

Why are there so many plant species in the Neotropics?

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Abstract The Neotropical region (tropical America) is the most species rich region on Earth. Several causes have been proposed to explain this extraordinary biodiversity, which may be very roughly classified into two major categories: ‘biotic’ (e.g. soil adaptations; biotic interactions with pollinators, dispersers and herbivores; niche conservatism; dispersal ability) and ‘abiotic’ (e.g. time; rainfall, temperature and area; mountain uplift; hydrological changes). In this paper we review the evidence for each of these postulated causes of diversification and provide general directions towards further testing. We highlight the need of more well-sampled and dated phylogenies and urge increased inter-disciplinary collaboration.

Keywords biogeography; botany; evolution; Neotropical biomes; Tropical America

■ THE NEOTROPICAL REGION: AN INTRODUCTION

In England any person fond of natural history enjoys in his walks a great advantage, by always having something to attract his attention; but in these fertile lands teeming with life, the attractions are so numerous, that he is scarcely able to walk at all.
Charles R. Darwin, 19 Apr. 1839, after leaving Brazil on board of HMS Beagle.

The word *Neotropic* (from the Greek *neos* = “new”) refers to the tropical region of the American continent, or “New World”—a term coined by Peter Martyr d’Anghiera in 1493 shortly after Christopher Columbus’s first voyage to the Americas (O’Gorman, 1972). As currently defined (Schultz, 2005), the Neotropical ecozone extends from central Mexico in the north to southern Brazil in the south, i.e., including Central America, the Caribbean islands and most of South America.

Geologically, the Neotropics are distributed across three tectonic plates: the North American, the Caribbean and the South American (Fig. 1), each with a very different geological history. The South American and African plates formed part of the giant palaeocontinent of Gondwana for hundreds of millions of years until its final break-up about 100 million years (Ma) ago (Scotese, 2001).

Precipitation and annual mean temperatures are generally high, but there is great regional variation. Whereas western Colombia in South America has amongst the highest precipitation in the world, with almost 9000 mm annually, other regions are extremely dry. In the Amazon Basin, precipitation ranges between 1500 and 3000 mm annually, averaging around 2000 mm in central Amazonia (Salati & Vose, 1984).

Before human colonisation, the rain forest of Amazonia accounted for about one third of the entire South American continent. There are however several other terrestrial biomes in the Neotropics that are noteworthy for their size and ecological

importance, such as the Cerrado and the Atlantic forest of eastern Brazil. The approximate distribution of major Neotropical biomes/ecosystems is given in Fig. 2, and Kricher (1999) provides an accessible overview of their characteristics and biodiversity.

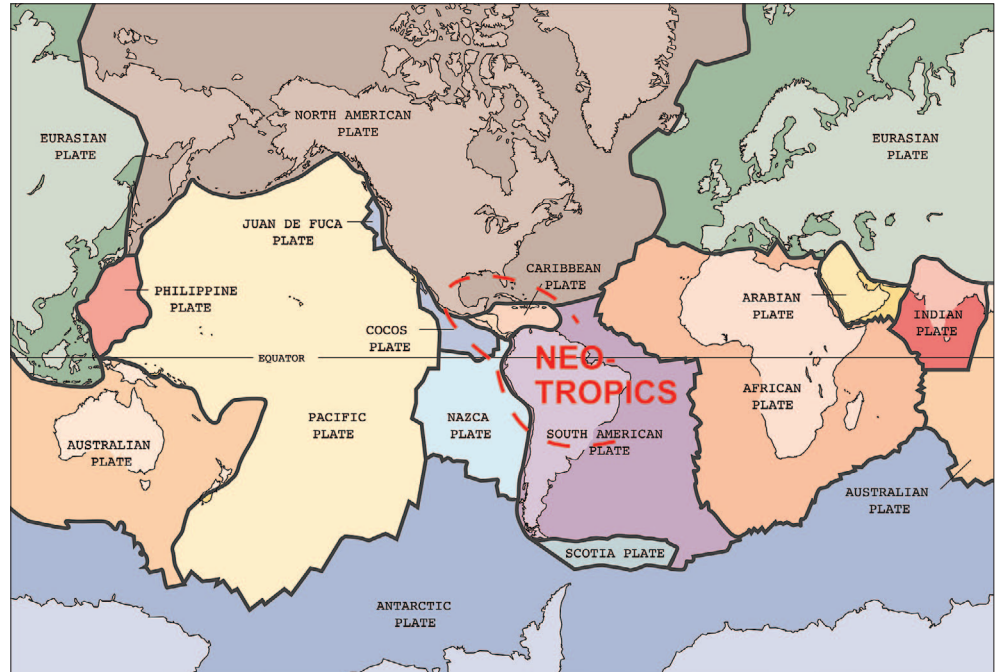
■ NEOTROPICAL PLANT BIODIVERSITY: PATTERNS AND HYPOTHESES

Distribution of plant diversity. — Ever since the early voyages of renowned explorers, such as Humboldt (1820), Darwin (1909) and Wallace (1852, 1853), the outstanding species richness found today in the Neotropics has remained elusive in our understanding of the evolution of life on Earth. Comprising around 90,000–110,000 species of seed plants, the Neotropics alone harbours about 37% of the world’s species. This is perhaps more than tropical Africa (30,000–35,000 spp.) and tropical Asia and Oceania combined (40,000–82,000 spp.; Gentry, 1982; Thomas, 1999; Govaerts, 2001). Explaining why there are so many species in the Neotropics is also relevant to further our knowledge on the global “latitudinal species gradient”—the fact that species richness tends to be higher at tropical latitudes (Hillebrand, 2004), a pattern that has sparked a long-standing search for ecological and evolutionary explanations (Kozak & Wiens, 2007; Mittelbach & al., 2007; Buckley & al., 2010).

Within the Neotropics, as in any other region, plant species are not distributed evenly. In a seminal paper, Gentry (1982) demonstrated that there are two main patterns of plant distribution, which he termed “Amazonian-centred” and “Andean-centred”. Typically, groups that are rich in species in one of these centres are relatively species-poor in the other. We propose to name it “the Gentry pattern”.

