

The role of immigrants in the assembly of the South American rainforest tree flora

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The Amazon lowland rainforest flora is conventionally viewed as comprising lineages that evolved in biogeographic isolation after the split of west Gondwana (*ca.* 100 Myr ago). Recent molecular phylogenies, however, identify immigrant lineages that arrived in South America during its period of oceanic isolation (*ca.* 100–3 Myr ago). Long-distance sweepstakes dispersal across oceans played an important and possibly predominant role. Stepping-stone migration from Africa and North America through hypothesized Late Cretaceous and Tertiary island chains may have facilitated immigration. An analysis of inventory plot data suggests that immigrant lineages comprise *ca.* 20% of both the species and individuals of an Amazon tree community in Ecuador. This is more than an order of magnitude higher than previous estimates. We also present data on the community-level similarity between South American and palaeotropical rainforests, and suggest that most taxonomic similarity derives from trans-oceanic dispersal, rather than a shared Gondwanan history.

Keywords: Amazon rainforests; molecular systematics; biotic interchange; long-distance dispersal

1. INTRODUCTION

The neotropics is species rich, both at the local and landscape scale. It contains an estimated 90 000 plant species, more than any other continental area (Thomas 1999), and the rainforests of the Amazon basin have the world's highest alpha-diversity as measured by the number of species of trees in a single hectare (1 hectare (ha) = 10⁴ m²) (Valencia *et al.* 1994; Romoleroux *et al.* 1997; De Oliveira & Mori 1999). The prevailing biogeographic model views the lowland South American flora as a product of Gondwanan vicariance, and assumes that the contribution of subsequent immigrant lineages to South America is negligible (Raven & Axelrod 1974; Gentry 1982). This idea has recently been challenged through recognition of the importance of interplate dispersal routes for tropical plants (Morley 2003) and fossil calibration of molecular phylogenies of major rainforest taxa. Our principal aim is to examine the contribution to the contemporary Amazon tree flora of lineages that have arrived in South America since its split from Africa (*ca.* 100 Myr ago).

We first review the possible migration routes by which plants may have arrived in South America since its split from Africa. We then evaluate phylogenetic evidence indicating that some tree groups assumed to be indigenous to South America are in fact, immigrants from other continents. We examine two related ideas promoted by Alwyn Gentry. First, that the contribution of immigrant taxa to South American rainforest is negligible (Gentry 1982).

Second, that most floristic similarities between rainforests in Africa and the neotropics derive from Gondwana vicariance (Gentry 1993). Based upon evidence from molecular phylogenies, we analyse the contribution of 'immigrant taxa', in effect those that entered South America after its split from western Gondwana, to an Amazon rainforest tree community in Ecuador. Then we analyse the community level floristic similarities between two neotropical forest inventory plots (Yasuní, Ecuador, and the BCI, Panama) with a tropical forest plot in Cameroon, in light of the immigration models reviewed here.

(a) *Splendid isolation?*

The conventional model of South American biotic history stems from palaeontological studies of mammals, and is encapsulated in the evocative title of Gaylord Simpson's (1980) book about South American mammalian evolution, '*Splendid isolation*'. This model regards South America as a biogeographically isolated landmass after its split from Africa (*ca.* 100 Myr ago; Goldblatt 1993; Pitman *et al.* 1993) until the closure of the Isthmus of Panama (*ca.* 3 Myr ago; Coates & Obando 1996), and thus explains the evolution of many South American endemic mammal families. The island continent model is central to studies of plant biogeography and features in Raven & Axelrod's (1974) seminal paper on angiosperm biogeography: 'clearly, the history of South American biota has been one of evolution in isolation of an initial West Gondwanaland stock shared with Africa' (p. 549). Despite refinements of plate tectonic theory over the past 30 years, the model of *in situ* South American floristic evolution remains the prevailing view (e.g. Burnham & Graham 1999; Young *et al.* 2002).

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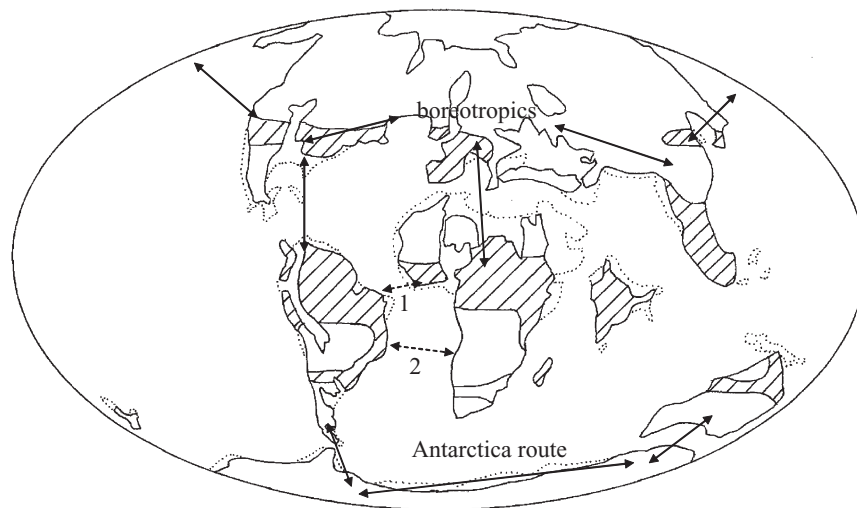


Figure 1. Early Tertiary, Early Eocene plate tectonic reconstruction and palaeogeography adapted, with permission, from Morley (2003, fig. 5), indicating closed canopy rainforests (cross hatched). Dotted lines approximate present-day coastlines. Dotted arrows indicate the approximate position of the Sierra Leone (1) and Walvis (2) ridges. Solid arrows indicate migration routes through and from the boreotropics and Antarctica.

Strictly speaking, the model is geologically accurate. By 85 Myr ago, it was estimated that an 800 km wide seaway isolated Africa and South America (Burnham & Graham 1999). At the same time, wide seas divided South and North America, a condition that had existed since the Early Jurassic (Burnham & Graham 1999). There is no firm geological evidence for any continuous land connections between South and North America until the closure of the Isthmus of Panama at 3 Myr ago. Biotically, however, the model of isolation may be too simplistic, as evidenced by several recent molecular phylogenetic studies of plants, which demonstrate arrivals in South America from the Late Cretaceous and through the Tertiary (e.g. Chanderbali *et al.* 2001; Renner *et al.* 2001). In many cases, the plant immigrants have become important elements of the neotropical flora, both in terms of species richness and ecological dominance.

