepts for the interpretation of apatite fission-track (AFT) ages. *Surface uplift* is the displacement of the Earth's surface with respect to the geoid. The displacement of the rock column with respect to the geoid is known as *rock uplift*. The difference between surface uplift and bedrock uplift is known as *exhumation* (S3). The AFT age indicates when a rock passed through the $\sim 60^\circ$ - 110°C temperature zone.

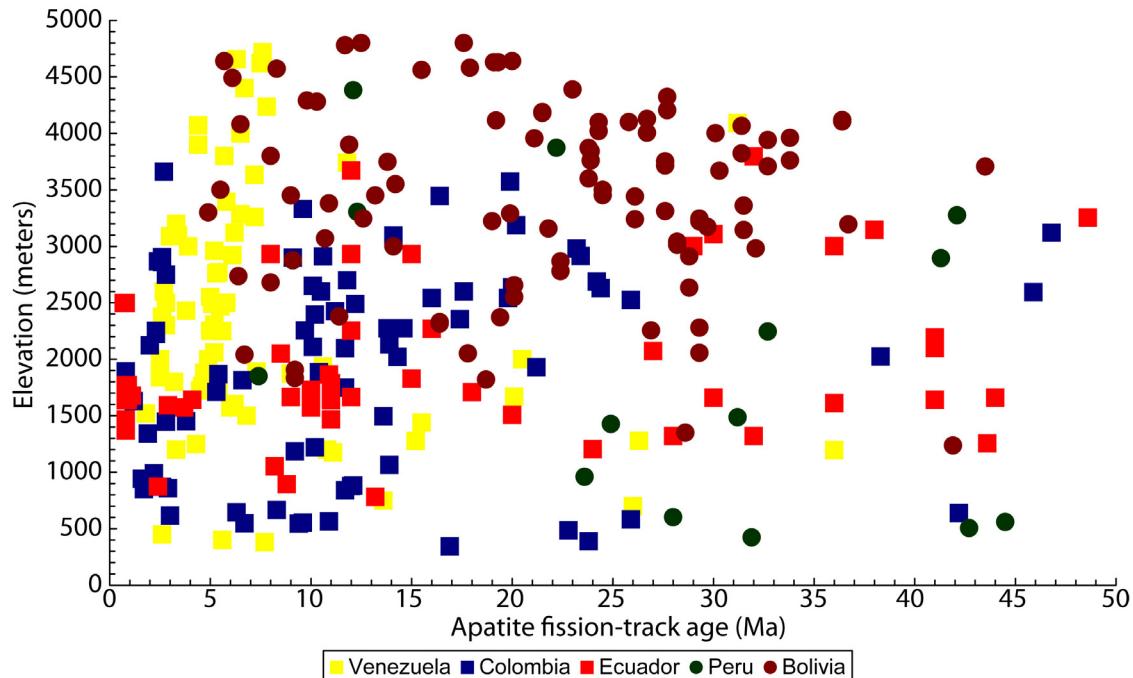


Figure S3. Distribution of AFT ages in relation to elevation across the Andes for areas shown as rectangles in Figure S1A. The spatial distribution of the data and the sampling philosophies prevent that age-elevation relationships can be translated in terms of exhumation rates. Only in some particular cases (Sierra Nevada and Sierra La Culata in Venezuelan Andes; Quetame and Garzon Massif at the Eastern Cordillera in Colombia; Real Cordillera at the Bolivian Andes) can exhumation rates be derived (see references for more detail).