Andean-centred groups have a centre of diversity in north-western South America and adjacent Central America. Gentry exemplified this pattern with Maas’s (1977) diversity map for the genus *Renealmia* (Zingiberaceae; Fig. 3). According to

Fig. 1. The Neotropical region extends from central Mexico in the north to southern Brazil in the south, thus occupying the North American, the Caribbean and the South American tectonic plates. (adapted from Wikimedia Commons).



Gentry's (1982) survey, as many as 38% of all Neotropical plant species may belong to Andean-centred groups. Amazonian-centred groups, on the other hand, are characterised by having a high number of species in the Amazon Basin. Gentry exemplified this pattern using Berg's (1972) diversity map for the tribe Olmedieae (Moraceae; Fig. 4). Amazonian-centred groups, according to Gentry, may comprise some 33% of all Neotropical plant species.

Because the great majority of Neotropical plant species (71% in Gentry's survey) belong to either one of these groups, Gentry concluded that "any explanation of the patterns of evolutionary diversification in these taxa will largely explain the richness of the Neotropical flora" (Gentry, 1982: 581). Although this was a bold and simplistic statement—hinting at an underlying belief that there should be a single explanation for Neotropical biodiversity—it set the stage for further exploration of factors responsible for the distribution patterns we observe today.

How did Neotropical biodiversity originate and evolve?

— Many mechanisms have been proposed to have played a role in the historical assembly and evolution of Neotropical biodiversity. These may be very roughly classified into two major categories: "biotic" (e.g., soil adaptations; interactions with pollinators, dispersers and herbivores; niche conservatism; dispersal ability) and "abiotic" (e.g., time; rainfall, temperature and area; mountain uplift; hydrological changes). Below we present a short overview of some of the main diversification mechanisms proposed, discuss their validity, and provide general directions towards further testing. (see Antonelli & al., 2010a for an overview of other "classical" hypotheses).

■ BIOTIC MECHANISMS

Soil adaptations. — Ecologists have long perceived and studied the correlation between edaphic variation and high species diversity, especially in tropical rain forests (e.g., Ashton, 1969; Gentry, 1981; Tuomisto & al., 1995, 2003b; Clark & al., 1999; Tuomisto & al., 2003a). Fine & al. (2005) showed that the majority of species in a phylogeny of tribe Protieae (Burseraceae) was strongly associated with only one of three main soil types in western Amazonia (clay, terrace soils and white

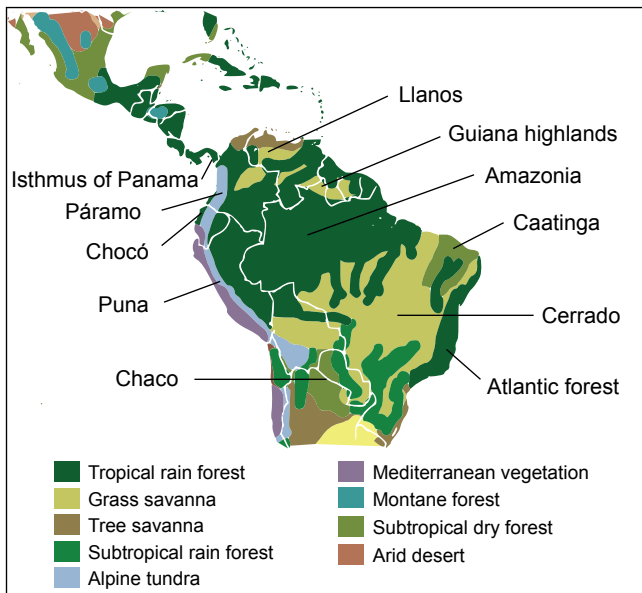


Fig. 2. Approximate natural distribution of major Neotropical biomes and vegetation types (adapted from Wikimedia Commons). Note that such maps differ widely in the literature in terms of resolution and delimitations. The Isthmus of Panama is also indicated.

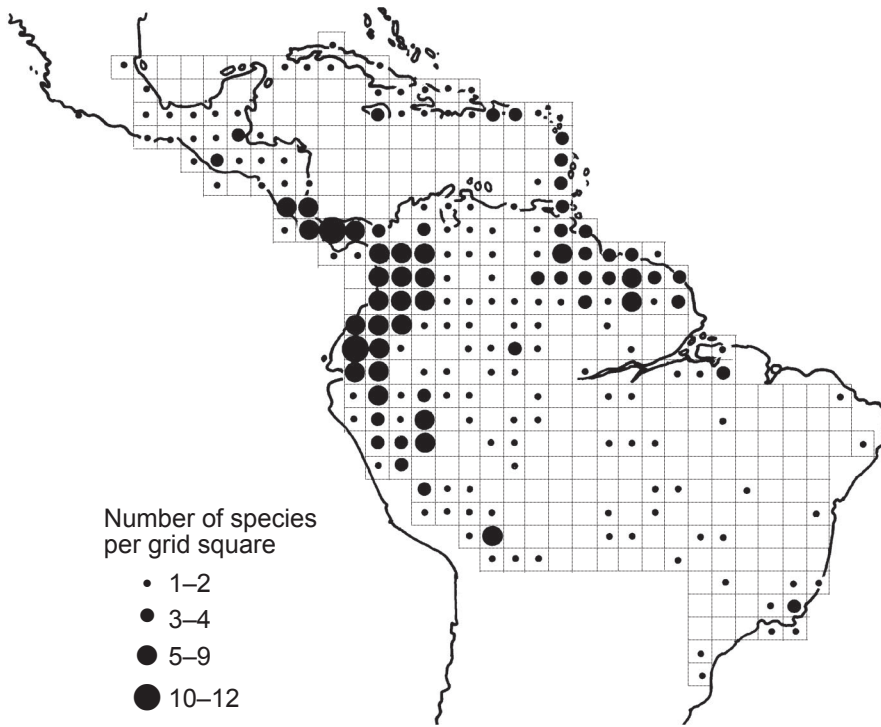


Fig. 3. Species diversity of a typical Andean-centred group: the genus *Renealmia* (Zingiberaceae). Redrawn from Maas (1977); the Trinidad grid square, mistakenly left blank by Maas was corrected in accordance with data in the text. Map by L. Andersson (unpublished).