Oceanic dispersal must be implicated in all cases of migration to South America during its long period of isolation. However, it is not necessary to invoke long-distance marine dispersal in every case. Although there is no unequivocal evidence for continuous land connections among the continents after their initial separations, it has been hypothesized that migration was possible through stepping stone migration along island chains: (i) between Africa and South America until the Late Cretaceous through islands of the Walvis Ridge – Rio Grande Rise and Sierra Leone – Ceará Rises (Morley 2000, 2003; Morley & Dick 2003); (ii) from North America through islands of the proto-Antilles (Iturralde-Vinent & MacPhee 1999; Graham 2003) and along a Central American land bridge in the Late Miocene (Bermingham & Martin 1998); and (iii) along a southern route from Australia through Antarctica (Morley 2003).

2. LAND CONNECTIONS TO SOUTH AMERICA

(a) African – South American connections

Based upon the simultaneous appearance of novel pollen types in Africa and South America, Morley (2000, 2003) suggested that transatlantic dispersal was facilitated until

the Maastrichtian (*ca.* 76 Myr ago) by putative island chains of the Rio Grande Rise – Walvis Ridge and the Ceará – Sierra Leone Rises (figure 1). Among the pollen taxa appearing simultaneously on either side of the south Atlantic are ancestral Proteaceae and Palmae (Arecaceae), Sapindaceae and Myrtales (Morley 2003). Parrish (1993) reviewed evidence from the Deep Sea Drilling Programme that shows shallow water and aerial volcanic features in both the Walvis Ridge and Rio Grande Rises during the Eocene. This corroborates subsidence estimations by Theide (1977) suggesting that the Rio Grande Rise may have been above sea level until the Oligocene. Thus it seems plausible that island chains may have been more extensive before these areas had subsided. Morley (2000, 2003) suggested that these island chains might have facilitated plant dispersal most effectively when sea levels were relatively low, for example at the end of the Turonian (*ca.* 88 Myr ago; Haq *et al.* 1988; Marcellari 1988). However, recent results from the Ocean Drilling Program (Zachos *et al.* 2004) failed to find evidence for dry land in the Late Cretaceous and Early Tertiary sediments along Walvis Ridge.

(b) North American – South American connections

(i) Proto-Greater Antilles

Geological and tectonic models for the Caribbean have been contentious, but Graham (2003) and Morley (2003) indicate that consensus is developing around the tectonic model of Pindell *et al.* (1988) and Pindell & Barrett (1990). This model suggests that the proto-Greater Antilles originated in the Early Cretaceous in the eastern Pacific Ocean adjacent to North and South America, which were separating. The Caribbean plate moved through the portal between the continents, carrying the submerged proto-Greater Antilles (figure 2). These only became islands after the Caribbean plate collided with the Bahamas plate, with the principal time of emergence in the Middle Eocene, *ca.* 50 Myr ago (Iturralde-Vinent & MacPhee 1999). In the Middle to Late Eocene, the proto-Greater Antilles may have provided an island corridor between North and South

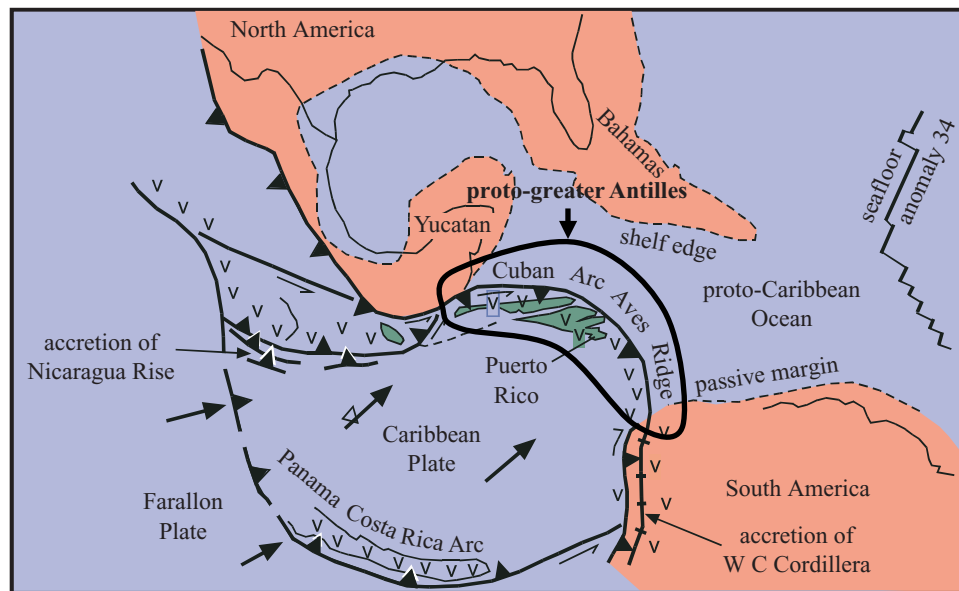


Figure 2. Campanian reconstruction of Middle America modified, with permission, from Morley (2003, fig. 6), highlighting the proto-Greater Antilles, which may have provided a filter-bridge in the Early Tertiary. Orange, thick continental crust; v symbols, volcanic arcs.

America. An arc of volcanic islands between North and South America may have provided a similar pathway somewhat earlier in the Late Cretaceous (Iturralde-Vinent & MacPhee 1999). Gentry (1982) suggested that some groups with strongly differentiated components in both tropical North and South America, such as Cactaceae, might reflect Late Cretaceous or Early Tertiary migration by these routes, with subsequent isolation until the closure of the Isthmus of Panama. Savage (1982) interpreted distributional patterns in frogs in the same way.

(ii) *Greater Antilles and Aves Ridge*

Iturralde-Vinent & MacPhee (1999) have proposed another migrational pathway comprising the Greater Antilles and the currently submerged Aves ridge (figure 3). GAARlandia may have existed for *ca.* 3 Myr at the Eocene–Oligocene boundary (35–33 Myr ago), and was not considered by earlier authors such as Raven & Axelrod (1974). The GAARlandia hypothesis has been invoked to explain the dispersal of *Styrax* (Fritsch 2001a), in addition to animal groups such as sloths (see MacPhee *et al.* 2000). GAARlandia provides a plausible link between North and South America because at this time, the western portion of the Greater Antilles was separated from Central America only by two narrow straits.