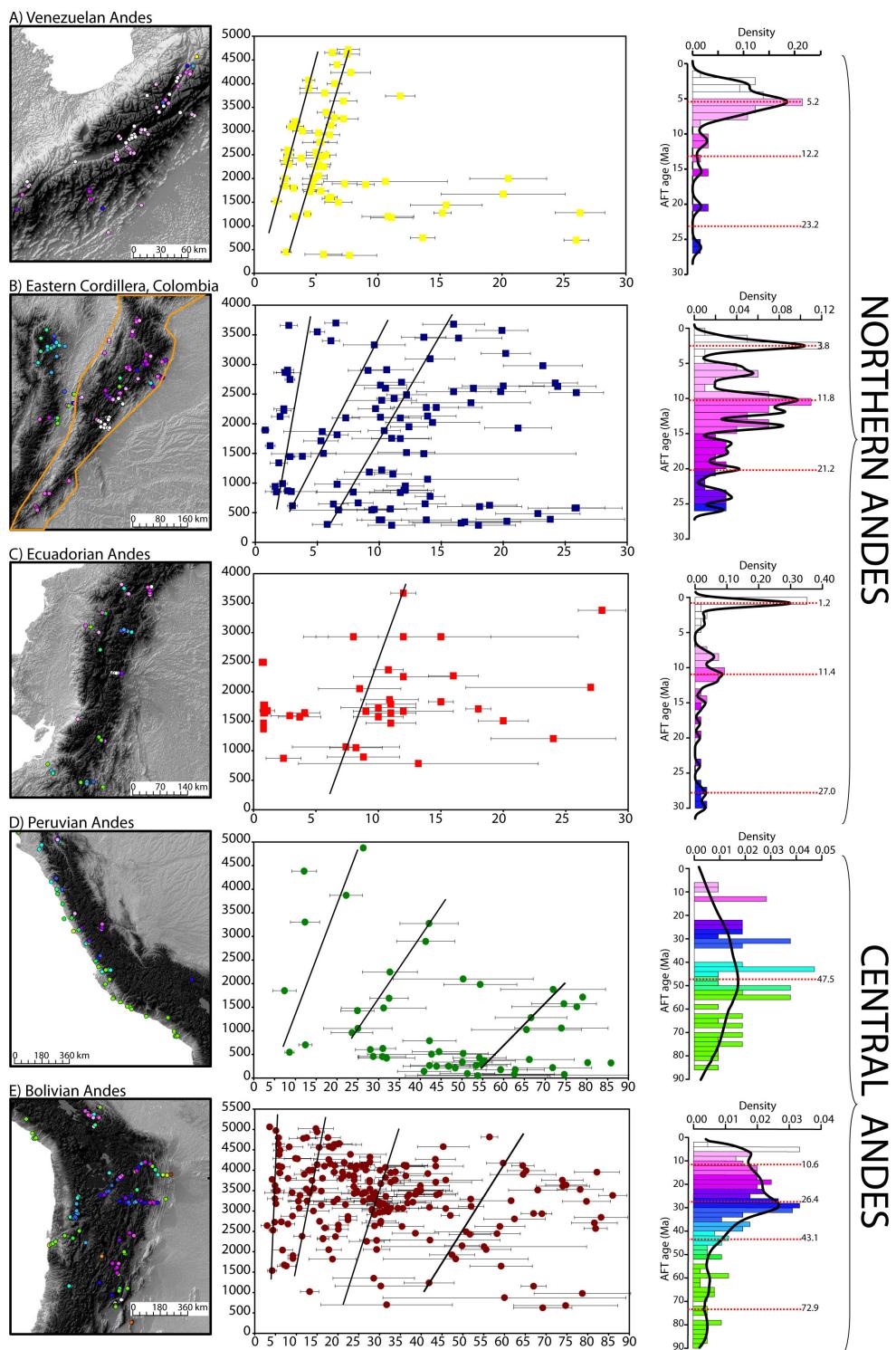


Figure S4. Comparison between age-elevation relationships and histogram for A) Venezuelan Andes; B) Eastern Cordillera, Colombian Andes; C) Ecuadorian Andes; D) Peruvian Andes and E) Bolivian Andes.