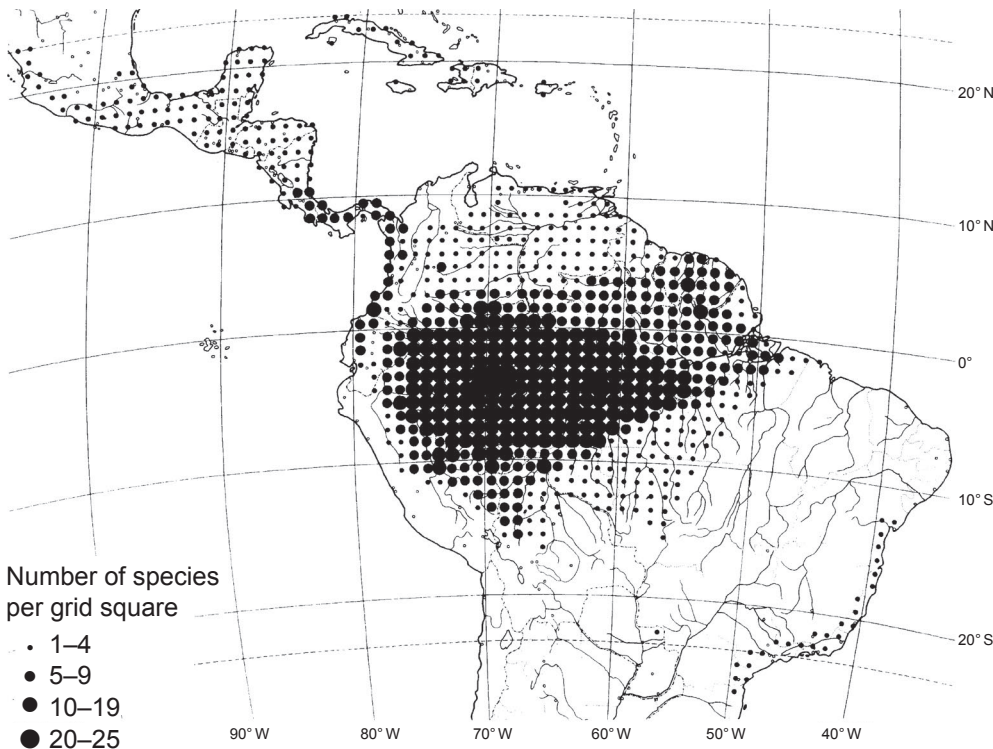


Fig. 4. Species diversity of a typical Amazonian-centred group: tribe Olmedieae (Moraceae). Compiled from maps of individual species distributions in Berg (1972) and localities listed by Berg (1998). Map by L. Andersson.

sand). Their study suggested that speciation by edaphic adaptation may have played an important role in the assembly of Amazonian biodiversity, but many similar studies are needed to ascertain the generality of the model.

Biotic interactions. — Interactions between plants and their pollinators, seed dispersal, and antagonists, and how such

interactions have promoted or constrained species diversification, constitute a complex and still poorly studied research topic for the Neotropics.

The pollination of many Neotropical species has yet not been recorded, although in many families (such as orchids) there appears to be high pollinator specificity (Van der Cingel &

Van der Cingel, 2001). Although a general pollinator can often be deduced from a plant's 'pollination syndrome', actual observation may provide novel insights into plant-pollinator interactions. Some species in the Campanulaceae genus *Burmeistera*, for instance, have been shown to be pollinated daytime by hummingbirds and at night by bats (Muchhala, 2003). The evolutionary consequences of pollinator specificity vs. generality, and the exact mechanisms underlying floral specialisation, constitute a growing and promising field of Neotropical research (e.g., Kay & al., 2005; Muchhala, 2007; Muchhala & Potts, 2007; Tripp & Manos, 2008; Armbruster & Muchhala, 2009; Alcantara & Lohmann, 2010, 2011; Muchhala & al., 2010).

Plants and their herbivores constitute more than half of the organisms in tropical forests (Kursar & al., 2009). Kursar & al. (2009) found strong selection for divergent defensive traits in the legume genus *Inga*. Their results suggest that plant-herbivore interactions may function not only be as an important driver of speciation, but also as a means of maintaining high species diversity. However, plant antagonists (herbivores and pathogens) could in theory lead to the opposite effect, constraining diversification if the diversity of antagonists increases with host diversity (Ricklefs, 2010).

Dispersal ability. — The development and increased use of molecular dating techniques has indicated that long-distance dispersals have occurred much more often among plants than once thought (Renner, 2004, 2005; Queiroz, 2005).

Dispersals into South America have probably produced a net increase of species numbers on the continent, despite extinction caused by competition between the new arrivals and the autochthonous biota. The most important wave of migration is that following the uplift of the Panama Isthmus in the Late Pliocene (~3.5 Ma), which connected South America to the north after some 100 million years of isolation. This event, known as the "Great American Biotic Interchange" (GABI), has been originally documented for mammals (Stehli & Webb, 1985), but recently its role has been investigated in other taxa through meta-analyses of dated phylogenies (Weir & al., 2009; Cody & al., 2010; Smith & Klicka, 2010). The available evidence suggests that many plant lineages arrived in South America prior to the final closure of the Isthmus (Cody & al., 2010), some considerably earlier (e.g., Antonelli & al., 2009; Erkens & al., 2009). These early dispersals might have been facilitated by "island hopping" across the proto-Greater Antilles in the Early Eocene (~50 Ma) and the Greater Antilles and the Aves Ridge (GAARlandia) around the Eocene/Oligocene boundary (33–35 Ma; Iturralde-Vinent & MacPhee, 1999), although the geological evidence for these island connections does not seem conclusive.