(iii) *Late Miocene Central American land bridge*

There is ample evidence that the Isthmus of Panama was completed as a terrestrial corridor *ca.* 3 Myr ago (Coates & Obando 1996), and that this event allowed a continental exchange of biota between North and South America. The profound effects of this biotic exchange are encapsulated in its usual title, the ‘Great American Interchange’ (Simpson 1980; Stehli & Webb 1985). However, geological evidence indicates that the staggered and gradual rise of the Isthmus influenced neotropical biogeography over a longer period of *ca.* 10 Myr (Stehli & Webb 1985; Zeh *et al.* 2003). The mammalian fossil record indicates some exchange of fauna

between North and South before 3 Myr ago. This is generally assumed to reflect a process of ‘island hopping’, but the existence of lineages of freshwater fishes in Panama dated at the end of the Miocene (4–7 Myr ago), derived from South American groups, implies an earlier, entirely dry land route, because these organisms cannot survive salt water (Bermingham & Martin 1998). The ‘Bermingham–Martin’ hypothesis has subsequently been used to explain the historical biogeography of the trans-Isthmian harlequin beetle-riding pseudoscorpion *Cordylochernes scorpioides* (Zeh *et al.* 2003).

(c) *The Antarctica route*

In the Late Cretaceous and Palaeocene, the landmasses now represented by South America, Antarctica, New Zealand, Australia, the South Sandwich Islands and South Georgia formed a continuous connection (Morley 2003; figure 1). This facilitated dispersal for taxa such as *Drimys*, Proteaceae, *Nothofagus* and Cunoniaceae (Morley 2003). Because of its near polar position, however, this is unlikely to have been a significant land bridge for megathermal (frost intolerant) plants. However, climates may have been sufficiently warm at the Late Palaeocene – Early Eocene thermal maximum for this to have acted as a migration route between South America and Australia for meso- and macrothermal taxa such as Bombacaceae (Malvaceae ‘baobabs’), Sapindaceae and Polygonaceae (Morley 2003).

3. SOURCE AREAS

In the survey of connections to South America, we indicated North America, Africa and Australasia as potential sources for migrant floras. However, these landmasses were themselves receiving immigrants from tropical south-east Asia and elsewhere. To understand contemporary floristic similarities between southeast Asia and South America, for example, we must consider the floristic connections that existed between Africa, North America and Eurasia during the Late Cretaceous and Tertiary. In this paper, we follow Morley (2003) and consider Australasia as

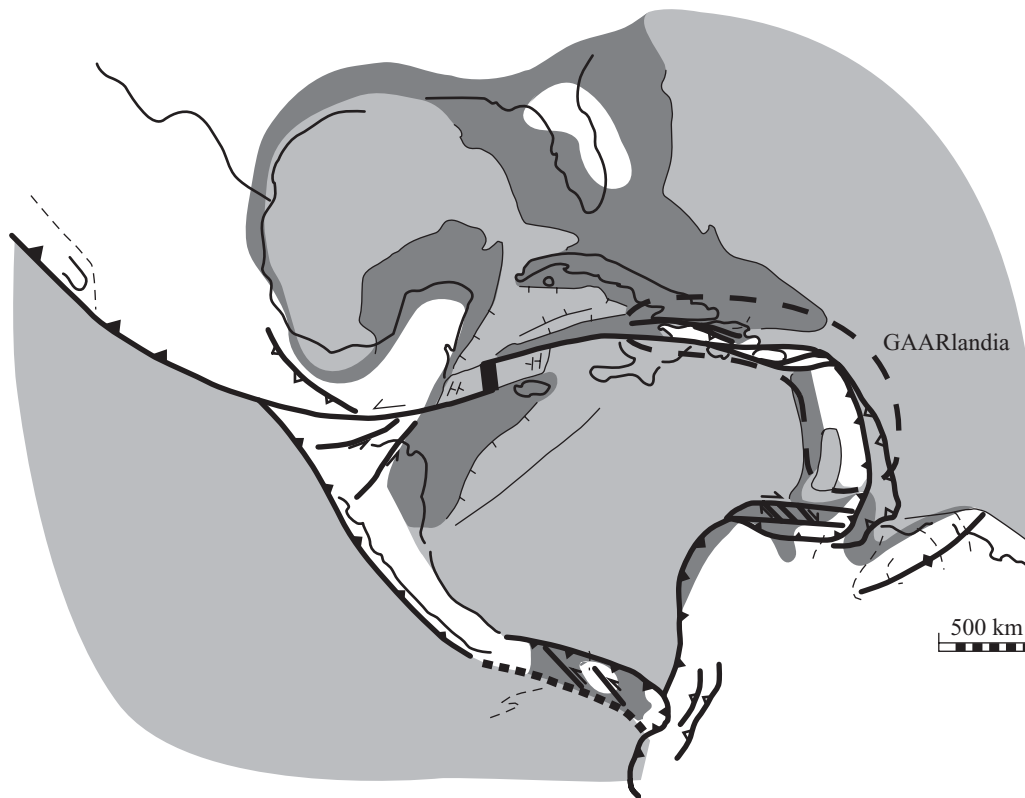


Figure 3. Caribbean tectonic reconstruction reproduced, with permission, following Pindell (1994, fig. 2.6L), highlighting the GAARlandia migration route. White, dry land and volcanic areas; dark grey, shallow water; light grey, deep water.

historically isolated, and receiving few immigrants from Southeast Asia, and do not discuss it further.

(a) Tropical Laurasia – boreotropical and Madrean–Tethyan vegetation

Under the ‘boreotropics hypothesis’ (e.g. Lavin & Luckow 1993) the proximity of the North American and Eurasian tectonic plates until the Late Eocene or Early Oligocene allowed plant dispersal over the North Atlantic, either through direct land connection or limited water gaps. It was also a time of thermal maxima, which would have allowed the survival of megathermal (‘tropical’) organisms at latitudes at which they do not occur today. The presence of tropical biomes at high latitudes is evidenced by Eocene fossil floras found in North America and Europe (reviewed by Wolfe 1975; Tiffney 1985*a,b*), which contain taxa closely related to extant species in tropical southeast Asia, Central America and the Antilles. The Beringian land bridge between North America and Asia would also have been a potential migration path for megathermal organisms (Wolfe 1975). The boreotropics hypothesis suggests wide migration of northern tropical elements between Eurasia, North America and Africa. The extent and duration of the boreotropical biome is unclear. Although there seems to have been floristic uniformity between European and North American mid- to high-latitude floras during the Eocene, many boreotropical taxa did not appear in Asia until the Miocene (Manchester 1999). This might reflect the poor Asian fossil record (Manchester 1999), but it is clear that boreotropical elements migrated at different times, and by the differing routes of the Beringian land bridge, the North Atlantic land bridge, and across Eurasia along the Tethys seaway (figure 1).