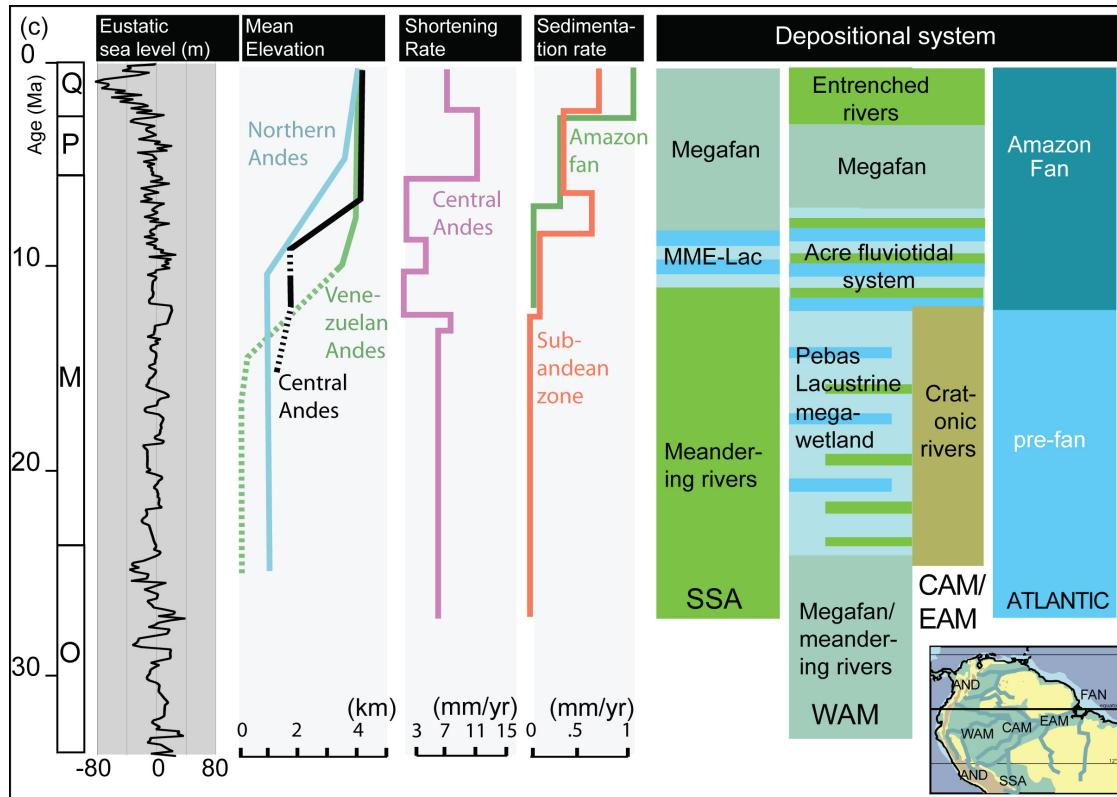


Figure S5. The sedimentary record of Amazonia and the Amazon submarine Fan indicates response to the tectonic evolution of the Andes.

Mean Elevation Central Andes (black line; (S74)), Northern Andes (pink line; (S4)) and the Central Venezuelan (Mérida) Andes (green line; (S35)). **Sedimentation rates** Central Andes (red line; (S75)); Amazon Fan (grey line; (S76)). **Shortening rates** Central Andes (S77) and refs therein. **Abbreviations:** Andes (AND); Western Amazonia (WAM); Central and Eastern Amazonia (CAM and EAM); Amazon Submarine Fan (FAN); Marginal Marine Embayment (MME); Southern Subandes (SSA); lac = lacustrine. Sea level curve according to (S78) but see for alternative curves (S79).