Repeated migrations from the north, which were almost always followed by in situ radiations (Hughes & Eastwood, 2006; Pirie & al., 2006; Erkens & al., 2007, 2009; Moore & Donoghue, 2007; Antonelli & Sanmartín, in press), added to inferred transatlantic dispersals directly from Africa (Lavin & al., 2004; Renner, 2004), suggests that dispersals from other landmasses have played an important role in the historical assembly of certain Neotropical biomes (Pennington & Dick, 2004; Pennington & al., 2006).

Niche conservatism. — The "tropical conservatism hypothesis" (Wiens & Donoghue, 2004; Wiens, 2007) suggests that there are more plant species in the Neotropics simply because more plant lineages originated and diversified there owing to the long-term climatic stability of the region (i.e., longer times for speciation) and the tendency of species to retain their climatic niches over evolutionary time. The inferred high dispersal ability of many lineages mentioned above, combined with the inference that many plant taxa show a high degree of niche conservatism (Crisp & al., 2009), support the idea that for plants it is often "easier to move than to evolve" (Donoghue, 2008: 11551). This might be an appropriate generalisation for some Neotropical biomes/ecosystems, such as seasonally dry tropical forests (see Pennington & al., 2006 for a detailed distribution map). Phylogenetic analyses indicate that a significant proportion of the species in these biomes belong to lineages that dispersed from distant regions with similar environmental conditions (i.e., they were "pre-adapted"), rather than arriving from neighbouring biomes such as Amazonia (Hughes & Eastwood, 2006; Pennington & al., 2009, 2010).

However, biome conservatism may not be a general rule for the entire Neotropics. Simon & al. (2009) showed that many lineages in the Cerrado have arrived from nearby ecosystems (rainforests, seasonally dry forests, subtropical grasslands and wetlands), independently adapting to fire conditions characteristic of this biome. Several other studies have similarly shown that considerable biotic interchange has occurred among Neotropical biomes and altitudinal zones within the same biome (e.g., Perret & al., 2006; Antonelli & al., 2009; Dušková & al., 2010; Hoorn & al., 2010).

Different biomes thus appear to have been assembled by different dominant processes, which could also be seen as they differ in their permeability to successful migrations (Pennington & al., 2010). Such differences may also become evident *within* biomes, as we gather more information from molecular phylogenies. In a recent review, for instance, Sklenář & al. (in press) showed that about half of the plant genera in the Páramos have a temperate origin, showing niche conservatism (i.e., they were pre-adapted to the Páramo climate), while the other half of the surveyed genera are likely of tropical origin and have adapted in situ. Quantifying the extent of biotic interchange in the Neotropics would help understand the historical assembly of biomes and pinpoint biological corridors for future conservation.

■ ABIOTIC MECHANISMS

Time. — The oldest evolutionary explanation to explain the extraordinary diversity of the Neotropical region is probably the "time hypothesis", the idea that the species richness of a region is correlated to the amount of time available for speciation within the region (Wallace, 1878; Mittelbach & al., 2007). According to this hypothesis, the geological isolation and long-term climatic stability of the South American continent would have favoured the gradual accumulation and/or preservation of lineages over time. After splitting from Africa

in the mid-Cretaceous (ca. 100 Ma), South America remained isolated from other tropical continents, until a new connection was established with North America via the uplift of the Panama Isthmus ca. 3.5 Ma. Simpson (1980) coined the term “splendid isolation” to refer to the fact that the mammalian fauna of South America evolved and diversified during nearly 90 million years in what was effectively an “island continent”. Also, compared to Australia and other Gondwanan landmasses, the Neotropical region has always been at about the same geographic latitude (close to the Equator), and therefore subjected to similar climatic conditions, so this long-term climatic stability would have favoured low extinction rates and the preservation of species over time (Stebbins, 1974; Mittelbach & al., 2007).

This “museum model of diversification”—the notion of the Neotropics as a museum of lineages—is supported by some recent palaeontological and phylogenetic evidence, showing that the origin of several evolutionary radiations (crown diversification) in present-day Amazonia can be traced back to the early Neogene or even earlier (Hoorn & al., 2010). However, other phylogenetic studies show evidence of a “cradle model” of diversification, with recent and rapid accumulation of species via high speciation rates, perhaps triggered by climatic shifts during the Pleistocene (Rull, 2011) or relatively recent tectonic events such as the Pliocene final uplift of the Andes (Gregory-Wodzicki, 2000; Hughes & Eastwood, 2006) or the uplift of the Panama Isthmus. Increasing evidence suggests that these two models are not mutually exclusive, with many tropical groups exhibiting features of both museum and cradle diversification and varying speciation and extinction rates in their evolutionary histories (McKenna & Farrell, 2006; Mittelbach & al., 2007; Antonelli & Sanmartín, in press).

Climate and area: Current patterns. — Ecologists have long recognised that high levels of rainfall, temperature and habitat heterogeneity are correlated with high species richness. Globally, a combined multipredictor model has been shown to explain 70% of the global variation in species richness (Kreft & Jetz, 2007). Such models may in fact account for the much debated latitudinal gradient in species richness (Kreft & Jetz, 2007), although dozens of alternative hypotheses have been proposed (Lomolino, 2005). It seems that climate plays an important role in determining species richness at large scales, whereas at smaller extents such correlation is often less evident or non-significant compared to a null expectation (Field & al., 2009).

The effect of area (range sizes) on species richness has been studied more in animals (e.g., Rahbek & Graves, 2001) than in plants (Field & al., 2009), perhaps due to our scarcer knowledge on range sizes for Neotropical plant species. The effect of area on diversity may be difficult to model and separate from other variables such as habitat heterogeneity (Kreft & al., 2006; Kisel & al., in press), but it appears to be a worse predictor of species richness than climate (Field & al., 2009) or other correlates such as diversification rates (Svenning & al., 2008).