The fossil record indicates that boreotropical vegetation was a mixture without modern analogue. The modern relatives of boreotropical taxa are found in habitats ranging from northern deciduous hardwood forests to tropical and paratropical rainforests (Tiffney 1985*a,b*). The climates supporting this vegetation cannot have been strongly seasonal, but there is evidence for a sclerophyllous ‘Madrean–Tethyan’ flora characteristic of more seasonal climates that ranged along the Tethyan coast from North America to southeast Eurasia and North Africa (Axelrod 1975). Fossil evidence shows sclerophyllous taxa entering the record in the Early Eocene, and this Madrean–Tethyan sclerophyll vegetation formed a broad and continuous belt across southern North America and Eurasia (figure 4) until it was disrupted by increased climatic cooling and drying at the end of the Oligocene (Axelrod 1975).

The boreotropical and Madrean–Tethyan areas offer a viable Early Tertiary migration route between the Asian, African and North American tropics. Earlier reviews of the boreotropics hypothesis (e.g. Lavin & Luckow 1993) envisaged the major arrival of boreotropical elements to South America after the closure of the Isthmus of Panama. However, the migration routes through the Lesser Antilles and the Late Miocene Central American land bridge offer earlier alternatives for both the boreotropical and Madrean–Tethyan floras.

4. INVESTIGATING THE HISTORICAL ASSEMBLY OF THE NEOTROPICAL FLORA

In addressing this problem, many authors, following the methods of Raven & Axelrod (1974), have attempted to designate the origin of a taxonomic group (typically a family) as being from west Gondwana or Laurasia (e.g. Gentry

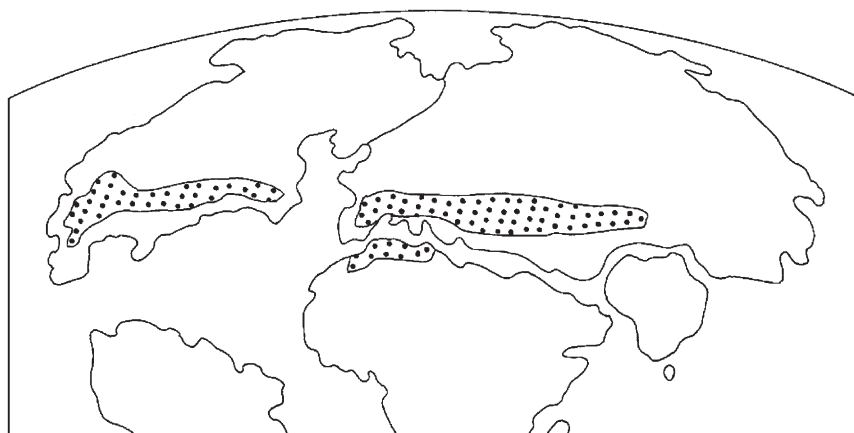


Figure 4. Early Tertiary continental positions and areas potentially occupied by Madrean–Tethyan sclerophyllous vegetation (stippled), modified, with permission, from Axelrod (1975, fig. 1).

1982; Wendt 1993; Burnham & Graham 1999). The inference is derived from several lines of evidence, including: current distribution, taking into account areas of maximum diversity and endemism; fossil distribution; degree of specialization of a taxon in a given area; assessment of systematic relationships based upon classical morphological taxonomic methods; and contemporary powers of dispersal. Given the publication of Raven and Axelrod's influential work soon after the general acceptance of plate tectonic theory, it is understandable that vicariance explanations took precedence. For example, for a pantropical distribution, which is both tempting and parsimonious to explain by Gondwanan vicariance, conflicting data such as a young fossil record and a systematic position implying recent origin, were assigned lesser importance. Examples are several families in asterid orders such as Lamiales, Gentianales and Boraginales, none of which has a pre-Eocene fossil record, but which were interpreted as originating earlier by Raven & Axelrod (1974), perhaps because of their wide distributions.

Several authors have used the Raven and Axelrod approach to infer the history of the neotropical flora. For example, Gentry (1982) used Raven & Axelrod (1974) to assign 145 neotropical families a Laurasian or Gondwanan origin. Considering the numbers of South American species in these families, he concluded that the Laurasian contribution to the South American flora was less than 10%, and even more insignificant for the lowland flora alone. This view of the South American lowland flora has been influential and supports the still widely accepted view of Gondwanan origins with little or no subsequent immigration.

(a) Evidence from molecular phylogenies

Raven & Axelrod's (1974) analysis of the relative age and specialization of families was based upon concepts of angiosperm relationships derived from morphology-based evolutionary taxonomies (e.g. Thorne 1968; Takhtajan 1969) that have been superseded by robust phylogenetic schemes from sequences of multiple chloroplast and nuclear genes (e.g. APG 1998; APG II 2003). This new source of information, in conjunction with the fossil record, offers a far more powerful instrument for assessing the age and origin of the lineages (stem groups) leading to

contemporary plant families. Part of this power stems from that fact that a molecular phylogenetic tree specifies exact sister group relationships, which increases the applicability of the fossil record. Sister lineages diverged at the same time, so the fossil record of one group can be used to date the stem lineage of its sister group, even if this lineage lacks fossils entirely (Magallón *et al.* 1999; Magallón & Sander-son 2001).

Studies integrating new molecular phylogenies of angiosperms with palaeobotanical information (e.g. Magallón *et al.* 1999), also offer some reassurance that the fossil record is not as incomplete and misleading as many authors assume, and that the phylogenies themselves are relatively accurate. There is a remarkable congruence between the fossil record and estimated phylogenetic relationships (e.g. Magallón *et al.* 1999). Families belonging to basally branching (i.e. inferred to be relatively ancient) lineages generally have a longer fossil record, whereas more apically placed (i.e. more recent) families generally have a more recent fossil record. An accurate phylogeny and a relatively complete fossil record explain this congruence between the molecular phylogenetic estimates and the fossil record. If the fossil record were badly incomplete, we would expect far more instances where putatively primitive lineages had only recent fossil records.

There is, however, some disagreement between the fossil record and molecular clock estimates on exact ages for some angiosperm lineages. Entire chloroplast genomes (Chaw *et al.* 2004), and combined nuclear 18S rDNA and chloroplast DNA *rbcL* and *atpB* genes (Wikstrom *et al.* 2001) provide somewhat older estimates than the fossil record for core eudicot clades, which account for 75% of extant angiosperms and most most rainforest trees. Our discussion encompasses the range of age estimates found in the literature.