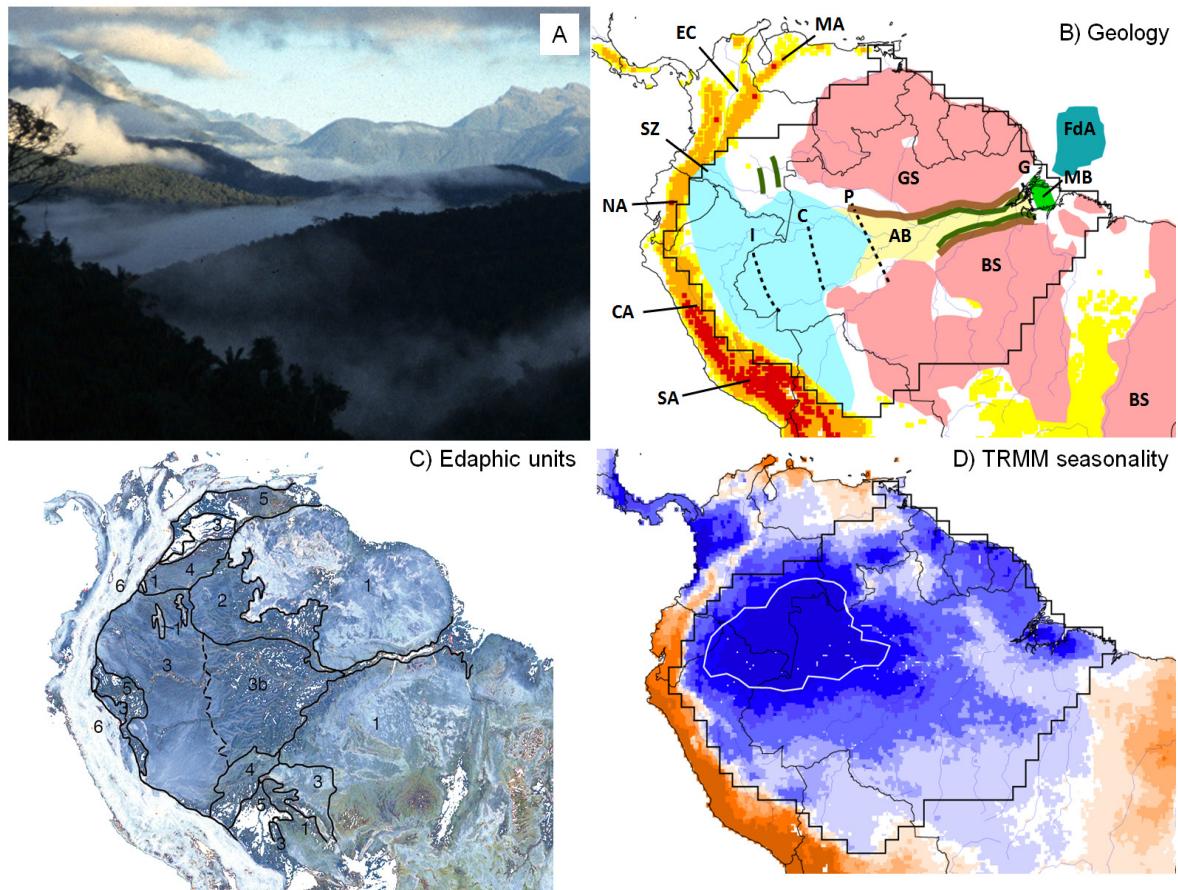


Figure S6 A) Pauji Yuyo, at the edge of Madidi National Park, Bolivia (altitude ca. 1,300 m, a biodiversity hotspot, image courtesy of Michael Kessler, University of Zürich, Switzerland). **B)** The geologic units of Neogene Andean origin (in light blue) occur in most of Western Amazonia. On the Atlantic side contemporary units (in light green) do not extend beyond the Gurupa (G) Arch. In Eastern Amazonia the Amazon (Proterozoic) craton (pink) is exposed; it is subdivided into the Guiana Shield (GS) and the Brazilian Shield (BS). An old rift (Proterozoic) rift divides the craton and stores some Paleozoic units (dark green & light brown). The fluvial (Cretaceous-Paleogene) Alter do Chão Formation (yellow) is exposed in Central Amazonia, but extends in the subsurface further to the west in up to the Caravari (C) Arch. Other codes used in this figure are: MB Marajó Basin; FdA: Foz do Amazonas Basin; I: “Iquitos Arch” (Sbut see 57);

P: Purus Arch; Altitude: yellow 500-1500m; orange 1500-4000m, red > 4000m. **C)** The Amazonian edaphic units represent a combination of habitats, in terms of scale and type of mosaic (modified after (S72)). The soils are labeled from 1- relatively ‘old cratonic’ (1) to ‘Andean young’ (6), with the exception of unit 4 (see ‘Methodology’ for further details). Unit 3 relates to Andean Neogene sediments, whereas unit 1 is linked to the Amazon Craton. Unit 4 coincides with the limits of the Amazon drainage and may date back to the late Miocene partitioning of the tropical lowland. Unit 5 is associated with areas of high denudation rates. **D)** Seasonality as indicated by the average yearly number of months < 100 mm of rain in 10 year (Data: Tropical Rainfall Measuring Mission, <http://trmm.gsfc.nasa.gov/>). The white polygon indicates the wettest, least seasonal area and also includes information on the amount of rain in the driest 3 month and 6 month period in 10 years.

Figure S7 Additional maps of diversity

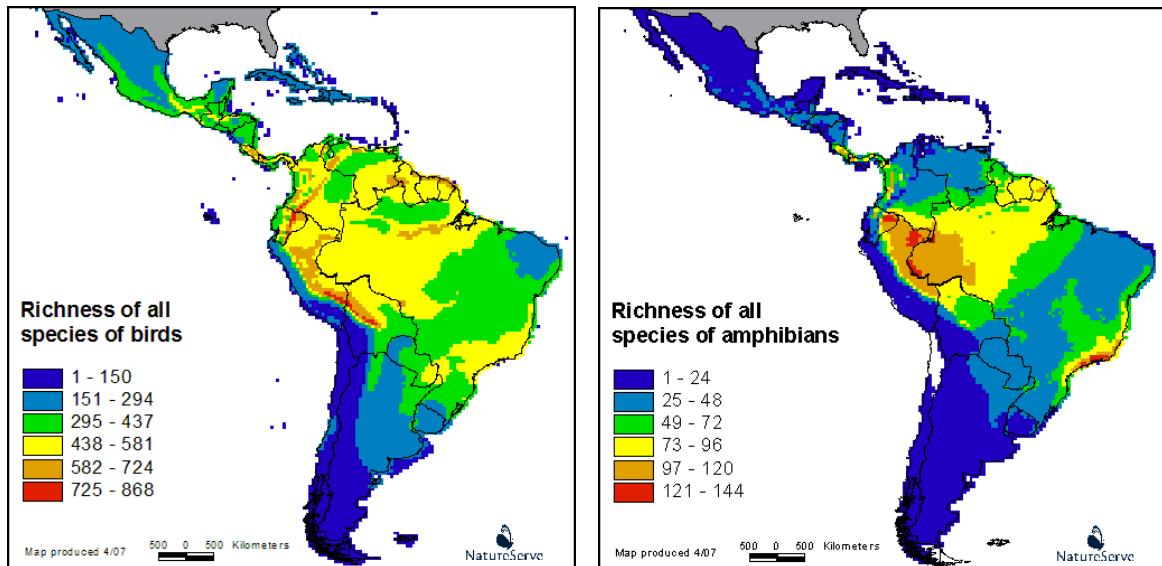


Figure S7.A, S7.B. Maps of species richness in birds and amphibians. Source ref (S80).

