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 is 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.

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 (29). 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.
(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 extinction [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.](www.sciencemag.org)
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 Amazon (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 depoosition 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 “Ace” system harbored a very rich aquatic vertebrate fauna that included mega-sized gharials, caimans, 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 xeranthran 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 megafauns 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).

**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 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).

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and fertility of floodplains further confirm the dynamics 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 seasonal 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.

References and Notes

23. See supporting material on Science Online.
29. K. E. Campbell Jr., Ed., The Paleogene Mammalian Fauna of Santa Rosa, Amazonian Peru (Natural History Museum of Los Angeles County, Los Angeles, 2004).
40. C. A. Quezada et al., Biogeosci. Discuss. 6, 3923 (2009).
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