Climate and area: Past responses to climate. — Although climate may thus be one of the most powerful global predictors of species richness today, its historical role in producing or maintaining Neotropical plant diversity is a matter of

contention. Analyses of fossil pollen show correlation between high global temperatures in the Eocene and high plant diversity in the Neotropics (Jaramillo & al., 2006), and indicate that global warming at the Paleocene/Eocene boundary (56.3 Ma) has resulted in increases in species numbers for several plant families (Jaramillo & al., 2010). However, a similar correlation is not evident for the Neogene, where the diversity of pollen morphospecies shows poor agreement with fluctuations in temperature (Hoorn & al., 2010).

Perhaps the most important and debated link suggested between climate and species richness in the Neotropics concerns the “refuge theory” for Amazonia. During the past ~2.6 Ma, the Earth went through some 20 major glacial periods (Gates, 1993). Based on the observation that the main centres of avian endemism in northern South America are situated in zones that today receive the highest levels of precipitation, Haffer (1969) suggested that the rainforest cover in Amazonia changed repeatedly in response to global climatic oscillations. According to his hypothesis, lowland forest was fragmented into isolated refugia during cooler (drier) periods and expanded and condensed again during warmer (wetter) interglacials. As a result, allopatric speciation in forest refugia was promoted.

This Pleistocene refuge theory gained early support with the emergence of similar distribution patterns in many taxa, including plants (Prance, 1973, 1978, 1982; Andersson, 1979). However, criticism started soon to accumulate in many directions, including the lack of evidence for widespread aridification in Amazonia, the demonstration that perceived endemism centres were often artefacts of sampling, and the fact that the age of many Neotropical clades as inferred by molecular dating analyses predates the onset of Pleistocene glaciations (Nelson & al., 1990; Bush, 1994; Knapp & Mallet, 2003). Recently, Hoorn & al. (2010) presented the most extensive review of the geological, fossil and molecular evidence for northern South America. Since most organism groups were already highly diverse prior to the onset of Pleistocene glaciations at 2.6 Ma, they concluded (Hoorn & al., 2010, 2011) that Pleistocene dynamics—either as postulated by the refuge theory or by alternative processes (Rull, 2005, 2011)—cannot be claimed responsible for the outstanding levels of Neotropical species richness. The refuge theory has later been modified to apply to the entire Cenozoic, based on the assumption that climatic fluctuations can lead to allopatric speciation (Haffer, 2008 and references therein). However, the lack of biogeographic signal in certain Amazonian phylogenies (e.g., Kursar & al., 2009) and recently developed null models of speciation (De Aguiar & al., 2009) challenge the view that allopatric speciation has been the dominant mode of speciation.

The effect of climatic fluctuations may have been more pronounced outside the Amazonian rainforest. Antonelli & al. (2010b) suggested that climate cooling following the Mid-Miocene climatic optimum probably increased the geographical extent of rocky savannas in the Cerrado, promoting the expansion and diversification of a group of orchids. Global cooling might have had a comparable effect on all southern continents, promoting the expansion of open habitats and establishment of fire regimes, triggering the diversification of

plants adapted to fire conditions (Simon & al., 2009; Crisp & al., 2010; Bytebier & al., 2011).

Mountain uplift. — Extending over 5000 km along the western coast of South America, the Andean Cordillera constitutes the largest mountain chain directly adjacent to a tropical rain forest. Its initial uplift can be traced back to the Cretaceous (Milnes, 1987), and is thought to have roughly proceeded from south to north and from west to east. In the central and northern Andes, most of the uplift took place in the last 25 Ma, intensifying between 10 and 5 Ma, and with some segments of the Eastern Cordillera in the northern Andes having risen as recently as 5–2 Ma (Gregory-Wodzicki, 2000; Garzione & al., 2008; Hoorn & al., 2010).

Andean uplift may have increased diversification in several important ways (see Hoorn & al., 2010 and references therein): (1) by increasing habitat heterogeneity in northern South America, and thus favouring adaptive radiations in newly formed montane habitats; (2) by creating a “biotic corridor” for taxa pre-adapted to montane conditions to increase their range; (3) by favouring allopatric speciation in montane taxa, separated by deep valleys and impassable ridges and peaks; (4) by producing geographic vicariance, and consequently genetic isolation, between lowland populations on both sides of the emerging mountains; (5) by acting as a “species pump”, as newly formed lineages in the Andes may have dispersed into other Neotropical biomes and further radiated; (6) by increasing nutrient deposition in western Amazonia, following denudation of the rising mountains by rainfall (see below).

Hydrological changes: The Pebas system. — Among many things, the Andean uplift changed the entire hydrological configuration of northern South America. The current settings, with the Amazon river flowing eastwards and the Andean mountains fully formed, was only established some 7–2.5 Ma (see Hoorn & al., 2010 and references therein; Wesselingh & al., 2010). There is now a general consensus that western Amazonia was dominated by aquatic settings, “the Pebas system”, between ca. 24 and 10 Ma (Hoorn & al., 2010) (Fig. 5). Whether the Pebas system was a single lake that covered up to 1 million km² (Wesselingh & al., 2002) or a river system surrounded by lowland *terra firme* (= dry soil) forest areas, such as the Brazilian Pantanal (Latrubesse & al., 2010), is however a matter of debate.

The nature of the Pebas system has important implications for our understanding of Neotropical plant evolution, since western Amazonia comprises sites with the highest alpha diversity measured in any tropical rainforest (Valencia & al., 1994). The existence of a single mega-lake would imply that in situ diversification of trees adapted to dry land necessarily post-dated its drainage (ca. 10–7 Ma), as pointed out by Antonelli & al. (2009). If diversification of clades endemic to western Amazonia are instead shown to extend further back than 11 Ma, and biogeographical and fossil analyses confidently indicate that they evolved in situ (instead of evolving elsewhere, such as in non-flooded montane habitats, and subsequently migrating), this would provide independent evidence that the Pebas system was a river system interspersed with *terra firme* areas, rather than gigantic lake. Interestingly, the few molecular