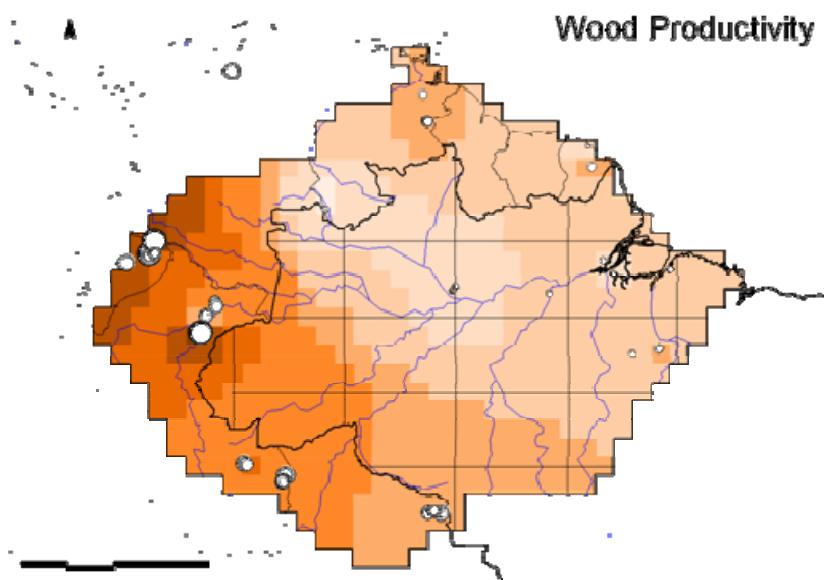


Figure S7.C. Map of biomass productivity ((S81), based on data of ref (S82)).

Table S1. Survey over approximate ages of living taxa (mainly genera or equivalent) reported from published molecular phylogenies, together with main elevation range and source publication. Records sorted as in Fig. 3B (arranged by major taxonomic category, then sorted by elevation range and decreasing age).

#	Category	Taxon	Crown Age	Elevation range **	Reference
1	Insecta : Coleoptera : Chrysomelidae [beetles]	Cephaloleia	68.2	lowland	(S83)
2	Insecta : Lepidoptera : Nymphalidae : Satyrinae [butterflies]	Hermeuptychia clade	21	lowland	(S84)
3	Insecta : Lepidoptera : Nymphalidae : Satyrinae [butterflies]	Paraeuptychia clade	19	lowland	(S84)
4	Insecta : Coleoptera : Copelatinae [beetles]	Copelatus & Aglymbus clade	16.4	lowland	(S85)
5	Insecta : Hymenoptera : Apidae [bees]	Melipona	15.4	lowland	(S86)
6	Insecta : Lepidoptera : Nymphalidae : Satyrinae [butterflies]	Taygetis clade	15	lowland	(S84)
7	Insecta : Lepidoptera : Nymphalidae : Phycoidina [butterflies]	Tegosa	16	montane	(S87)
8	Insecta : Hymenoptera : Apidae [bees]	Bombus clade 1	7.2	highland	(S88)
9	Insecta : Hymenoptera : Apidae [bees]	Bombus clade 2	3.2	highland	(S88)
10	Insecta : Lepidoptera : Nymphalidae : Phycoidina [butterflies]	Eresia sensu latu	21	mixed	(S87)
11	Insecta : Lepidoptera : Nymphalidae : Ithomiini [butterflies]	Ithomia	14.4	mixed	(S89)

12	Insecta : Lepidoptera : Nymphalidae : Ithomiini [butterflies]	Napogenes	12.7	mixed	(S89)
13	Arachnida : Buthidae [scorpion]	Tityus	10.2	montane	(S90)
14	Pisces: Teleostei : Cichlasomatini [cichlids]	Cichlasoma + Aequidens	26	lowland	(S91)
15	Pisces: Teleostei : Cichlasomatini [cichlids]	Aequidens	19	lowland	(S91)
16	Pisces: Osteichthyes : Gymnotidae [knifefishes]	Gymnotus carapo group	15.2	lowland	(S92)
17	Amphibia : Anura : Dendrobatidae [poison frogs]	Allobates	26.1	mixed	(S93)
18	Amphibia : Anura : Dendrobatidae [poison frogs]	Dendrobates	25.8	mixed	(S93)
19	Amphibia : Anura : Dendrobatidae [poison frogs]	Anomaloglossus	17.4	mixed	(S93)
20	Amphibia : Anura : Dendrobatidae [poison frogs]	Colostethus clade 2	16.3	mixed	(S93)
21	Amphibia : Anura : Dendrobatidae [poison frogs]	Mannophryne	16	mixed	(S93)
22	Amphibia : Anura : Dendrobatidae [poison frogs]	Aromobates	15.7	mixed	(S93)
23	Amphibia : Anura : Dendrobatidae [poison frogs]	Colostethus clade 1	12.1	mixed	(S93)
24	Amphibia : Bolitoglossine [salamanders]	Bolitoglossa	11	mixed	(S94)
25	Amphibia : Anura : Dendrobatidae [poison frogs]	Hyloxalus	9.6	mixed	(S93)
26	Amphibia : Anura : Dendrobatidae [poison	Phyllobates	9.6	mixed	(S93)

