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History and Geography of Neotropical Tree Diversity

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Keywords

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Abstract

Early botanical explorers invoked biogeographic history to explain the remarkable tree diversity of Neotropical forests. In this context, we review the history of Neotropical tree diversity over the past 100 million years, focusing on biomes with significant tree diversity. We evaluate hypotheses for rain forest origins, intercontinental disjunctions, and models of Neotropical tree diversification. To assess the impact of biotic interchange on the Amazon tree flora, we examined biogeographic histories of trees in Ecuador's Yasuní Forest, which suggest that nearly 50% of its species descend from immigrant lineages that colonized South America during the Cenozoic. Long-distance and intercontinental dispersal, combined with trait filtering and niche evolution, are important factors in the community assembly of Neotropical forests. We evaluate the role of pre-Columbian people on Neotropical tree diversity and discuss the future of Neotropical forests in the Anthropocene.

1. INTRODUCTION

Woody plant diversity exhibits a striking latitudinal gradient, especially in the Americas. Diversity peaks in the Neotropics, which supports as many as 24,500 tree species (with diameters ≥10 cm) (Slik et al. 2015). The lowland rain forests of the Amazon basin harbor the most concentrated tree diversity, with individual hectares containing up to 644 species (with diameters ≥1 cm) (Valencia et al. 2004). For comparison, approximately 300 tree species occur in eastern North America (Fine & Ree 2006). Explaining the local coexistence of so many tree species is a central problem of community ecology (e.g., Hubbell 2001).

Wallace (1878) hypothesized that tropical tree diversity accumulated over "countless past ages" (p. 122) within climatically stable environments. Indeed, lowland tropical forests were not displaced by glaciers, as in Europe and North America, both of which lost many tree genera during the Pliocene–Pleistocene (Latham & Ricklefs 1993). Wallace's reference to time also implied that tree diversity in the tropics is older than in temperate zones, an idea that is supported by phylogenetic comparisons of North and South American tree taxa (Kerkhoff et al. 2014; however, for the Southern Hemisphere temperate flora, see Rezende et al. 2017).

The Pleistocene refuge theory (PRT) (Haffer 1969) challenged Wallace's idea by positing Quaternary climate change as a driving force of tropical speciation. In reviewing ideas about tropical plant diversification, Stebbins (1974) used the term "cradle" to describe elevated speciation associated with the refuge theory and the term "museum" for Wallace's model of species accumulation through deeper time. Although these models have multiple interpretations and are not mutually exclusive (Eiserhardt et al. 2017), they highlight the influence of time and environmental change on biotic diversification and provide an intellectual framework for phylogenetic studies (e.g., Couvreur et al. 2011b, Koenen et al. 2015, Richardson et al. 2001).

Over the entirety of the Cenozoic, the climate and geology of the Neotropics have been far from stable (Hoorn & Wesselingh 2011). The emergence of the Isthmus of Panama, the formation of the Amazon river, and the uplift of the northern Andes, for example, have profoundly influenced climate, speciation, and biotic interchange (Graham 2010, Hoorn & Wesselingh 2011), but the precise association of these events with biotic diversification often is unclear (Baker et al. 2014).

This review is motivated by several guiding questions. How long have Neotropical tree lineages and biomes existed to accumulate such enormous species diversity? How was the Neotropical tree flora assembled? How has biogeographic history influenced the community structure and ecology of present-day Neotropical forests? How did pre-Columbian people impact Neotropical tree diversity? What is the future of Neotropical forests in the Anthropocene?

2. SCOPE

We focus on four Neotropical biomes that contain substantial tree diversity: (*a*) lowland rain forest; (*b*) lower to upper montane forests; and the drier vegetation types, including (*c*) seasonally dry forest and (*d*) savanna (**Figure 1**). Tropical rain forests have high (>25 m), closed, evergreen canopies and generally occur in locations with annual precipitation greater than ∼2,000 mm and with little to no dry season. Most Neotropical montane forests occur between 1,200 and 2,800 m, although small pockets of wind-protected forest may occur at >4,000 m in the Andes (Kappelle 2004). Seasonally dry forests have a closed, deciduous canopy and are typically confined to richer soils, whereas savannas occur on less fertile soils, are fire-prone, have evergreen tree cover up to 80%, and have grass cover greater than 50% (Pennington et al. 2018).

Under a standard definition (but see Feeley & Stroud 2018), the tropics are bounded by the Tropics of Cancer and Capricorn (**Figure 1**). These latitudes contain the most distant points from the equator in which sunlight may be directly overhead. However, tropical vegetation was
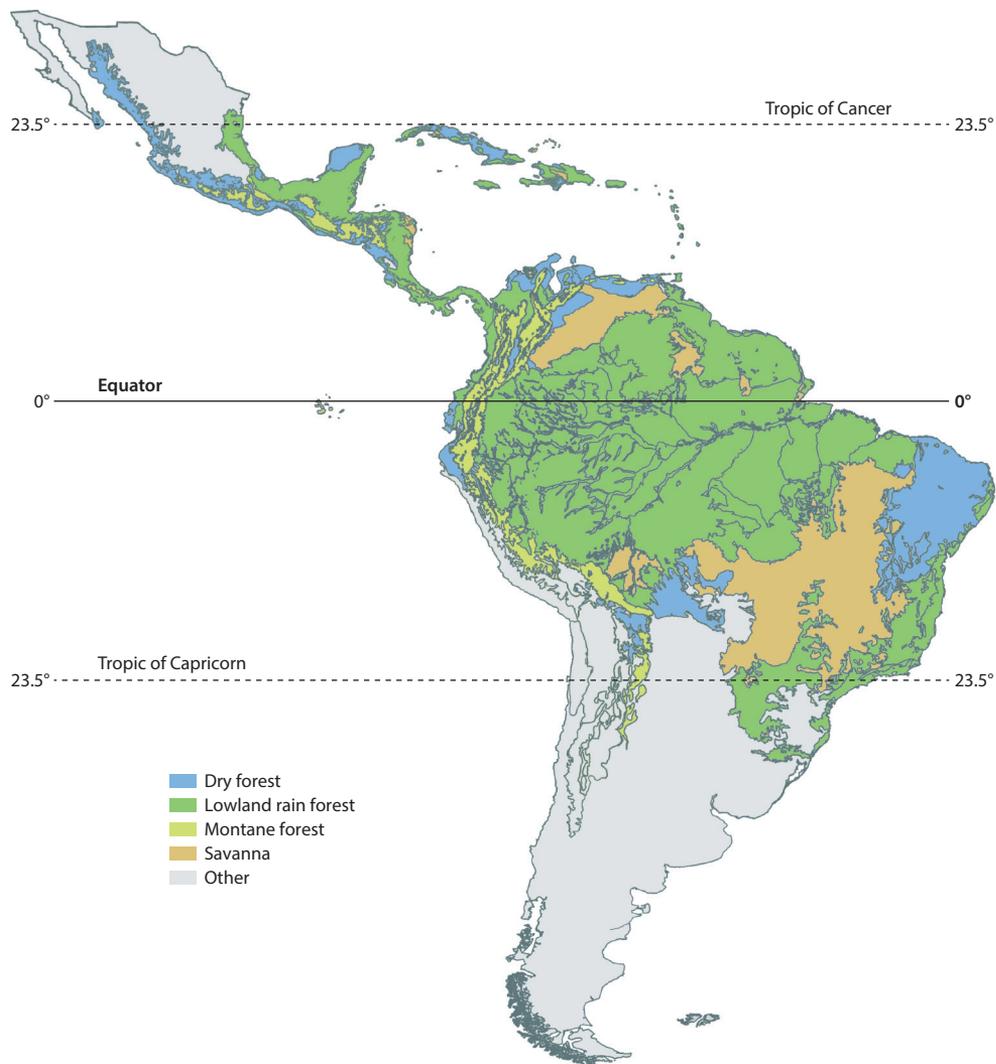
Figure 1