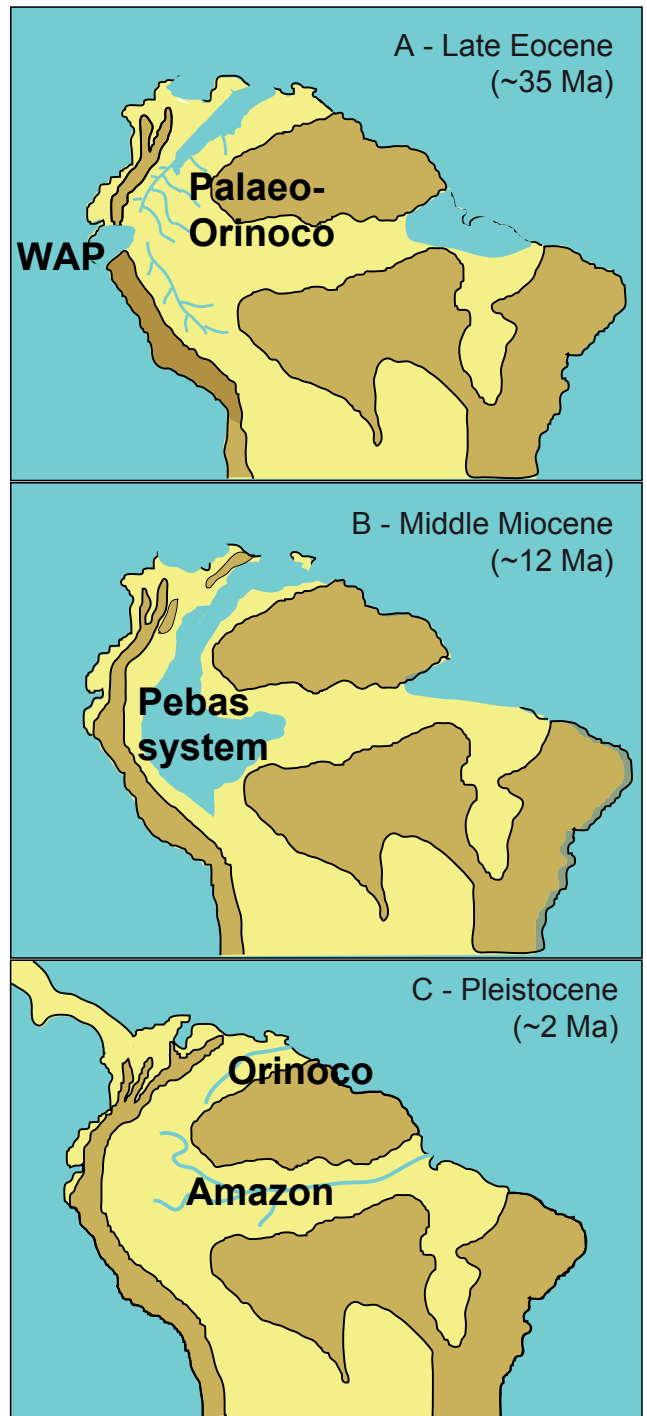


Fig. 5. Simplified landscape evolution of northern South America in the last 35 Ma (adapted from Antonelli et al., 2009; Hoorn & al., 2010). **A**, A northwards flowing fluvial system (the Subandean River System or palaeo-Orinoco) dominates the drainage of western Amazonia and the foreland Andean basins. A lowland corridor occasionally invaded by marine settings (the Western Andean Portal, WAP) may have limited biotic dispersal between the Northern and Central Andes. **B**, The Pebas system dominates western Amazonia. The WAP is uplifted, facilitating the dispersal of Andean taxa. **C**, South America is connected to Central America, the Pebas system is completely drained, and dispersal of terrestrial organisms is facilitated across most of the region. Light yellow, lowlands; brown, montane areas; blue, aquatic settings.

dating studies that have dealt with a representative number of Amazonian trees seem to support the former scenario, i.e., recent and rapid radiation for the genera *Inga* (Richardson & al., 2001; Lavin & al., 2006) and *Gutteria* (Erkens & al., 2007). However, biogeographical analyses necessary for testing this scenario may be complicated by recent range expansion into western Amazonia of species that once surrounded the Pebas system (“dispersal overwrite”; Pennington & Dick, 2010).

Hydrological changes: The Western Andean Portal. — Many plant families, such as Campanulaceae (Ayers, 1999), Calceolariaceae (Molau, 1988), Tropaeolaceae (Sparre & Andersson, 1991), Loasaceae, Passifloraceae, Grossulariaceae (Weigend, 2002, 2004), Clusiaceae (M.H. Gustafsson, pers. comm.) and Alstroemeriaceae (Hofreiter & Rodríguez, 2006), show a conspicuous disjunction between the Northern and Central Andes. These families contain genera or species groups mostly restricted to either north or south of a zone in southern Ecuador/northern Peru (~3°–5° S; Fig. 5), referred to as the “Western Andean Portal” (WAP, Antonelli & al., 2009), but also Huancabamba Depression, Huancabamba Deflexion, Marañón Portal, Guayaquil Gap, Northern Peruvian Low or Pirua Divide, all seemingly referring to roughly the same area (Antonelli & al., 2009).

From the Eocene to the Middle Miocene (~40–12 Ma), episodic marine incursions from the Pacific have been suggested to penetrate the WAP, which at the time was a lowland corridor separating the Northern from the Central Andes. Marine incursions probably ended in connection with the uplift of the Eastern Cordilleras of the Central and Northern Andes from the Middle Miocene onwards (13–11 Ma; Hoorn & al., 1995, 2010; Hungerbühler & al., 2002), allowing the Andes to be permanently connected by highlands. This may have created a new migration route between the Northern and Central Andes for organisms adapted to montane conditions (Antonelli & al., 2009). Prior to the establishment of this “Andean highway”, however, the WAP probably constituted a dispersal barrier for montane taxa, leading to species diversification on either side of the WAP but rather few dispersals across it. It should be noted, however, that by the time the WAP uplifted the northern Andes may have attained only about half of their present height (Gregory-Wodzicki, 2000), meaning that truly high altitude (Páramo) taxa were probably absent.