	frogs]				
27	Amphibia : Anura : Dendrobatidae [poison frogs]	Ameerega	6	mixed	(S93)
28	Amphibia : Bolitoglossine [salamanders]	Oedipina	6	mixed	(S94)
29	Amphibia : Anura : Dendrobatidae [poison frogs]	Epipedobates	4	mixed	(S93)
30	Reptilia: Squamata : Spaerodactylidae [geckos]	Gonatodes	35	lowland	(S95)
31	Reptilia : Scincidae [skinks]	Mabuya	14.5	mixed	(S96)
32	Reptilia : Serpentes : Leptodeira [snakes]	Leptodeira	3.9	mixed	(S97)
33	Mammalia : Xenarthra : Pilosa [anteaters]	Vermilingua	41	lowland	(S98)
34	Mammalia : Xenarthra : Pilosa [sloths]	Folivora	22	lowland	(S98)
35	Mammalia : Primata : Cebidae [monkeys]	Saguinus	13.3	lowland	(S99)
36	Mammalia : Primata : Pitheciidae [monkeys]	Callicebus	12.3	lowland	(S99)
37	Mammalia : Chiroptera : Phyllostominae [bats]	Tonatia	12.1	lowland	(S100)
38	Mammalia : Chiroptera : Diclidurini [bats]	Peropteryx	11.7	lowland	(S101)
39	Mammalia : Primata : Pitheciidae [monkeys]	Pithecia	10.7	lowland	(S99)
40	Mammalia : Chiroptera : Phyllostominae [bats]	Lophostoma	7.8	lowland	(S100)
41	Mammalia : Chiroptera : Diclidurini [bats]	Saccopteryx	7.7	lowland	(S101)
42	Mammalia : Primata : Cebidae [monkeys]	Callithrix	7.7	lowland	(S99)
43	Mammalia : Chiroptera : Diclidurini [bats]	Diclidurus	6.9	lowland	(S101)
44	Mammalia : Primata : Pitheciidae [monkeys]	Chiropotes	4	lowland	(S99)

45	Mammalia : Primata : Cebidae [monkeys]	Saimiri	3.7	lowland	(S99)
46	Mammalia : Primata [monkeys]	Ateles	3.6	lowland	(S102)
47	Mammalia : Rodentia : Echimyinae [rodents]	Isothrix	2.7	lowland	(S103)
48	Mammalia : Rodentia : Echimyinae [rodents]	Makalata	2.3	lowland	(S103)
49	Mammalia : Rodentia : Cricetidae [rodents]	Zygodontomys	1.2	lowland	(S104)
50	Mammalia : Xenarthra [armadillos]	Dasypodidae	35	pre-montane	(S98)
51	Mammalia : Primata : Atelidae [monkeys]	Ateles	4.3	pre-montane	(S99)
52	Mammalia : Primata : Cebidae [monkeys]	Cebus	7.3	mixed	(S99)
53	Mammalia : Primata : Aotidae [monkeys]	Aotus	6.7	mixed	(S99)
54	Mammalia : Primata [monkeys]	Alouatta	5.1	mixed	(S105)
55	Aves : Bucconidae [puffbirds]	Nonnula	16	lowland	(S106)
56	Aves : Tyrannidae	Myiopagis	9.5	lowland	(S107)
57	Aves : Troglodytidae [wrens]	Thryothorus clade 1	8.1	lowland	(S108)
58	Aves : Psittacidae [parrots]	Gypsitta	7.8	lowland	(S109)
59	Aves : Troglodytidae [wrens]	Thryothorus clade 2	7	lowland	(S108)
60	Aves : Psittacidae [parrots]	Amazona	6.7	lowland	(S110)
61	Aves : Cardinalidae [cardinals]	Cardinalis	5.7	lowland	(S111)
62	Aves : Ramphastidae [toucans]	Ramphastos	4.8	lowland	(S112)
63	Aves : Accipitridae [birds of prey]	Buteogallus	4.3	lowland	(S113)
64	Aves : Accipitridae [birds of prey]	Leucopernis	3.5	lowland	(S113)
65	Aves : Bucconidae [puffbirds]	Notharchus tectus complex	3.1	lowland	(S106)

66	Aves : Bucconidae [puffbirds]	Nyctastes	3.1	lowland	(S106)
67	Aves : Bucconidae [puffbirds]	Malacoptila	14	pre-montane	(S106)
68	Aves : Furnariidae [ovenbirds]	Thripadectes-Clibanornis subclade	13	pre-montane	(S114)
69	Aves : Thamnophilidae [antbirds]	Myrmotherula clade 1 including Myrmochanes	11.4	pre-montane	(S108)
70	Aves : Galbulidae [jacamars]	Galbula	11	pre-montane	(S106)
71	Aves : Thamnophilidae [antbirds]	Myrmeciza	10.5	pre-montane	(S108)
72	Aves : Dendrocolaptinae [woodcreepers]	Xiphorhynchus	10.4	pre-montane	(S108)
73	Aves : Rhamphastidae [toucans]	Pteroglossus	10.3	pre-montane	(S115)
74	Aves : Galbulidae [jacamars]	Brachygalba	9.3	pre-montane	(S106)
75	Aves : Tityridae	Schiffornis	9.1	pre-montane	(S116)
76	Aves : Thamnophilidae [antbirds]	Myrmotherula clade 2	9	pre-montane	(S108)
77	Aves : Thraupidae [tanagers]	Cyanerpes	7.4	pre-montane	(S108)
78	Aves : Dendrocolaptinae [woodcreepers]	Dendrocincla	7.3	pre-montane	(S108)
79	Aves : Bucconidae [puffbirds]	Monasa	7.1	pre-montane	(S106)
80	Aves : Dendrocolaptinae [woodcreepers]	Dendrocolaptes	6.4	pre-montane	(S108)
81	Aves : Cardinalidae [cardinals]	Cyanocompsa	6.2	pre-montane	(S117)
82	Aves : Arini	Brotogeris	5.1	pre-montane	(S118)
83	Aves : Gracidae [curassows]	Crax	4.5	pre-montane	(S110)
84	Aves : Icteridae [blackbirds]	Agelasticus	4.3	pre-montane	(S108)