Biome map adapted from the ecoregion classification of Olson et al. (2001), but with the tropical regions reclassified into the tropical montane forest, lowland rain forest, savanna, and dry forest biomes. Classification of the savanna and dry forest biomes follows Pennington et al. (2018). Because of scale, small areas of some biomes embedded within other biomes (e.g., isolated savannas in Amazonia, patches of dry forest within Brazilian savannas) cannot be depicted.

not always confined to this equatorial belt. Palms and crocodilians nearly reached the Arctic Circle (60–65°N) during the Paleocene (Graham 2010, Wolfe 1975), and what we know as tropical and temperate trees mingled at midlatitudes to form a nonanalog biome known as the Boreotropical flora (Wolfe 1975) that extended across the Northern Hemisphere. We loosely use climatic definitions (e.g., megathermal and tropical) to describe the high-latitude distribution of thermophilic taxa during much of the Cenozoic. Our assumption is that megathermal or tropical vegetation—wherever it is located—requires year-round warmth (average monthly temperature of ≥18°C for lowland plants) and an absence of extended freezing.

3. ORIGIN OF NEOTROPICAL RAIN FOREST

As anticipated by Wallace, historical models of tropical biome distributions for South America (Jaramillo & Cárdenas 2013) and globally (Fine & Ree 2006) have proven useful for predicting levels of tree diversity under a time-integrated biome area hypothesis (Fine & Ree 2006). Though no definitive evidence exists of modern tropical biomes before the Cenozoic, fossil and phylogenetic evidence suggest that forms of lowland rain forest and tropical montane forest may have existed in the mid-Cretaceous, roughly 100 Ma (Burnham & Johnson 2004; Davis et al. 2005; Graham 2010, 2011; Morley 2000).

At 100 Ma, South America was beginning to separate from Africa, and Laurasia was biotically connected across North America and Eurasia. Global surface air temperatures were ~7°C warmer than present and sea levels were 100–300 m higher (Graham 2010). Angiosperm orders diversified, as did early palms (Couvreur et al. 2011a) and understory trees (Davis et al. 2005) that are indicative of multi-strata rain forest.

Increased leaf vein density—a key innovation—enabled mid-Cretaceous angiosperms to photosynthesize and transpire more efficiently than other seed plants and dominate most terrestrial ecosystems (Boyce et al. 2010). However, the large seeds associated with shade tolerance, leaf drip tips, and large tree trunks with modern wood anatomy do not appear until the Cenozoic (Burnham & Johnson 2004, Morley 2000). Because of the extreme warmth and aridity of the equatorial tropics in the Cretaceous, proto-tropical moist forests may have been confined to mid-latitudes (Morley 2000). Indeed, gymnosperms and ferns dominate late Cretaceous floras from South America (Jaramillo & Cárdenas 2013).

An essentially modern rain forest first appeared shortly after the Cretaceous–Paleogene (K/Pg) extinction event, approximately 64.1 Ma. This was Colorado's Castle Rock flora (Johnson & Ellis 2002). The earliest South American rain forest appeared by 58 Ma and left many fossils in the Colombian Cerrejón flora (Wing et al. 2009). Although the Castle Rock flora had Asian affinities, Cerrejón had approximately 20% family-level overlap with present-day Neotropical rain forests. The Paleogene (Paleocene + Eocene) was a period of global expansion of angiosperm-dominated forests at midlatitudes and the equatorial region (Jaramillo et al. 2010, Morley 2000). A second marked increase in angiosperm leaf venation occurred at that time, providing even greater plant–climate feedback and facilitating expansion of modern rain forests (Feild et al. 2011). The first modern dry forests and savannas appeared much later, in the Miocene/Pliocene (Graham 2011).

The fossil record suggests that tropical forests expanded, and diversity increased, during the warmest periods of the Cenozoic (Jaramillo & Cárdenas 2013, Jaramillo et al. 2010). The Cerrejón rain forest persisted through the abrupt warmth of the Paleocene–Eocene Thermal Maximum (PETM) (approximately 53 Ma)—the warmest time of the Cenozoic—in which temperatures increased by approximately 5°C over a remarkably brief 20-thousand-year period. Although some pollen types disappeared at the PETM, some new pollen taxa appeared during this rapid warming period, maintaining diversity (Jaramillo et al. 2010). Although Jaramillo et al. (2010) suggested that warming may have caused evolutionary change manifested in the pollen turnover, this macroevolutionary scenario is unlikely because 20 thousand years seems too brief for the evolution of genera and families of plants with novel pollen morphologies. An alternative hypothesis is that the PETM warming facilitated biome displacement and mixing that maintained local tree diversity.

4. GLOBAL CONNECTIONS

Floristic connections between the tropical regions have long been recognized (Givnish & Renner 2004). A recent phylogenetic classification of the world's tropical forests (Slik et al. 2018) showed a close relationship between the lowland tree floras of Africa and the Neotropics and between the
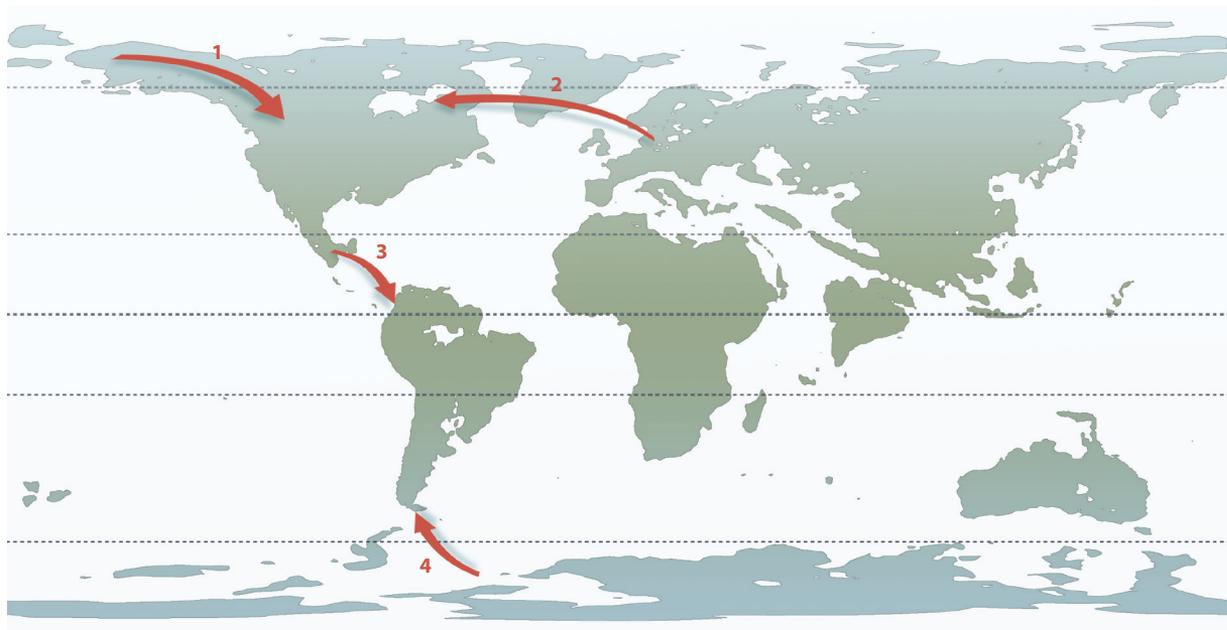
Figure 2