Biogeographic interpretations of Raven & Axelrod (1974) should now be re-examined in the light of this new evidence because it highlights inaccuracies, especially in families now established as having relatively recent origins. For example, the order Lamiales (*sensu* Magallón *et al.* 1999) is determined as *ca.* 44 Myr ago (Magallón *et al.* 1999) to *ca.* 74 Myr ago (Wikstrom *et al.* 2001). This undermines the Gondwanan vicariance explanation for the distribution of the Lamiales families Bignoniaceae

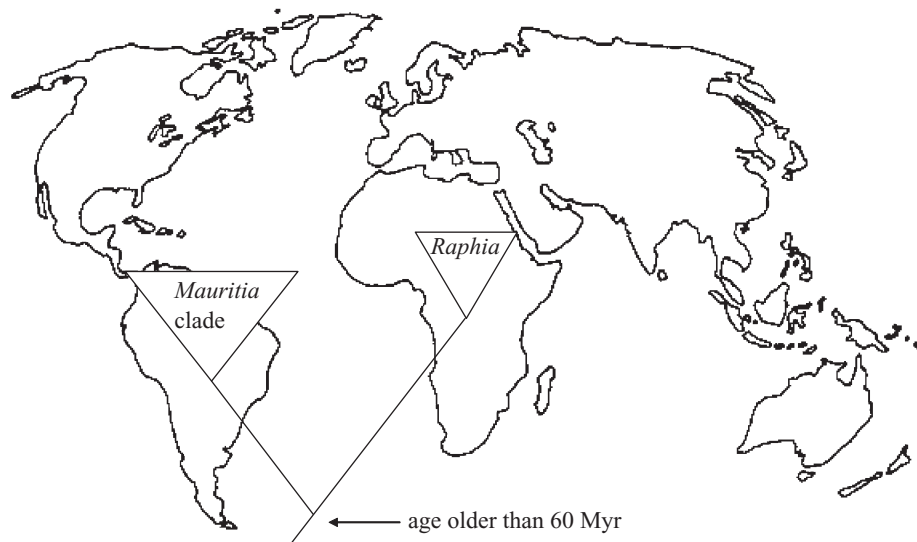


Figure 5. Gondwanan phylogenetic pattern of reciprocal monophyly, as exemplified by calamoid palms (Baker & Dransfield 2000).

and Gesneriaceae, first suggested by Raven & Axelrod (1974), and followed by subsequent authors (e.g. Gentry 1982; Hilliard & Burt 2002). Likewise, Gondwanan explanations for the transatlantic distributions of Melastomataceae *sensu stricto* (i.e. excluding Memecylaceae) and Malpighiaceae have been refuted by molecular phylogenetic studies coupled to fossil calibrated molecular clock analyses (Renner *et al.* 2001; Davis *et al.* 2002).

(b) Hypothesis testing using molecular phylogenies

Hypotheses of geographical origin and migration contain implicit assumptions about phylogenetic relationships. It is possible to reconstruct the phylogeny for a group and determine whether the phylogenetic estimate fits a biogeographic scenario. Furthermore, and most pertinent in the context of this volume, different biogeographic scenarios involve events of different ages, and calibrating phylogenies with a time dimension adds a second level of biogeographic testing. In this paper, we are interested in testing hypotheses about source areas and migration routes which have led to the assembly of the South American flora.

(i) Gondwanan origin

If South American taxa are descendants of west Gondwanan lineages that have evolved *in situ* without subsequent transatlantic dispersal, we might expect them to be monophyletic, with monophyletic sister groups in Africa and/or Madagascar. This pattern of reciprocal monophyly (*sensu* Cunningham & Collins 1994, 1998) is displayed by calamoid palms (Baker & Dransfield 2000; Baker *et al.* 2000a,b), where the three endemic neotropical genera *Mauritia*, *Mauritiella* and *Lepidocaryum* form a monophyletic group, with the African *Raphia* as its sister group (figure 5). Because of the Late Cretaceous – Early Tertiary fossil pollen record attributable to this group in both South America and Africa, Baker & Dransfield (2000) suggested that the divergence of *Raphia* and its neotropical relatives was linked to the opening of the Atlantic Ocean. Corroborating evidence that calamoid palms were present before the split of west Gondwana is suggested by their basal position in a palm family phylogeny (Asmussen &

Chase 2001), and a date of origin for palms just older than 100 Myr ago (Bremer 2000).

The same pattern of reciprocal monophyly would be predicted if filter dispersal was possible until the Maastrichtian through putative island chains along the Walvis Ridge – Rio Grande Rise or Sierra Leone – Ceará Rises. Because of the relatively close timing of the break-up of west Gondwana (*ca.* 96 Myr ago) and the availability of the possible island dispersal routes (96–76 Myr ago; Morley 2003), distinguishing these scenarios by dating phylogenies is difficult. For either, the divergence of the sister groups should date at least to the Late Cretaceous (figure 5). Baker & Dransfield (2000) did not attempt to date their phylogeny of calamoid palms, but the high degree of ITS sequence divergence between the neotropical and African taxa does suggest antiquity.

A dated phylogeny of Lauraceae (Chanderbali *et al.* 2001) provides compelling evidence for an influence of the break-up of west Gondwana on the distribution of this family. The South American *Chlorocardium–Mezilaurus* clade occupies a basal and isolated position in the family. Its putative Gondwanan origin is supported by a molecular rate analysis of ITS and rpl16 datasets. However, the lack of continental monophyly in more derived Lauraceae groups favours a role of Tertiary dispersal in explaining the pantropical distribution. Such overlapping patterns of diversification and dispersal may be common, meaning that simple patterns of South American – African/Madagascan reciprocal monophyly, such as that found in the calamoid palms, may be rare.