85	Aves : Thamnophilidae [antbirds]	Cercomacra	4.1	pre-montane	(S108)
86	Aves : Troglodytidae [wrens]	Campylorhynchus	3.8	pre-montane	(S108)
87	Aves : Cardinalidae [cardinals]	Caryothraustes	3.6	pre-montane	(S111)
88	Aves : Thamnophilidae [antbirds]	Terenura	3.6	pre-montane	(S108)
89	Aves : Galbulidae [jacamars]	South American Jacamerops	2.7	pre-montane	(S106)
90	Aves : Momotidae [motmots]	Electron	2.4	pre-montane	(S106)
91	Aves : Dendrocolaptinae [woodcreepers]	Xiphocolaptes	2.2	pre-montane	(S108)
92	Aves : Corvidae [jays]	Cyanocorax	2.1	pre-montane	(S119)
93	Aves : Momotidae [motmots]	Northern South America Baryphthengus martii clade	1.6	pre-montane	(S106)
94	Aves : Furnariidae [ovenbirds]	Tarphonomus-Berlepschia clade	21.8	montane	(S114)
95	Aves : Furnariidae [ovenbirds]	Margarornis-Premoplex clade	18.9	montane	(S114)
96	Aves : Rhinocryptidae [tapaculos]	Scytalopus	11	montane	(S108)
97	Aves : Furnariidae [ovenbirds]	Asthenes subclade	10.8	montane	(S114)
98	Aves : Thraupidae [tanagers]	Diglossopsis	9.1	montane	(S120)
99	Aves : Corvidae [jays]	Cyanolyca	8	montane	(S121)
100	Aves : Thraupidae [tanagers]	Diglossa	7	montane	(S108)
101	Aves : Strigidae [owls]	Aegolius	5.9	montane	(S117)
102	Aves : Thraupidae [tanagers]	Hemispingus clade 2	5.7	montane	(S108)
103	Aves : Accipitridae [birds of prey]	Geranoaetus	4.5	montane	(S113)
104	Aves : Emberizidae [brunch-	Chlorospingus	3.7	montane	(S108)

	finches/tanager]				
105	Aves : Thraupidae [tanagers]	Piranga leucoptera/rubriceps clade	3.7	montane	(S122)
106	Aves : Parulidae [warblers]	Myioborus	3.6	montane	(S123)
107	Aves : Troglodytidae [wrens]	T. ochraceus/rufulus/ solstitialis clade	3.6	montane	(S117)
108	Aves : Thraupidae [tanagers]	Hemispingus clade 1	3.5	montane	(S108)
109	Aves : Emberizidae [brunch-finches]	Buarremon	1	montane	(S124)
110	Aves : Thraupidae [tanagers]	Sicalis	8	highland	(S108)
111	Aves : Thraupidae [tanagers]	Poospiza	5.2	highland	(S108)
112	Aves : Furnariidae [ovenbirds]	Dendrocolaptinae- Xenops clade	27.7	mixed	(S114)
113	Aves : Thraupidae [tanagers]	Saltator	10.7	mixed	(S108)
114	Aves : Picidae [woodpickers]	Veniliornis & Picoides "small" clade	9.9	mixed	(S125)
115	Aves : Thraupidae [tanagers]	Tangara including Thraupis	9.4	mixed	(S108)
116	Aves : Thraupidae [tanagers]	Tachyphonus	8.4	mixed	(S108)
117	Aves : Thamnophilidae [antbirds]	Drymophila	8	mixed	(S108)
118	Aves : Thamnophilidae [antbirds]	Thamnophilus	7.9	mixed	(S108)
119	Aves : Troganidae	Trogon personatus & T. collaris/aurantiiventris clade	7.8	mixed	(S126)
120	Aves : Motacillidae	Anthus South American clade	7.2	mixed	(S108)
121	Aves : Icteridae [blackbirds]	Cacicus including Clypticerus & Ocyalus	7.1	mixed	(S108)
122	Aves : Psittacidae [parrots]	Pionus	6.9	mixed	(S127)
123	Aves : Thraupidae [tanagers]	Conirostrum	5.8	mixed	(S108)