Eocene land surface map (50 Ma) showing the locations of intercontinental migration corridors: (1) Beringia, (2) North Atlantic Land Bridge, (3) Antillean Land Bridge (also known as GAARlandia), and (4) Magellan Land Bridge. Map adapted from Scotese (2001).

montane tree communities of the Neotropics and of tropical Asia. These floristic patterns can be partly explained by the five intercontinental dispersal routes described below (Graham 2018) in addition to continental drift and long-distance dispersal (LDD).

4.1. Boreotropical Dispersal

High-latitude (Laurasian) migration is an important and widely cited explanation for pantropical tree disjunctions (Davis et al. 2002, Lavin & Luckow 1993). The two northern land bridges are Beringia and the North Atlantic Land Bridge (NALB) (Wolfe 1975) (**Figure 2**; **Table 1**). Because NALB was 10° lower in latitude than Beringia during the Paleocene and contained a

Table 1   Putative land bridges available for intercontinental dispersal of plants into the Neotropics

Migration route	Summary description
North Atlantic Land Bridge (NALB)	Continuous land between Europe and North America until approximately 59 Ma. Migration of subtropical and warm temperate taxa until early Eocene (>65 to ∼47 Ma).
Beringian Land Bridge (BLB)	Possible land bridge during warm–temperate Paleogene, though primarily of temperate deciduous taxa. BLB developed throughout the Tertiary.
Antillean Land Bridge (ALB) (also known as GAARlandia)	An archipelago for stepping-stone dispersal since the latest Eocene, but no strong evidence of a continuous land bridge has been found.
Magellan Land Bridge (MLB)	Possible land bridge for dispersal of Austrotropical elements during the Paleogene.
Isthmus of Panama	The conventional first emergence of the Isthmus of Panama is at 3.5 Ma, but some geological and biogeographic evidence suggests mid-Miocene connections.

Descriptions and timelines mainly follow Graham (2018).

more thermophilic flora, it is considered more likely to have facilitated tropical biotic interchange between Eurasia and North America (Graham 2018) (**Table 1**).

Laurasian taxa dispersing between Eurasia and North America could have reached South America before the closure of the Isthmus of Panama (see below) by LDD or though stepping-stone dispersal across the Antillean islands. However, a continuous land bridge spanning the Greater Antillean and Aves Ridge (GAARlandia) (Iturralde-Vinent & MacPhee 1999) at approximately 35–33 Ma is not supported by geological evidence (Graham 2018).

Lavin & Luckow (1993) proposed a phylogenetic test of the Boreotropical dispersal hypothesis for Neotropical plants in which (*a*) the Neotropical lineage must be nested within a tropical Asian or African clade, and (*b*) high-latitude North American fossils must be found. Several tropical tree clades meet these criteria, including the families Melastomataceae, Burseraceae, and Meliaceae, and some clades of Lauraceae, Chrysobalanaceae, and Annonaceae (see **Table 2** for references). Malpighiaceae, however, probably originated in South America and spread to the Paleotropics via the Boreotropical NALB (Davis et al. 2002).

Many questions about these high-latitude dispersal routes remain unanswered, some of which pertain to the nature of the Boreotropical flora itself. Although some authors have described the Boreotropical flora as tropical or megathermal (e.g., Johnson & Ellis 2002, Morley 2000), the seasonality of daylength and temperature made it a nonanalog climate and biome. Paleogene floras along the NALB are in fact dominated by temperate angiosperms (e.g., Fagaceae, *Acer*, Betulaceae) and conifers (*Abies*, *Larix*, *Picea*, *Pinus*, and *Thuja*) (Graham 2018, Wolfe 1975). Graham (2018) suggested that trees in this biome had not yet evolved the distinctive tropical and temperate forms that exist today. Indeed, important tropical tree families have lineages adapted to cold and seasonal environments. Examples in northern temperate forests include *Asimina* (Annonaceae), *Cephalanthus* (Rubiaceae), *Zanthoxylum* (Rutaceae), *Sassafras* and *Lindera* (Lauraceae), and *Catalpa* (Bignoniaceae). Possibly similar to the Boreotropical flora, Mexican cloud forests contain a mixture of tropical and temperate taxa such as palms, hickories (*Carya*), and maples (*Acer*) (Wendt 1993). Putative Boreotropical lineages (e.g., Melastomataceae, Lauraceae) are common elements of tropical montane forests.

When the Boreotropical biome was most extensive (early to mid-Eocene), the NALB had already broken up and was more of a stepping stone than a land bridge for thermophilic trees (**Figure 1**). Given the pervasiveness of oceanic dispersal (see Section 4.4), it is likely that some thermophilic lineages migrated to North America via oceanic currents rather than across either boreal land bridge.

4.2. Austrotropical Dispersal

During the Paleogene, Antarctica was partly forested and contained a mixture of temperate and tropical plant lineages, which Graham (2018) has described as Austrotropical. The Magellan Land Bridge (MLB), which connected South America and Australasia via Antarctica, lasted up to the Oligocene (approximately 37 Ma) (**Figure 2**). Southern Hemisphere taxa associated with the MLB include Cunoniaceae, Proteaceae, Myrtaceae, and some groups of Lauraceae; the conifers Podocarpaceae and Araucariaceae; and tree ferns (e.g., Cyatheaceae) (de la Estrella et al. 2018, Rezende et al. 2017). Relatively few Southern Hemisphere migrants have become important in the lowland Neotropical flora (Wilf et al. 2013), although *Weinmannia* (Cunoniaceae), *Podocarpus*, and tree ferns are important taxa in Andean montane forests.