(ii) Laurasian boreotropical or Madrean–Tethyan origin with entry to South America through the proto-Greater Antilles, GAARlandia, Late Miocene land bridge and Isthmus of Panama

A good example of how to use phylogenetic hypotheses in this biogeographic context was provided by Lavin & Luckow (1993), who asked whether elements of the tropical North American flora were derived from South American Gondwanan stock, or from northern boreotropical vegetation. These two biogeographic hypotheses imply different area cladograms, which can be produced by

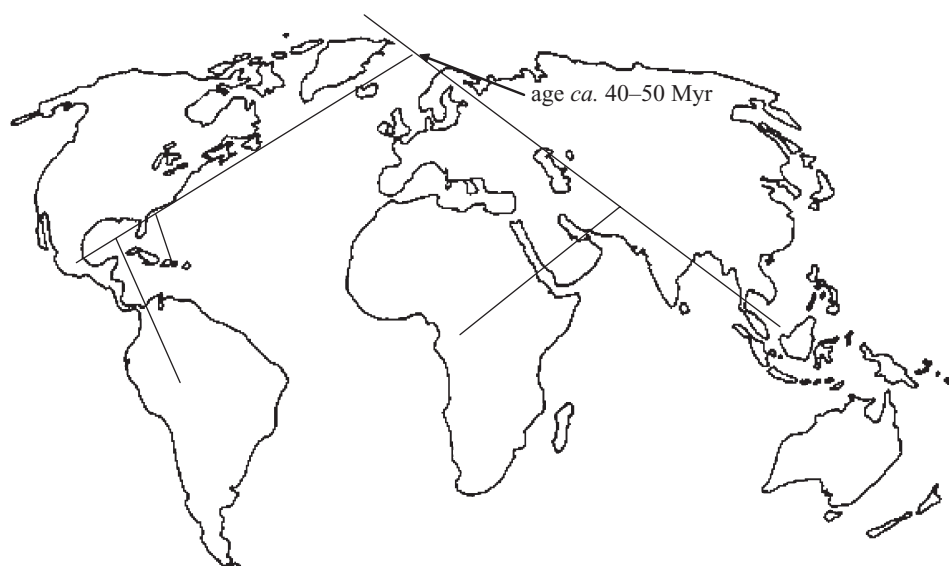


Figure 6. One potential boreotropical phylogenetic pattern, modified from Lavin & Luckow (1993), showing a South American group derived from tropical North American relatives, and with Old World sister groups.

reconstructing phylogenies for groups with species in the requisite areas of South America, tropical North America, and with tropical Old World sister groups. Subsidiary evidence can be gathered from the fossil record; a Gondwanan explanation would predict Cretaceous fossils in South America or Africa (unfortunately, Cretaceous fossils are scarce for South America; Burnham & Graham 1999; Burnham & Johnson 2004); a boreotropical explanation would predict Early Tertiary fossils in North America, Europe or Asia. Calibrating phylogenies with a time dimension now allows a further distinction of the hypotheses. A Gondwana explanation would predict a date of *ca.* 90–76 Myr ago (the separation of Africa and South America, plus putative island chain connections) for the divergence of Old and New World groups, whereas a boreotropical explanation would predict a date of *ca.* 40–50 Myr ago. These are the approximate dates for the existence of a north Atlantic land bridge and temperatures high enough for megathermal taxa to migrate through the Beringian land bridge (Tiffney 1985*a,b*; Wolfe 1975).

Boreotropical groups may have ultimately arrived in South America through the Proto-Antilles, GAARlandia, the late Miocene Central American land bridge, or as part of the Great American Interchange. These alternatives are not mutually exclusive, and they all predict the same cladogram topology: South American groups derived from tropical North American relatives with Old World sister groups (Lavin & Luckow 1993; figure 6). Furthermore, confidence limits in assigning dates to cladogram nodes are too wide to confidently distinguish between the Late Miocene land bridge (4–7 Myr ago) and the closure of the Panama Isthmus (3 Myr ago). An arrival in the Eocene or Early Oligocene boundary (*ca.* 50–33 Myr ago) might, however, be indicative of a Proto-Antillean or GAARlandia route. Confidently distinguishing these two Antillean scenarios by assigning dates will also be difficult.

Laurasian origins of South American taxa have been suggested for Annonaceae (Doyle & Le Thomas 1997; Richardson *et al.* 2004), Lauraceae (Chanderbali *et al.* 2001), and some groups of Leguminosae (Fabaceae)

(Lavin & Luckow 1993). The example of Lauraceae is particularly instructive in that there is little doubt from the fossil record dating from the Mid-Cretaceous (Chanderbali *et al.* 2001) and its basal phylogenetic position in the angiosperms (e.g. APG 1998; APG II 2003), that this is a relatively ancient angiosperm family. Chanderbali *et al.* (2001) show that the South American *Chlorocardium–Mezilaurus* clade is basally branching in the Lauraceae phylogenetic tree, consistent with a primitive presence of Lauraceae in South America (see above). However, a neotropical diversification containing species-rich genera such as *Ocotea* (200 species) and *Nectandra* (100 species) that are abundant in lowland South American rainforests is nested within less species-rich African, Madagascan and Macaronesian lineages. Chanderbali *et al.* (2001) hypothesize that this transatlantic distribution cannot have been achieved by west Gondwanan vicariance because it is far too young (*ca.* 23 Myr ago), but rather was the result of migration through Laurasia, probably in Madrean–Tethyan sclerophyll vegetation. Given the antiquity of Lauraceae, the species in these neotropical genera might be considered prime candidates to have accumulated by the ‘museum’ model, where high species diversity is attained over long time-scales with low rates of extinction. However, they are clearly the result of recent radiation. This again emphasizes that ancient biogeographic events such as Gondwanan vicariance should not necessarily be sought to explain the distribution and diversification of lineages and species within ancient families.

(iii) Antarctica route

This southern route does not appear to have been important for lowland tropical plants. However, certain elements of the Andean flora may have used it to enter South America during the Tertiary. An example is Cunoniaceae, of which *Weinmannia* is an important genus in Andean montane forests. A phylogeny of *Weinmannia* (Bradford 2002) is insufficiently resolved to determine whether the neotropical species of this genus can be considered immigrants, but the extensive Palaeogene fossil record of

Cunoniaceae, including *Weinmannia*, from southern Australia, plus Late Cretaceous fossil wood from Antarctica (reviewed by Bradford *et al.* 2004), implies that this family probably migrated along this southern route.

(iv) *Long-distance, trans-oceanic dispersal*

The 'island' model of South American biotic isolation until the closure of the Isthmus of Panama denies a major role for long-distance, trans-oceanic dispersal in contributing to the neotropical flora through the Cenozoic. This would surprise early biogeographers such as Darwin (1859) and Darlington (1957) who emphasized the primacy of dispersal explanations in explaining the global distribution of organisms. Acceptance of continental drift provided an alternative, potentially universal explanation that did not need to invoke *ad hoc* dispersal scenarios for each taxon. This viewpoint was popularized by the field of cladistic or vicariance biogeography (e.g. Nelson & Platnick 1981), which attempts to seek common patterns in the distributions of unrelated organisms.