124	Aves : Dendrocolaptinae [woodcreepers]	Campylorhamphus	5.5	mixed	(S108)
125	Aves : Icteridae [blackbirds]	Psarocolius	5.2	mixed	(S108)
126	Aves : Thraupidae [tanagers]	Sporophila clade 2	5	mixed	(S108)
127	Aves : Trogonidae	Pharorrhachrus	4.8	mixed	(S126)
128	Aves : Cardinalidae [cardinals]	Amaurospiza	4.5	mixed	(S117)
129	Aves : Dendrocolaptinae [woodcreepers]	Lepidocolaptes	4.2	mixed	(S108)
130	Aves : Thraupidae [tanagers]	Sporophila clade 1	4.2	mixed	(S108)
131	Aves : Emberizidae [brunch-finches]	Atlapetes	3.7	mixed	(S117)
132	Aves : Momotidae [motmots]	Momotus	3.1	mixed	(S106)
133	Aves : Thamnophilidae [antbirds]	Thamnistes superspecies	3.1	mixed	(S108)
134	Aves : Thraupidae [tanagers]	Ramphocelus South American clade	2.6	mixed	(S108)
135	Aves : Fringillidae [finches]	Carduelis	1.6	mixed	(S128)
136	Plants : Annonaceae	Anaxagorea	40	lowland	(S129)
137	Plants : Meliaceae	Cedrela South American clade 3	22.6	lowland	(S130)
138	Plants : Arecaceae : Attaleinae [palms]	Syagrus rain forest clade	17.1	lowland	(S131)
139	Plants : Arecaceae : Chamaedoreeae [palms]	Chamaedorea	16.8	lowland	(S132)
140	Plants : Fabaceae : Papilioideae [legumes]	Andira & Hymenolobium clade	16.3	lowland	(S133)
141	Plants: Annonaceae	Guatteria	6.7	lowland	(S134)
142	Plants : Arecaceae : Ceroxyloideae [palms]	Phytelephas	6	lowland	(S135)
143	Plants : Fabaceae :	Mimosa Mimadenia	5.6	lowland	(S133)

	Mimosoideae [legumes]	clade				
144	Plants : Rubiaceae	Joosia	13.7	pre-montane	(S136)	
145	Plants : Rubiaceae	Ladenbergia	11.8	pre-montane	(S136)	
146	Plants : Polygonaceae	Ruprechtia	10	pre-montane	(S137)	
147	Plants : Fabaceae : Papilioideae [legumes]	Centrolobium	9.9	pre-montane	(S138)	
148	Plants : Annonaceae	Malmea	9.5	pre-montane	(S139)	
149	Plants : Rubiaceae	Cinchona	9	pre-montane	(S136)	
150	Plants : Annonaceae	Mosannonia	8.6	pre-montane	(S139)	
151	Plants : Anacardiaceae	Loxopterygium	8	pre-montane	(S137)	
152	Plants : Annonaceae	Klarobelia	7.7	pre-montane	(S139)	
153	Plants : Annonaceae	Crematosperma	7.2	pre-montane	(S139)	
154	Plants : Rubiaceae	Stilpnophyllum	6.1	pre-montane	(S136)	
155	Plants : Lejeuneaceae [liverworts]	Marchesinia	23.6	montane	(S140)	
156	Plants : Onagraceae	Fuchsia Andean radiation	22.3	montane	(S141)	
157	Plants : Fabaceae : Papilioideae [legumes]	Poissonia	18.1	montane	(S137)	
157	Plants : Chloranthaceae	Hedyosmum Tafalla	17.6	montane	(S142)	
158	Plants : Fabaceae : Mimosoideae [legumes]	Mimosa Weberbaueri clade	7.6	montane	(S133)	
159	Plants : Fabaceae : Papilioideae [legumes]	Coursetia C. gracilis – C. grandiflora clade	7.2	montane	(S143)	
160	Plants : Arecaceae : Ceroxyloideae [palms]	Ceroxylon	7	montane	(S135)	
161	Plants : Fabaceae : Mimosoideae [legumes]	Mimosa Pectinatipinna clade	3.5	montane	(S133)	

162	Plants : Valerianaceae	Valeriana Paramo clade	10.6	highland	(S144)
163	Plants : Poaceae [grasses]	Loliinae American clade 1	4.2	highland	(S145)
164	Plants : Boraginaceae	Lithospermum	3.8	highland	(S146)
165	Plants : Poaceae [grasses]	Loliinae American clade 2	3.8	highland	(S145)
166	Plants : Cyperaceae [sedges]	Oreobolus	3.7	highland	(S147)
167	Plants : Fabaceae : Papilioideae [legumes]	Lupinus Andean clade	1.8	highland	(S148, 149)
168	Plants : Gentianaceae	Halenia Weddeliana clade	0.8	highland	(S150)

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