4.3. The Great American Biotic Interchange

During the >90 million years following its separation from Africa, South America was considered to have developed an endemic biota in relative isolation from other continents (Gentry 1982,

Raven & Axelrod 1974). Mexico and the islands that were to form Central America contained relatively little forest, and by the late Cenozoic, they were a refuge for the Boreotropical flora (Wendt 1993). The Isthmus of Panama (**Table 1**) was the first continuous land bridge of the Cenozoic connecting North and South America, and its completion gave rise to the Great American Biotic Interchange (GABI).

In an influential article, Gentry (1982) noted that Central American rain forests are dominated by widespread tree species with probable South American (Amazon basin) origins. He inferred substantial migration from South America into Central America but little in the opposite direction except, possibly, for montane floras. Because of this asymmetry, Gentry regarded the present-day Amazon flora as Gondwanan, as described above, with little influence of migration from other tropical continents.

Recent geological advances have challenged conventional views on the age of the Isthmus of Panama and of GABI and suggest an older, mid- to late Miocene land bridge (Montes et al. 2015; but see O'Dea et al. 2016 and responses). In line with the new geological hypothesis, Bacon et al. (2015) inferred a spike of plant migration events across the Isthmus of Panama during the mid- to late Miocene. The Bacon et al. (2015) study used the divergence times of widespread species and clades as a proxy for the timing of their migration between the continents. However, the origins and divergences for many of their clades may be explained by other events. For example, Bardon et al. (2013) attributed the origin of Neotropical Chrysobalanaceae to oceanic dispersal from Asia. Furthermore, the Bacon et al. (2015) study did not consider stem lineage ages (the time of earliest possible migration), meaning that earlier dates of migration are feasible. Thus for plants, an earlier land bridge might have had little relevance because any disjunctions between Central and South America can be explained by LDD (Cody et al. 2010), as discussed in the next section.

4.4. Long-Distance Dispersal

One of the most intriguing advances in the field of biogeography over the past two decades is an increasing acceptance of LDD as an explanation for intercontinental tropical disjunctions. Transoceanic LDD—hypothesized to be generally achieved via marine currents—is an alternative explanation to vicariance and land bridge hypotheses (Givnish & Renner 2004, Renner 2004).

An example of LDD is provided by the rain forest tree *Symphonia globulifera*, which is broadly distributed in the Neotropics and in tropical Africa. *S. globulifera* has a distinct pollen type with earliest records from the Eocene (approximately 54 Ma) of West Africa. *S. globulifera* pollen appears abruptly approximately 30 million years later in the mid-Miocene (approximately 15 Ma) in offshore sediments of eastern Brazil and Venezuela (reviewed in Dick et al. 2003), at which time South America was an island continent. The species has no apparent adaptations to water dispersal, and its seed desiccates in salt water. A possible dispersal scenario for *S. globulifera* involves rafting of living branches or trunks within the flotsam dislodged by major rivers. Successful raft-dispersal events are rare, but integrated over the span of millions of years such improbable events do occur. This mode of dispersal, also called sweepstakes or waif dispersal, is the most likely explanation for the migration of caviomorph rodents, primates, lizards, and other nonswimming vertebrates to the New World (discussed in Renner 2004)

Higher-level phylogenetic studies of tropical trees have similarly concluded that marine dispersal has played a central role in pantropical distributions (e.g., **Table 2**). It is thought that LDD often acts in concert with conserved ecological niches, meaning that lineages tend to occupy similar environments on different continents (Crisp et al. 2009).

Table 2 Important immigrant clades in the Yasuní Forest inventory plot

Migrant clade	Reference(s)	Number of migrant genera and species in the plot	Migration hypotheses
Fabaceae	Schrire et al. 2005	37, 114	Late Cretaceous origin in Madrean–Tethyan biome, implying Boreotropical and oceanic dispersal to SA.
Lauraceae	Chanderbali et al. 2001, Huang et al. 2016	12, 75	Boreotropical origin of *Cinnamomum/Persea* groups. Early Miocene long-distance dispersal of species-rich *Ocotea* (18 spp. in plot)
Melastomataceae	Renner et al. 2001	10, 63	Boreotropical origin. Oligocene marine dispersal into South America.
Sapotaceae	Rose et al. 2018	7, 53	Indo-Malaysian origin of stem (∼102 Ma) and crown (∼58 Ma) clades with some Boreotropical fossils.
Annonaceae	Couvreur et al. 2011b	13, 39	Boreotropical and marine dispersals from NA and Africa to SA. Ages of two main clades: ∼65.5 Ma (Long Branch Clade) and ∼32.8 Ma (Short Branch Clade).
Meliaceae	Koenen et al. 2015	5, 37	Crown origin ∼59 Ma in OW, possibly of deciduous and tropical montane ancestors. Marine dispersal to Neotropics.
Arecaceae	Baker & Couvreur 2013	15, 23	Early divergence in Laurasia (∼100 Ma) with four dispersals to SA from NA (∼80 Ma and ∼40 Ma) and Africa (∼65 Ma).
Chrysobalanaceae	Bardon et al. 2013	4, 21	Single (marine) dispersal from Paleotropics ∼28 Ma for Neotropical clade.
Burseraceae	Weeks et al. 2005	5, 18	Paleocene NA origin (stem ∼60 Ma).
Lecythidoideae	Rose et al. 2018	5, 13	Neotropical stem clade (∼59 Ma) and crown clade (∼43 Ma) with sister clades in OW.

Abbreviations: NA, North America; OW, Old World; SA, South America.

4.5. Immigrant Lineages in the Yasuní Forest—A Case Study

Pennington & Dick (2004) quantified the so-called immigrant lineages to the 50-hectare Amazon Yasuní forest dynamics plot in Ecuador (Valencia et al. 2004), where immigrants were defined as species belonging to clades that arrived from outside of South America when it was still isolated in the Cenozoic. Along with known migrants such as *S. globulifera* and species from conventionally accepted temperate clades (Cannabaceae, Rhamnaceae, Rosaceae, Magnoliaceae, Styracaceae), the migrant group included clades that were previously considered likely Gondwanan (Raven & Axelrod 1974): Fabaceae, Melastomataceae, and some genera of Lauraceae and Annonaceae. The authors estimated that 21% of the Yasuní tree species, and a similar percentage of total stem numbers in the forest plot, belonged to these immigrant clades.

Recent work has revealed additional immigrant clades. In **Table 2**, we present a revised list of the most diverse immigrant lineages and their contribution to the genus- and species-level taxonomic diversity of the Yasuní plot. The newly recognized immigrant clades include additional genera of Annonaceae (Couvreur et al. 2011b) and Lauraceae (Huang et al. 2016); the families Lecythidaceae and Sapotaceae (Rose et al. 2018), Burseraceae (Weeks et al. 2005), Meliaceae (Koenen et al. 2015, Muellner et al. 2006), Arecaceae (Baker & Couvreur 2013), Chrysobalanaceae

(Bardon et al. 2013), Staphyleaceae (Harris et al. 2017), and Urticaceae (Wu et al. 2018); and the genera *Zanthoxylum* (Rutaceae) (Appelhans et al. 2018) and *Ardisia* and *Cybianthus* (Primulaceae) (Rose et al. 2018). Including the temperate immigrants mentioned previously, nearly half (547 of the 1,140) of the known tree species of Yasuní descend from immigrant lineages.