Evidence from molecular phylogenies does, however, indicate that such 'waif' or 'sweepstakes' dispersal across very wide physical barriers as the Atlantic ocean has indeed occurred in multiple taxa and explains disjunctions at species, generic and higher taxonomic levels (Lavin *et al.* 2004; Renner 2004). It is remarkable that some of these examples are of plants that show little adaptation for over-water dispersal, such as the rainforest tree *Symphonia globulifera* (Dick *et al.* 2003), whose large, recalcitrant seeds cannot survive immersion in salt water. In all these cases, trans-oceanic dispersal is inferred because the node on a phylogenetic tree that marks the movement from one continental area to the other has a geological date that does not correspond with the availability of any stepping stone migration route. Renner (2004) presented 11 examples of transatlantic distributions at various taxonomic levels (species, genus, tribe) that are all dated at 11 Myr ago or less, and therefore explicable only by long-distance dispersal. For legumes, Lavin *et al.* (2004) show that out of 59 trans-oceanic crown clades, only eight are older than 25 Myr ago. This strongly implies that most have developed their distributions by long-distance dispersal.

We predict that as more studies are published, further well-corroborated examples of recent transatlantic dispersal to and from the neotropics will appear. For example, chloroplast DNA restriction site data (Pennington 2003) and ITS sequences (Skema 2003) indicate that *Andira inermis* reached Africa from the neotropics within the past few million years. *Renealmia* (Zingiberaceae) is the only genus of the ginger family indigenous to the neotropics, where there are *ca.* 56 species. This genus is also distributed in Africa, where there are *ca.* 15 species. ITS sequence data for a handful of neotropical and African species (M. F. Newman, unpublished data) show that the African and neotropical species are separated by remarkably short branch lengths, implying that the biogeographic patterns in this genus have been attained by recent trans-oceanic dispersal followed by rapid speciation.

Frequent long-distance trans-oceanic dispersal may obliterate underlying biogeographic patterns caused by continental vicariance or biogeographic bridges or filters. Lavin *et al.* (2004) conclude that this is the case in Leguminosae, where there are no clear repeated patterns of area

relationships. Schrire *et al.* (2004) suggested that structure in legume phylogeny is more explicable by ecological setting, and Lavin *et al.* (2004) further suggest that the frequency of long-distance dispersal between habitats is the principal determinant of legume phylogenetic patterns. Whether the frequency of long-distance dispersal seen in legumes is found to be typical of other groups can only be verified by more empirical data. However, it is also invoked to explain some distribution patterns in Annonaceae and Rhamnaceae (Richardson *et al.* 2004). Conversely, such dispersal must have been rare in calamoid palms. Legumes, however, dominate neotropical rainforests, dry forests and woody savannahs, and understanding that long-distance, trans-oceanic dispersal has been instrumental in shaping the distribution of this family is important to our understanding of the historical assembly of these biomes.

(c) *The historical assembly of the Amazonian rainforest flora: a re-evaluation*

The examples above demonstrate that the South American flora has received immigrant taxa throughout the Cenozoic from Laurasia, Africa and Australia, by stepping stone migration and long-distance dispersal. Clearly, the contribution of immigrant taxa to the South American rainforest flora also merits re-evaluation, as suggested by the authors of many of the studies reviewed (e.g. Chanderbali *et al.* 2001; Renner *et al.* 2001). One approach is to duplicate the analysis presented by Gentry (1982), and re-assign areas of origin to all Amazonian rainforest families in light of new molecular and biogeographic evidence of their geographical origins. This approach is not yet feasible, however, because insufficient phylogenies are available. Furthermore, the approach may be flawed, in that subfamilial groups may have multiple continental origins, as Chanderbali *et al.* (2001) have shown for the Lauraceae.

Given these uncertainties, we restrict ourselves to four major families that are important elements of Amazonian forests, and for which reasonable phylogenetic information is available: Leguminosae (Schrire *et al.* 2004), Annonaceae (Richardson *et al.* 2004), Lauraceae (Chanderbali *et al.* 2001) and Melastomataceae *sensu stricto* (Renner *et al.* 2001). For Lauraceae and Annonaceae, the neotropical genera identified as arrivals from Laurasia are listed in Appendix A. Legumes are the dominant tree family of South American rainforests and their global fossil record indicates a Late Cretaceous or Early Tertiary origin (Herendeen *et al.* 1992; Magallón *et al.* 1999; Schrire *et al.* 2004), with the oldest molecular clock based estimate at 74–79 Myr ago (Wikstrom *et al.* 2001; Chaw *et al.* 2004). Schrire *et al.* (2004) suggest that the seasonally dry margins of the Tethys seaway are the ancestral area for legumes, implying that all South American taxa must be considered immigrants. The classification of all legumes as immigrants would be disputed by some authors (e.g. Raven & Polhill 1981; Morley 2000, 2003), and the putative Madrean–Tethyan origin hypothesized by Schrire *et al.* (2004) is not inferred by a clear optimization of an ancestral area, but from inference of historical ecological preferences. Renner *et al.* (2001) indicated that all South American Melastomataceae *sensu stricto* are derived from Laurasian boreotropical ancestors. Morley & Dick (2003) considered this family as possibly Gondwanan, but their preferred biogeographic scenario is an African origin for South American

species, which therefore does not alter their status as immigrants.

Some other less ecologically important families have a clear Laurasian origin based upon published phylogenies or their fossil record, and it seems reasonable to assume that their South American species are immigrants. We consider these families to be Ulmaceae (*Ampelocera*, *Celtis*, *Trema*), Rhamnaceae (*Colubrina*, *Rhamnidium*, *Zizyphus* (see Richardson *et al.* 2004)), Rosaceae (*Prunus*), Staphyleaceae, (*Huertea*, *Turpinia*), Magnoliaceae (*Talauma*) and Styracaceae (*Styrax* (Fritsch 2001b)).

We assessed the percentage of species that can be considered immigrants to an Amazon rainforest tree community (1 cm or greater diameter at breast height) represented in a 25 ha forest inventory plot in Yasuni National Park, Ecuador (see Valencia *et al.* (2004) for a description of this inventory plot). We adopted a conservative approach for the Lauraceae, by excluding the 30 undetermined morphospecies. Out of the staggering 1104 tree species thus far identified in the Yasuni plot, 232 (21%) belong to families and genera that we classify as immigrant. Even if we do not consider legumes as immigrants, 11% of the Yasuni species consist of Cenozoic immigrants. We can also assess the immigrant contribution to the Yasuni flora in terms of numbers of individuals (1 cm or greater in diameter) found in the 25 ha plot. Out of 152 353 individuals (Valencia *et al.* 2004), 30 156 (20%) are accounted for by the 232 immigrant species. These results stand in stark contrast to the view of Gentry (1982, p. 577), who claimed that less than 10% of the entire neotropical flora, and 'virtually none' of the lowland rainforest flora, had Laurasian (i.e., immigrant) origin.