Hydrological changes: The palaeo-Orinoco and the Gentry pattern. — To date, no studies have attempted to explain the formation of the Gentry pattern (see above; Figs. 3 and 4). Gentry’s own idea was that this pattern arose by differentiation from an originally more uniform pattern, and that the uniform pattern was a remnant of a more or less continuous West Gondwanan rain forest flora (Gentry 1982). Based on these premises, species richness of Andean-centred groups in northwestern South America was explained as a consequence of evolutionary radiation in certain lineages in response to environmental changes caused by the Andean orogeny. Gentry did not discuss at all how or when a diversity centre would have been formed in the central Amazonian basin.

Distributional disjunctions of organisms are commonly formed by the influence of a geographic barrier, but no such

barrier exists today between the Andes and the Amazon Basin. It could therefore be assumed that eco-physiological constraints acted instead as barriers for lowland organisms, at the same time as taxa already adapted to montane habitats were unable to compete with lowland-adapted taxa at lower altitudes. However, as emphasized by Gentry (1982), while the representation of Andean-centred taxa is highest in the Andes, most species occur along the base and slopes of mountains, rather than at high altitudes. It is thus conceivable that if no geographic barrier existed between the Andes and Amazonia, biotic interchange between these two areas would have taken place continuously, which in turn should have promoted speciation through gradual adaptation to slightly different altitudes (Smith & al., 1997). However, if this was the case for most taxa, no clear biogeographical pattern should be observed today separating Andean-centred and Amazonian-centred groups.

From the Cretaceous until the end of the Oligocene (ca. 112–24 Ma), a fluvial system referred to as the palaeo-Orinoco dominated the drainage of northwestern Amazonia and the foreland Andean basins towards Lake Maracaibo, on the Caribbean coast (Fig. 5). Then, in the Early Miocene (ca. 23 Ma), geotectonic changes in the Amazon Basin associated with the ongoing uplift of the Eastern Cordillera in the Central Andes caused western Amazonia to gradually become submerged, creating the Pebas system (see above). Further uplift, affecting mainly the Eastern Andean Cordilleras, presumably caused the areas west of the Guiana Shield to emerge, closing the Caribbean connection of the palaeo-Orinoco and shifting the drainage of the Amazon Basin eastwards, causing the demise of the Pebas system (Hoorn & al., 2010; Wesselingh & al., 2010) (Fig. 5C).

A remarkable fit can be observed between the hydrological scenario outlined here (Fig. 5) and the distributional patterns depicted in Figs. 3 and 4. It seems therefore possible to speculate that the “missing” long-lasting barrier needed for creating the disjunction between Andean-centred and Amazonian-centred groups could have been the palaeo-Orinoco and its successor, the Pebas system.

The WAP and the palaeo-Orinoco are of special relevance for understanding the biogeography and distribution of Neotropical plants, because they could potentially be used to test the role of ecological constraints vs. historical barriers in shaping current patterns of plant distributions. If they indeed constituted dispersal barriers, biogeographical analyses based on dated phylogenies of groups distributed across these presumed barriers (e.g., Antonelli & al., 2009; Santos & al., 2009) should infer very few dispersals before the disappearance of the barriers, followed by a significant increase in dispersals. If no significant shifts in dispersal rates can be detected, this would favour the idea that eco-physiological constraints (niche conservatism) played a more important role in determining the disjunct patterns observed today. Phyloclimatic modelling of niche preferences (Yesson & Culham, 2006), especially in combination with realistic palaeoclimatic reconstructions (e.g., Sepulchre & al., 2006) and biogeographic inference taking into account phylogenetic uncertainty and dynamic biogeographical settings (Smith, 2009) could provide further insights on the issue.

■ USING DATED PHYLOGENIES TO HELP UNDERSTAND NEOTROPICAL DIVERSIFICATION

A major problem in evolutionary studies is how to determine the actual cause(s) of speciation. We have outlined here some—but certainly not all—of the major mechanisms and hypotheses proposed for explaining Neotropical diversification, but there is no consensus regarding how (or even whether) they can be tested. Dated molecular phylogenies (molecular chronograms), especially in conjunction with information from the fossil record, can help test some of the hypotheses that contain a strong temporal prediction, such as (1) that a large proportion of South American species have been “inherited” from Gondwana, i.e., they existed already before the separation of South America and Africa ca. 100 Ma; or (2) that the high levels of Neotropical diversity originated as a consequence of Pleistocene dynamics, i.e., in the last 2.6 Ma.

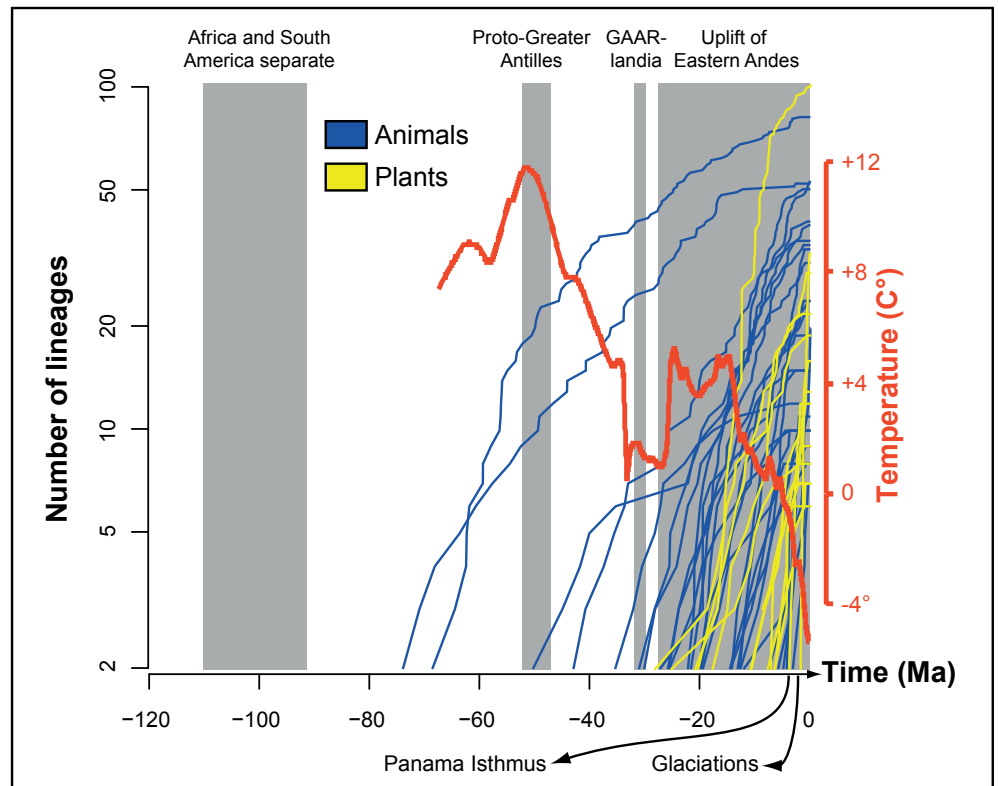
To illustrate how this may be done, we present here (Fig. 6) a number of lineage-through-time (LTT) plots of dated Neotropical phylogenies of plants and animals (Antonelli & al., in prep.). The principle of LTT plots is simple: the number of lineages in a molecular chronogram, or the logarithm of that number, is plotted as a function of time. Although this graphical method has limited statistical value in testing hypotheses (Nee & al., 1992; Paradis & al., 2004), it has been widely used in the literature for visualising the temporal pattern of lineage accumulation over time from reconstructed (i.e., including extant taxa only) phylogenies. A visual inspection of Fig. 6 makes