These results contrast with Gentry's (1982) view that the contribution of Laurasian (i.e., immigrant) taxa to South American rain forest was "virtually none" (p. 577). The immigrant families in **Table 2** include four of the five most common families across the Amazon basin (Fabaceae, Sapotaceae, Lecythidaceae, Burseraceae) and the nine most common genera (ter Steege et al. 2006). These immigrant families contribute disproportionately to the stem numbers, species diversity, and biomass of Amazon forests. Most of these clades were present in South America long before GABI, suggesting an initial origin through oceanic dispersal.

These biogeographic histories should be considered hypotheses, and they may be refuted in future studies. For example, Antonelli et al. (2009) posited a North American origin of the Rubiaceae, which was in conflict with Manns et al. (2012), whose analyses support a South American origin. Zerega et al. (2005) proposed a possible immigration history of Neotropical Moraceae but suggested that this hypothesis needed further testing.

4.6. Biogeographic Influences on Community Assembly

Evidence has been found that GABI—and biogeographic interchange more generally—has increased the functional trait and species diversity of trees in South and Central American forests. Sedio and colleagues (2012, 2013) found that 22 species of *Psychotria* on Barro Colorado Island (BCI), Panama, (**Figure 3**) were derived from two clades: a drought-tolerant clade that originated in South America and likely arrived in Panama via GABI and a more mesic clade from Central America (Sedio et al. 2013). On BCI, the genus shows community phylogenetic clustering, whereas the South American and Central American clades segregate along moisture gradients within the forest (Sedio et al. 2012).
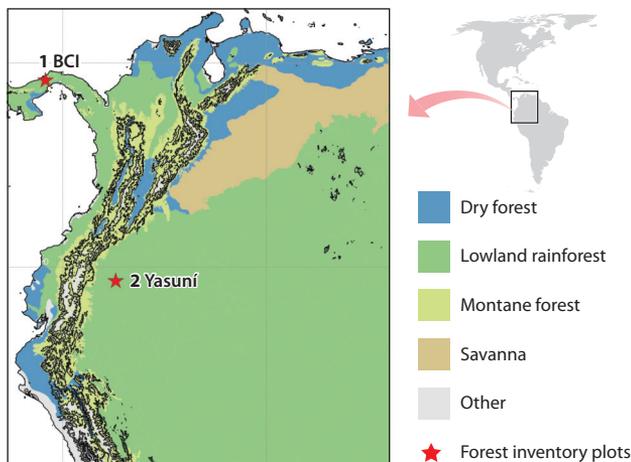

Figure 3

Detail of **Figure 1** showing northwestern South America. Ecological dispersal barriers that impede biotic interchange for lowland rainforest (*green*) east and west of the Andes include montane forest (*light green*), savannas (*brown*), and dry forest (*blue*). Forest inventory plots mentioned in text: (1) Barro Colorado Island (BCI), Panama, and (2) Yasuní forest dynamics plot.

That drought-tolerant trees migrated from Amazonia may seem counterintuitive, as Amazon forests tend to be wetter than the more seasonal forests of lower Central America. This may be partially explained by the fact that migrating Amazon trees had to pass through ecological barriers including the high-elevation Andes—which at present do not have passes lower than approximately 2,000 m—and the arid Colombian and Venezuelan savannas and dry forests (**Figure 3**). If the high Andes were an effective barrier, only species able to tolerate drought may have successfully migrated through these drier areas north of the cordillera (Coronado et al. 2014).

To understand community-level effects of biogeographic filtering, Bemmels et al. (2018) performed a trait-based analysis of >1,000 woody plant species (trees, shrubs, and lianas) with occurrences in Yasuní Ecuador and/or BCI Panama—representing east- and/or west-of-Andes species and populations. The authors found that a widespread (i.e., east- and west-of-Andes) geographic distribution was correlated with population abundance—possibly providing more opportunities for dispersal under a neutral model (Hubbell 2001)—and with environmental tolerance, as reflected in their occurrence in dry habitats and at high elevations. Their study suggested that dispersal combined with trait filtering channeled Neotropical tree migration, with implications for the phylogeography of widespread rain forest species (Coronado et al. 2014, Dick et al. 2013), regional species pools, and trait diversity. For example, Bemmels et al. (2018) suggested that Central American rain forests contain more ecological generalists than Amazon forests, as initially proposed by Gentry (1982). Remarkably, 70% of the woody species studied by Bemmels et al. (2018) have widespread Neotropical distributions, and ≥25% occurred at least occasionally in dry ecoregions, including savannas. Future efforts focused on determining the geographic origins of these widespread species may further test Gentry's hypothesis.

LDD has implications for Hubbell's (2001) neutral theory. The spread of rain forest tree species from single, or a few, propagules is analogous to the point-mutation speciation model of neutral theory, which also predicts the rate of spread of new species by stochastic dispersal. Using neutral theory assumptions, Leigh (2007) estimated that the probability of *S. globulifera* spreading through the Amazon—even over 20 million years—was virtually zero. Leigh obtained similar probabilities for higher-level clades (e.g., *Ocotea* in the Lauraceae) that appeared in the Amazon basin during the Neogene. The widespread distribution of dominant tree species in Amazonia (ter Steege et al. 2013) adds to the evidence that neutral theory does not apply to a large proportion of Neotropical tree diversity. This may be because these species are not competitively neutral or because the disturbance history of the rain forest has enabled immigrants to spread faster than predicted by neutral theory (Pennington & Lavin 2016).

5. PATTERNS AND DRIVERS OF REGIONAL DIVERSIFICATION

Two approaches have been used to understand the relative roles of dispersal and regional diversification in the assembly of Neotropical tree communities—phylogenetic studies of individual clades and community phylogenetics.

In an example of the first approach, Lavin et al. (2004) used a phylogenetic analysis of woody legume clades to reconstruct biogeographic assembly within the succulent-dominated dry biome of the Antilles, the mainland Neotropics, and Africa. Genus-level disjunctions were attributed to transoceanic sweepstakes dispersal. However, rates of immigration are low, as evidenced by geographically structured phylogenies and clade endemism. Further studies of clades endemic to such tropical dry forests in the New World show similar patterns of geographic phylogenetic structure (reviewed in Hughes et al. 2013, Pennington et al. 2009), and a general pattern emerges that successful immigration may be more frequent in rain forests than it is in dry forests (Pennington & Lavin 2016).

Using a community phylogenetic approach, Coronado et al. (2015) found that tree species of seasonally dry forest communities are more strongly phylogenetically clustered than those found in rain forest and savanna communities. Strong adaptive barriers may keep migrants from becoming established in this biome—potentially because of its erratic rainfall or distinctive edaphic conditions.

Dexter et al. (2017) bridged both approaches by examining phylogenies of Amazon forest trees in *Inga*, the tribe Protieae (Burseraceae), *Swartzia* (Fabaceae), and *Guatteria* (Annonaceae) and by using community phylogenetic metrics to evaluate the structure of local communities of each clade. Their study shows that tree communities within the Amazon basin have a random phylogenetic structure and are assembled by widespread dispersal.