Our calculations probably underestimate the immigrant contribution to the Amazonian flora. As is the case for Lauraceae, Annonaceae and Melastomataceae *sensu stricto*, we predict that elements of families previously considered 'Gondwanan' will be identified as South American immigrants as more phylogenies become available. For example, a phylogeny of *Manilkara* (Sapotaceae; Clayton 2003) indicates that this genus arrived in the neotropics by a boreotropical route. This calls into question the assumption that all of Sapotaceae, another ecologically dominant Amazonian family (54 species in the Yasuni plot), can be considered essentially 'Gondwanan' (Gentry 1982). Similarly, a phylogeny of *Ficus* (Moraceae; Weiblen 2000), which sampled only three of *ca.* 150 neotropical species, showed two to be sister species and basally divergent within the genus, but one (*F. pertusa*) to be nested high within an Asian clade, consistent with a recent neotropical arrival.

(d) *How similar are neotropical and tropical African rainforest communities?*

There have been many reviews of biotic relationships between the neotropics and tropical Africa (e.g. Meggers *et al.* 1973; Goldblatt 1993). In many cases these have emphasized floristic differences. For example, Thorne (1973) listed 111 seed plant genera restricted to tropical and subtropical Africa, Madagascar and the neotropics, but he estimated that these are fewer than 2.5% of the 4500 genera found on either continent. Considering more wide-ranging pantropical genera did not make the genera shared between South America and Africa exceed 10% of the total generic flora (Thorne 1973). However, Gentry (1993)

pointed out that the composition of ampho-Atlantic rainforest communities showed much higher levels of similarity. He highlighted that the family-level composition of rainforests on both continents was almost identical, and that Leguminosae, Moraceae, Lauraceae and Annonaceae are dominant rainforest tree families on both continents. Gentry also pointed out strikingly high levels of generic similarity; for example, an average of 31% of genera found in a series of 0.1 ha sample plots in Africa are also present in the neotropics, and he indicated that the existence of additional shared genera was potentially obscured by provincial nomenclature.

Given that the earliest fossils of many species-rich eudicot families such as legumes that are important components of tropical rainforests date only to the Late Cretaceous (Magallón *et al.* 1999; Lavin *et al.* 2004), the occurrence of shared genera between Africa and South America is probably most often the result of oceanic dispersal. In a similar fashion to Gentry (1993), we have compared species lists of the CTFS forest inventories in BCI, Panama (50 ha), and Yasuni, Ecuador (25 ha) with lists from Iturí, Democratic Republic of Congo (40 ha), and Korup, Cameroon (50 ha). Out of 174 genera in the BCI plots, 30 (17%) are found in the African plots, whereas 43 out of 333 genera in Yasuni (13%) are also found in Africa. If we expand the comparison to other palaeotropical rainforests in Asia through reference to distribution information in Gentry (1996) and Mabberley (1993), we find that 105 (32%) of the Yasuni genera are found in the palaeotropics.

Gentry (1993, p. 542) explained the community-level similarities between South American and African rainforests in terms of Gondwana vicariance: '...the strong floristic similarities seen when individual sites or communities are compared strongly suggest that today's forests result to a much greater extent from common origin than from chance immigration'. By contrast, we hypothesize that these similarities also reflect the relatively recent arrival of immigrant taxa by both long-distance dispersal and the migration routes we have reviewed. The analysis for Leguminosae by Lavin *et al.* (2004) suggests that long-distance dispersal has been the predominant force shaping the distribution of this family. Whether this is the case for other tree families that are ecologically important in Amazonia will be determined only by the availability of thoroughly sampled, dated phylogenies. These will enable us to disentangle the relative contributions of continental vicariance, filter bridge migration routes and long-distance dispersal in the historical assembly of the rainforest floras.

Finally, we ask why does the model of 'splendid isolation' apply more weakly to the South American flora than to its vertebrate fauna? We think the answer lies in the greater capacities of plants to disperse over long distances and establish founder populations. The traits that distinguish them from vertebrates include seed dormancy, asexual reproduction and the capacity to form their own rafts and waifs. Because the fossil record of South American plants provides a relatively poor documentation of the floristic interchange (e.g. Burnham & Graham 1999; Morley & Dick 2003), the new advances in molecular systematics will provide strong inferences about the role of immigration in the assembly of this species-rich biome.

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APPENDIX A. NEOTROPICAL GENERA OF LAURACEAE AND ANNONACEAE THAT ARE NOT PRIMITIVELY SOUTH AMERICAN

Annonaceae	<i>Bocageopsis</i>
Annonaceae	<i>Crematosperma</i>
Annonaceae	<i>Desmopsis</i>
Annonaceae	<i>Ephedranthus</i>
Annonaceae	<i>Klarobelia</i>
Annonaceae	<i>Malmia</i>
Annonaceae	<i>Mosannonia</i>
Annonaceae	<i>Onychopetalum</i>
Annonaceae	<i>Oxandra</i>
Annonaceae	<i>Polyalthia</i>
Annonaceae	<i>Pseudephedranthus</i>
Annonaceae	<i>Pseudomalmea</i>
Annonaceae	<i>Pseudoxandra</i>
Annonaceae	<i>Ruizodendron</i>
Annonaceae	<i>Sapranthus</i>
Annonaceae	<i>Stenannonia</i>
Annonaceae	<i>Tridimeris</i>
Annonaceae	<i>Unonopsis</i>
Lauraceae	<i>Aiouea</i>
Lauraceae	<i>Aniba</i>
Lauraceae	<i>Dicypellium</i>
Lauraceae	<i>Endlicheria</i>
Lauraceae	<i>Kubitzkia</i>
Lauraceae	<i>Licaria</i>
Lauraceae	<i>Nectandra</i>
Lauraceae	<i>Ocotea</i>
Lauraceae	<i>Paraa</i>
Lauraceae	<i>Pleurothyrium</i>
Lauraceae	<i>Rhodostemonodaphne</i>
Lauraceae	<i>Umbellularia</i>
Lauraceae	<i>Urbanodendron</i>

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GLOSSARY

- BCI: Barro Colorado Island
 CTFS: Center for Tropical Forest Sciences
 GAARlandia: Greater Antilles and Aves Ridge
 ITS: internal transcribed spacer