evident that both the “Gonwana” and “Pleistocene” hypotheses may be discarded as the major causes of Neotropical biodiversity: (1) prior to the separation of Africa and South America, no modern Neotropical clades (of the ones analysed here) existed (i.e., no most recent common ancestors can be traced back to Gondwanan times); and (2) by the time Pleistocene climatic changes began, most modern groups had already begun to diversify (Hoorn & al., 2011).

Dated phylogenies can thus be used to test simple temporal hypotheses of diversification, as well as to provide insights into the historical assembly of species-rich biomes (Pennington & al., 2006, 2010; Simon & al., 2009). Nevertheless, there are many limitations and caveats associated with molecular-dating analyses, and results are highly influenced by taxon sampling, methodology, and fossil calibrations (e.g., Linder & al., 2005; Renner, 2005; Ricklefs, 2007). As pointed out by Pennington & Dick (2010) a further and perhaps even harder problem to tackle is that several of the proposed hypotheses of diversification overlap in time, such as the Andean uplift, climatic fluctuations, and postulated island chains between South and North America (Fig. 6).

Phylogenetic correlation analyses (e.g., Pagel & Meade, 2006; Freckleton & al., 2008) could be increasingly used to test whether increases in diversification rates can be associated with specific events, such as dispersal into a new region or acquisition of a morphological “key innovation” (e.g., Ree, 2005; Moore & Donoghue, 2007, 2009; Antonelli & al., 2011; Antonelli & Sanmartín, in press; Humphreys & al., in press). However, they too are sensitive to a series of potential pitfalls

Fig. 6. Lineage-through-time (LTT) plots for a representative sample of dated phylogenies of Neotropical organisms (from Antonelli & al., in prep.), depicting 14 plant and 30 animal phylogenies. The shaded boxes represent the approximate duration of some geological and geographic events suggested to have fostered the dispersal and radiation of Neotropical organisms. Global temperature curve from Zachos & al. (2001). GAARlandia: Greater Antilles and Aves Ridge.



including poor taxon sampling, and it is exceptionally difficult to separate speciation and extinction rates from net diversification estimates (Crisp & Cook, 2009; Cusimano & Renner, 2010; Rabosky, 2010). Finally, such analyses can still only provide correlational links, whereas substantial theoretical and experimental work may be necessary to distinguish between correlation, causation, and effect, with an acceptable level of confidence (e.g., Armbruster & Muchhala, 2009).

■ GAINED INSIGHTS, CURRENT CHALLENGES AND FUTURE PERSPECTIVES

Gentry (1982) suggested that the Andean uplift has played a central role in generating the “excess” of species found in the Neotropics as compared to other tropical regions. Thirty years later, technological and other intellectual advances have provided us with new tools to pursue the question outlined in the title of this paper. The evidence gathered so far from molecular phylogenies and the fossil record has confirmed the key role of geotectonic processes in re-shaping northern South America and setting the stage for species diversifications (Hoorn & al., 2010), but it has also pointed out that Neotropical biodiversity is the product of many distinct, and often interacting, evolutionary processes—several of which we are just beginning to realise and understand. It is also important to emphasise that the processes and events that have led to increases in biodiversity may not necessarily be the same as those that maintain it over longer time scales.

Big problems demand big science. We need to advance the way we accumulate and use evidence from as many organismic groups as possible, creating phylogenies that are densely sampled both taxonomically and genetically (e.g., by using new ultra-high-throughput DNA sequencing technologies and plant material from ecological inventory plots). Increased taxon sampling in phylogenies, besides improving our estimates on the biogeography and diversification of a clade, may lead to an appreciation of the true diversity of the Neotropics including “cryptic” species (Condon & al., 2008; Smith & al., 2008). At the same time, we need to put our results into a broader perspective, developing methods that can test the generality of postulated hypotheses across individual studies (e.g., Field & al., 2009). Substantial insights are to be gained through inter-disciplinary scientific collaborations (integrating, for instance, botany and zoology; biology, geology, palaeontology and climatology; ecology, classical taxonomy and molecular systematics).

The origins and evolution of Neotropical diversity have intrigued scientists for centuries, and will most probably continue to do so for centuries to come. However, we now face an unprecedentedly difficult task, as much of this diversity is at considerable risk of disappearing due to habitat destruction and climate change (Hubbell & al., 2008; Svenning & Condit, 2008). As biologists we must actively contribute to disseminate our knowledge on biodiversity, how it has evolved, and how the gathered evidence can help us in choosing the most effective conservation measures (Hendry & al., 2010).

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