6. ANDEAN–AMAZON DIVERSIFICATION AND VICARIANCE

An increase in tectonic activity during the Neogene (Miocene + Pliocene) generated the modern Andean–Amazon landscape (Hoorn & Wesselingh 2011). Fully half of South American plant species occur in montane and slope habitats of the Andes (45,000 species, 44% of which are endemic; Gentry 1982, Myers et al. 2000), even though these environments are young and cover a sliver of area compared with the vast lowlands of Amazonia. Alpine habitats provided opportunities for stepping-stone migration by temperate plants and bursts of diversification (Hughes & Eastwood 2006, Luebert & Wiegend 2014). Canopy and understory trees speciated in the slope forests (Gentry 1982), in some cases facilitated by adaptations to hummingbird and large bee pollinators at mid-elevations (Gentry 1982, Lagomarsino et al. 2016).

The Andes may have also played an important role in rain forest vicariance. In Ecuador, 30% of lowland vascular plant species are distributed east and west of the Andes (Jørgensen & León-Yánez 1999), which Peter Raven (in Jørgensen & León-Yánez 1999) attributed to vicariance by the uplifting Andes. This fascinating hypothesis implies that Amazon forests have maintained species and ecological associations since approximately 5–10 Ma, when the rising northern Andes would have become too high (greater than ~2,500 m) for lowland rain forest plants. The alternative explanation is recent or more ancient cross-Andean dispersal. Presently the high elevations of the northern Andes and aridity of the Venezuelan llanos form migration barriers for rain forest trees (**Figure 3**).

On the basis of molecular divergence time estimates of east- and west-of-Andes populations of 12 rain forest species, Dick et al. (2013) found that 9 species (including *S. globulifera*) showed genetic divergences consistent with Neogene vicariance or ancient dispersal. Interestingly, species with phylogeographic structure indicative of recent dispersal (e.g., *Ceiba pentandra*, Dick et al. 2007) are ecological generalists that occur in both rain forests and seasonally dry forests. Species able to tolerate drought may be better able to migrate through seasonally dry areas to the north of the Andes (Bemmels et al. 2018, Coronado et al. 2014; see Section 4.6) and in the lowest area of the Andean cordillera, the Huancabamba Depression in northern Peru and southern Ecuador (Quintana et al. 2017).

7. DIVERSIFICATION PROCESSES WITHIN AND AMONG BIOMES

The concept of adaptive radiation has been influenced heavily by studies of islands, where it is often associated with ecological opportunity and niche shifts. However, on and between continents, some authors have suggested that plants generally track similar major habitats or biomes even after LDD and through diversification, which is the concept of phylogenetic niche conservatism (Crisp et al. 2009). When niches are conserved, allopatry provides the simplest explanation for speciation. Niche evolution, however, can be inferred when congeneric species are adapted to

distinct biome types. For example, 72 of the 90 dominant woody genera of Brazilian Cerrado savannas also have species in rain forests (Pennington et al. 2006). Simon et al. (2009) showed that four woody clades endemic to the Brazilian Cerrado were assembled by evolutionary transitions from surrounding biomes, implying parallel adaptations to frequent fires in the Cerrado savannas (e.g., corky bark, ability to root sprout).

More recently, Antonelli et al. (2018), on the basis of a meta-analysis of Neotropical angiosperm, fern, and vertebrate phylogenies, have shown that a much higher proportion (47%) of successful long-distance colonization events involved a shift in major biome (e.g., wet to dry) than those involving no biome shift (7%), contradicting the largely Southern Hemisphere and intercontinental study of Crisp et al. (2009). However, 46% of the colonization events in the Antonelli et al. (2018) study were ambiguous as to whether a biome shift was involved, so niche conservatism could still characterize most successful angiosperm colonization events over evolutionary timescales.

Speciation involving major niche shifts between biomes is one process of ecological speciation, and other workers have made progress on studying both abiotic and biotic niche shifts within biomes, particularly within the Amazon rain forest. Some of the edaphic heterogeneity in the Amazon basin, such as islands of white-sand vegetation (Adeney et al. 2016), has been involved in speciation in trees of the Burseraceae family (Fine et al. 2005), as inferred by sister species occurring on different soil types and by evidence for strong selective pressure by insect herbivores in different edaphic environments (Fine et al. 2004). Divergence in defenses against insect herbivores has also been implicated in diversification in the species-rich legume genus *Inga* (Kursar et al. 2009), for which closely related species differ markedly in their defense traits and co-occurring species in a community are more divergent in defense traits than would be expected by chance, suggesting strong local selection by specialized herbivores.

In the cases of both *Inga* and Burseraceae species, it is not clear whether ecological selection pressure has initiated speciation—the initial impetus may be allopatry resulting from dispersal. The biogeography of both groups is heavily influenced by dispersal (Dexter et al. 2017; see Section 5), with local communities of each comprising unrelated species such that their phylogenetic structure does not differ from random. It is possible that effective dispersal in both groups may initiate speciation by isolating peripheral populations—a peripatric speciation process (Dexter et al. 2017, Pennington & Lavin 2016)—with subsequent strong selective pressures speeding the process of population divergence and leading to eventual speciation.

8. PALEOCLIMATES: BEYOND REFUGIA

The PRT posited that reduced precipitation during glacial periods created a rain forest/savanna matrix across Amazonia, which promoted allopatric speciation of rain forest organisms (Haffer 1969)—even acting as a speciation pump over numerous glacial and interglacial cycles. The theory was so broadly accepted by botanists and zoologists alike that prominent Amazon conservation efforts in the 1980s focused on putative Pleistocene refuges as areas most likely to have large numbers of endemic species.

The PRT endures as one of the most influential ideas of Amazon biogeography. However, many of its underlying assumptions have been challenged or discarded. For example, the extensive fragmentation of rain forest by savanna during the last glacial maximum (LGM) is not supported by palynological data from one western Amazon lake (Colinvaux et al. 1996) or from the oceanic sediments near the mouth of the Amazon (Haberle 1999), which do not document increased grass pollen. Some predicted and observed areas of endemism used as evidence for the location of LGM refuges were artefacts of higher botanical collection intensity near cities and

major herbaria (Nelson et al. 1990). A recent review (Fiaschi & Pirani 2009) found no evidence of areas of plant endemism in the Brazilian Amazon as predicted by the refuge model.

Despite these challenges, elements of the PRT persist and merit continued research. Glacial/interglacial cycles did impact tropical climates—for example, average tropical surface air temperatures were approximately 5°C cooler than present. It is unclear how precipitation was distributed during the LGM, however, or the vegetation's response to it—particularly in Amazonia.

Some evidence suggests that species composition of Amazon rain forests changed during the LGM. Pollen cores from the western Amazon (Colinvaux et al. 1996), for example, show an increase in *Podocarpus*, a gymnosperm more commonly found along Andean slopes. Furthermore, important clades of rain forest trees did speciate rapidly during the Pleistocene, including *Inga* (Richardson et al. 2001), *Trichilia*, and *Guarea* (Koenen et al. 2015). However, *Inga* species do not show the spatial patterns of clade endemism (Dexter et al. 2017) expected under the specific refuge model, and whether climate change was the driver for speciation in any of these groups is not clear.

A possible game changer in the interpretation of Quaternary paleoclimates comes from isotopic data in stalagmites (speleothems) collected from Brazilian caves (Cheng et al. 2013, Cruz et al. 2005). These isotope data show fluctuations in precipitation on 20-thousand-year cycles roughly matching the periodicity of Earth's precessional cycle. The data largely reflect dynamics of the Andean low-level jet, an air current that picks up moisture in the Atlantic and carries it across Amazonia, dropping precipitation in its return path along the Andean slopes and toward southeast Brazil. Levels of precipitation are partly controlled by the intensity of summer solar radiation over the Atlantic—hence, the role of the precession. Unlike glacial–interglacial cycles, which extend only through the Quaternary, these orbital cycles are constant throughout the Cenozoic.

Precession-forced rains caused the western Amazon and Brazil's southern Atlantic forests to be as wet or wetter during the LGM than today, while the eastern Amazon and northern Atlantic forest would have been drier (Cheng et al. 2013). This pattern of spatially heterogenous precipitation provides a different interpretation of the Colinvaux et al. (1996) finding of continuous forest cover in the western Amazon through the LGM, which the authors generalized to the broader Amazon basin. A prediction of such coupled spatial patterns of rainfall is that past biogeographic connections should occur through what is now a dry corridor separating the eastern Amazon/northern Atlantic forest, on the one hand, and the western Amazon and southern Atlantic forest, on the other hand (Prates et al. 2016). A phylogeographic study of lizards provides some evidence of these historical connections (Prates et al. 2016), but this history has not yet been tested with respect to rain forest trees.

When modeling paleoclimatic impacts on vegetation, it is critical to consider edaphic conditions. For example, savannas occur on low pH, nutrient-poor soils, and seasonally dry forests develop on higher pH, and more nutrient-rich, soils. The lack of widespread expanses of richer, high-pH soils in Amazonia, and across the Neotropics in general, may explain why suggestions of much more widespread seasonally dry forests in Pleistocene glacial periods (Prado & Gibbs 1993) have not been corroborated in all areas. Pennington et al. (2000) suggested that fragmentation of these dry forests during wet interglacial periods might have driven speciation; however, dated phylogenies show pre-Pleistocene diversification (e.g., Särkinen et al. 2012), and the low floristic similarity among disjunct areas of dry forest and the high levels of plant species endemism in each area are suggestive of long isolation.

The vanishing refuge model (VRM) (Damasceno et al. 2014, Vanzolini & Williams 1981) invokes not only geographic isolation of populations (as in standard PRT) but also ecological divergence in refuge areas where, for example, forest is gradually replaced by savannas—hence the term "vanishing refuge." The VRM was originally proposed to avoid an assumption of parapatric

speciation models that postulate divergence of populations in the face of gene flow, which at that time was thought to be unlikely. In an excellent article that tests the VRM for lizard species first studied by Vanzolini & Williams (1981), Damasceno et al. (2014) outlined a series of predictions and tests for the VRM, which include paleo-habitat modeling and genetic tests for divergence in the absence of gene flow. Such genetic tests, which are needed to exclude the possibility of parapatric divergence, require hundreds of genetic loci, and such depth of data is now feasible using next-generation sequencing. We are, however, unaware of any studies in Neotropical plants that test the VRM, but it is a plausible model to explain the existence of sister species that have parapatric distributions in different habitats, for example, in the rain forests of Amazonia and the Cerrado savannas of central Brazil. Such studies should be a priority for future research.

9. PRE-COLUMBIAN HUMAN LEGACIES (UP TO 1491 AD)

Deforestation and remote sensing in the southwestern Amazon have uncovered extensive geoglyphs established for ceremonies, indicating the existence of sophisticated societies and anthropogenic landscapes in pre-Columbian times (Watling et al. 2017). The degree to which pre-Columbian people shaped modern forest composition is an active area of research (Clement et al. 2015, Levis et al. 2017). One question relates to the impact of pre-Columbian people on the distribution and relative abundances of tree species.

Paleobotanical evidence suggests that pre-Columbian people expanded the geographic ranges of some important species either directly by planting or indirectly by altering ecological conditions (e.g., by burning vegetation). For example, the palm species *Mauritia flexuosa* first appears in the Venezuelan Gran Sabana in association with anthropogenic charcoal (Rull & Montoya 2014). By eliminating megafauna, humans removed agents of seed dispersal of large-seeded tree species, thought to include cultivated trees such as the Brazil nut (*Bertholletia excelsa*) and edible palms (e.g., *M. flexuosa*) (Doughty et al. 2016).

Ross (2011) found higher local abundances of useful tree species near densely used Mayan sites than in less densely used sites—more than 1,000 years since the Mayans had abandoned them. This suggests a remarkable millennial-scale persistence of abandoned forest gardens. Levis et al. (2017) examined the abundance of tree species used by people within a network of >1,100 Amazon forest inventory plots and found that forests near archeological sites were more enriched with species used by people compared with plots farther away from archeological sites. In the Levis et al. (2017) study, 20 of the 77 useful species (out of 4,962 species total) were members of an ecologically dominant group of 227 tree species that account for approximately 50% of stems in networks of Amazon plots (ter Steege et al. 2013). The 5 edible palm species ranked in the top 10 of most abundant tree species, with highest abundances near archeological sites. Levis et al. (2017) suggested that native peoples shaped forest structure across the entirety of the Amazon basin—an idea with popular appeal reminiscent of the PRT during the 1990s.

In spite of this appeal, the pre-Columbian domesticated Amazon hypothesis requires careful examination. First, it is difficult to disentangle recent and prehistoric influences. For example, the most abundant non-palm tree in the Levis et al. (2017) study is the rubber-producing tree *Hevea brasiliensis*, which was not especially useful for preindustrial peoples but became economically important in the mid-nineteenth century. Second, the Amazon forest plots are spatially correlated with archeological sites (McMichael et al. 2017b), which also overlap with high modern human densities (McMichael et al. 2017a). Third, definitions for what constitutes useful or cultivated species are vague. Nearly every woody plant may have some use, but only 14 Amazon tree species show evidence of artificial selection by humans (Clement 1999). Finally, many of the most important cultivated or used species are short-lived. Detailed demographic studies may reveal whether

or not it is realistic to conclude that enriched species would persist in high abundance over the hundreds of years since European colonization.

A key approach to address some of these issues would be to expand forest plot networks to cover representative habitat types and areas remote from modern people and archeological sites. This would require greater dialogue and collaboration between biologists and archeologists (Clement et al. 2015). In addition, detailed phylogeographic and population genetic studies of widespread species would be powerful tools for testing whether widespread distributions predated human influences.

10. A GLIMPSE INTO THE ANTHROPOCENE

Species-rich Neotropical forests have persisted over virtually the entirety of the Cenozoic, starting not long after the K/Pg extinction event, and through periods of abrupt warmth and more gradual climate change. How will Neotropical tree diversity fare in the Anthropocene?

Increased atmospheric CO_2 and warmth are linked to extreme climatic events—droughts, floods, winds—creating more disturbance generally. A recent study showed that drought-tolerant species have increased in abundance across the Amazon basin over the past 30 years (Esquivel-Muelbert et al. 2019). These drought-tolerant species, like the Amazon clade of *Psychotria* in Panama (Sedio et al. 2013; see Section 4.6), may have biogeographic origins in drier parts of the Amazon. Biogeographic mixing across regions with different soils and climates may be necessary to maintain species-rich forests under climate change, but given extensive habitat destruction by humans, this may not be possible.

Neotropical montane forests are especially vulnerable to the combined impacts of warming and habitat change. Andean tree species are already showing evidence of narrowed elevational ranges in response to anthropogenic warming (Fadrique et al. 2018), reflecting increased mortality at the lower elevations in which these species occur. The mortality may be caused by pest pressure, drought sensitivity, or other biotic and/or abiotic factors. Understanding these causes is essential to designing conservation programs.

In addition to its effects on climate, increased atmospheric CO_2 directly affects plants by altering photosynthetic efficiency. Rising atmospheric CO_2 is hypothesized to favor growth of woody plants that photosynthesize using the C3 pathway over grasses that photosynthesize using the C4 pathway (Bond & Midgley 2012), suggesting that encroachment by trees should occur in savanna types by fertilizing their growth, enabling saplings to escape fires and reach maturity. Such woody encroachment has been observed across the globe, on the basis of both point observations on the ground (Stevens et al. 2017) and broad-scale remote sensing products (McNicol et al. 2018). This finding suggests that even in the absence of land use change, the balance of savanna and forest in the Neotropics will change in future.

11. DISCUSSION

We have highlighted research on the history of tree lineages that compose Neotropical forests, along with the history of the forests themselves, over a 100-million-year span. Important elements of this history include the diversification and dominance of angiosperms, and the development of environmental conditions favorable to tropical forests. Neotropical rain forests, in particular, have harbored species-rich tree communities beginning with their oldest Paleocene fossil records (Wing et al. 2009). Dispersal was likely important in the assembly of the earliest Neotropical rain forests, as recorded in the turnover of pollen at the PETM (Jaramillo et al. 2010), and dispersal has continued to enrich them, as exemplified by the analysis of the Yasuní Forest. Such biotic

interchange has impacted tree communities through biogeographic filtering and trait-based assembly over evolutionary timescales.

The Yasuní Forest also illuminates the debate about historical human influence on Neotropical forests. The Huaorani people live there and hunt monkeys and other seed-dispersing animals. The soils contain pottery shards 500–1,000 years old and charcoal from 7,700 years ago (Valencia et al. 2004). Although humans may have left their imprint on the ecology of Yasuní in unknown ways, the species and higher-level taxonomic diversity of its tree community were shaped over a period much older than the human species, and this is the case elsewhere in the Neotropics.

11.1. Museums and Cradles Revisited

The most abundant genus in the Yasuní plot is *Inga*, with 44 species. *Inga*'s history of explosive recent speciation epitomizes Stebbins's (1974) cradle model, with most of the 300 extant species of *Inga* having formed during the Quaternary. This history contrasts with that of *Symphonia*, which is older than the crown clade *Inga* but has just one recognized species on two continents. *S. globulifera* is an example of a depauperon (Donoghue & Sanderson 2015)—a lineage that has failed to diversify significantly or one in which extinction has left few species. Depauperons receive relatively less attention from ecologists and evolutionary biologists because of their low diversity. In cases like *S. globulifera*, however, they may have cryptic genetic divergence that can help to uncover biogeographic histories. Because of their phylogenetic isolation, depauperons are unlikely to share genes with other species through hybridization and introgression, but they may have important functional traits that allow them to endure environmental changes, including climate warming (Dick et al. 2013). They may become the successful lineages of the future as climates change in uncertain ways.

In the Yasuní Forest, the legume genus *Brownea* is an example of a museum lineage that has steadily accumulated diversity over the course of the Cenozoic (Schley et al. 2018). *Guarea* and *Trichilia*, however, are young and species-rich like *Inga* (Koenen et al. 2015). Although Stebbins (1974) developed the museum and cradle dichotomy, he recognized that biomes can have both kinds of clades, and clades themselves can be museums and cradles with periods of rapid speciation and steady diversification or decline (Eiserhardt et al. 2017).

11.2. Information in the Branch Tips

Our review has emphasized deep-time phylogenies with passing mention of population-level studies. In many cases, higher-level phylogenies lack adequate species sampling needed to fully understand causes of shifts in diversification rates and evolutionary biome switching, and in line with other authors (e.g., Eiserhardt et al. 2018, Hughes et al. 2013), we see great promise in working with fully sampled species phylogenies, ideally using hundreds of independent genomic loci. Some new techniques of DNA sequencing do not require high-molecular-weight DNA and broaden the possibility of achieving dense taxonomic sampling using herbarium specimens.

Opportunities to reconstruct more refined Neogene and Quaternary biogeographic histories are available using phylogeographic approaches, which can take advantage of the hundreds to thousands of widespread Neotropical tree species with Neogene histories (Dick et al. 2003, 2013). Most population-level studies have been restricted to relatively abundant tree species to facilitate sampling. Reduced representation genomic sequencing can provide robust estimates of within- and among-population genetic diversity from a few individuals (Nazareno et al. 2017a). This raises the possibility of studying rare species (i.e., most Amazon tree diversity) and more carefully examining the causal mechanisms of divergence at landscape scales. Population-level approaches

have been used to test Wallace's riverine barrier hypothesis (Nazareno et al. 2017b) and the PRT (Barthe et al. 2017). They could also be used to test hypotheses about the timing and symmetry of GABI (Bemmels et al. 2018, Gentry 1982). Combined with densely sampled phylogenies that can pinpoint ancestor-descendent species relationships (Pennington & Lavin 2016), we see a great opportunity to use these methods to study diversification across heterogeneous edaphic landscapes, which are being revealed in new detail through remote sensing (Asner et al. 2017).

11.3. Botanical Exploration

The Yasuní Forest case study also highlights the value of continued botanical exploration. Since the plot was established in the mid-1990s, 20 new tree species have been described (R. Valencia, personal communication), including a new genus of Lauraceae, aptly named *Yasunia*. Frequent discoveries highlight the urgency for taxonomic research, training, and further exploration. A new generation of systematists—preferably from Latin American countries—is needed to describe the hundreds of species that await discovery both in the field and in herbaria (Bebber et al. 2010). Unfortunately, legitimate concerns about sharing commercial benefits from biodiversity have influenced policy and made permission to collect scientific samples much more difficult to obtain in some biodiverse countries. Large-scale clearing of tropical forests for economic exploitation continues apace, and fieldwork has never been more urgently needed to collect herbarium specimens and tissue for genomic analyses, which will be essential to document tropical diversity and to understand its origin and evolution.

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