REVIEW ARTICLE

Biogeographical patterns of plants in the Neotropics – dispersal rather than plate tectonics is most explanatory

MAARTEN J. M. CHRISTENHUSZ FLS¹,²* and MARK W. CHASE FLS²

¹Botany Unit, Finnish Museum of Natural History, University of Helsinki, Helsinki, Finland
²Jodrell Laboratory, Royal Botanic Gardens, Kew, Surrey TW9 3DS, UK

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The phylogenetic relationships of some Neotropical plant groups have proved to be different from expectation assuming plate tectonics as the underlying model, and these unanticipated relationships (and their timing) have required further work to explain how they came into existence. Well-known Neotropical families, such as Bromeliaceae and Cactaceae, have one to a few species in Africa, but these can be explained by recent long-distance dispersals; the estimated ages of the Transatlantic crown and stem clades of these families are of relatively recent origin, so long-distance dispersal is the only possible explanation and plate tectonic explanations are not viable. Other families with a crown age appropriate to be explained by plate tectonics did not seem to have distributions indicating an involvement of long-distance dispersal, but the advent of molecular systematics and molecular clocks has shown this to be otherwise. Families exhibiting this pattern include Fabaceae and Lauraceae (and many others), and in spite of the unlikely dispersal qualities of their generally large seeds, they exhibit many instances of long-distance dispersal occurring throughout their evolutionary history; in fact, long-distance dispersal is the most probable explanation to account for the current distributions of the great majority of land plant families. One factor that sometimes is overlooked is the boreotropics hypothesis, which may explain more recent connections between American, African and Asian floristic components. However, in some old lineages with small propagules that appear well adapted to long-distance dispersal, such as Marattiaceae and Orchidaceae, we find a pattern suggesting that tectonics is the primary factor, with clades clearly restricted to one tropical region. These patterns appear to have little to do with dispersability and it is probable that their conforming to expected (tectonic) biogeographical patterns has to do with their specialized life-history strategies that have acted to make intercontinental establishment unlikely even though dispersal almost certainly occurs. Molecular studies have identified additional, unanticipated clades, and these fit into the relictual category with what may be an overlay of old long-distance dispersal events. Examples at the ordinal level are Crossosomatales and Huerteales, and we expect future studies to identify more of these relict and unexpected clades at many taxonomic levels. Overall, molecular systematic studies and molecular clocks have demonstrated that there are many more connections between the Neotropics and Palaeotropics, both Asia and Africa, than previously would have been thought under a plate tectonic model. © 2012 The Linnean Society of London, Botanical Journal of the Linnean Society, 2013, 171, 277–286.


INTRODUCTION

The Neotropical flora has many plant groups that appear to be unique to the area. South America was part of Gondwana, and after break up of Gondwana (c. 155–65 Mya; Jokat et al., 2003) it was physically isolated until the formation of the Isthmus of Panama (c. 18–5 Mya; Knowlton & Weigl, 1998) connected it to North America, although exchange of plants and animals from the Northern Hemisphere is now known to have occurred long before this date (see *Corresponding author. E-mail: maarten.christenhusz@helsinki.fi
many examples below). The origins, relationships and distribution of Neotropical plant families and genera have therefore always elicited great interest.

In historical biogeography, there are two established theories to explain biotic distributions: dispersal and vicariance. In the dispersalist view, organisms spread from a centre of origin and by chance cross natural barriers (such as oceans, deserts, mountain ranges) that are unlikely to be frequently traversed. Thus, they manage to become established beyond the range of their former predators, diseases, pollinators, seed dispersers, symbionts, etc. After dispersal and establishment, evolution of the source and founder populations takes place independently, usually resulting in speciation. Centres of origin as a concept has been widely criticized as ad hoc, and the earlier close association of this concept with dispersalist views led some authors to reject dispersal as equally ad hoc (e.g. Nelson & Platnick, 1981). However, dispersal hypotheses can be rigorously tested independently, and do not depend on assuming a centre of origin for a taxon.

The vicariance hypothesis assumes that a species was already dispersed over a wide area and subsequently becomes fragmented as geographical or biotic barriers develop. In explaining general biogeographical patterns, the major vicariant factor is continental drift (plate tectonics). Even though these two schools of thought have been viewed as competing and views have been strongly polarized among biogeographers in the past (de Queiroz, 2005; Encyclopaedia Britannica, 2012), most distributions can be explained by a combination of dispersal and vicariant events. Prior to the advent of molecular systematics, most biogeographers thought that vicariance must be the underlying mechanism accounting for most of the diversity observed today, with dispersal operating much more sporadically and more recently (Lomolino, Riddle & Brown, 2006).

Dating of molecular phylogenetic trees, particularly with multiple fossil constraints and Bayesian approaches (Bell, Soltis & Soltis, 2005, 2010), and increased knowledge of species distribution patterns allows us to assess dispersability of Neotropical plant families. Here we review the historical biogeography of many plant groups and show that the biogeography of plants is not always as straightforward as has previously been assumed.

VICARIANCE THROUGH PLATE TECTONICS

Plate tectonics was frequently considered to be the primary agent responsible for the distribution of widespread plant families (e.g. Raven & Axelrod, 1975), especially families with a fossil record old enough to suggest a Gondwanan origin. However, there are few good examples that show geographical persistence of groups over sufficiently long periods of time to explain continental separation of clades through plate tectonics. This would have to involve old plant lineages with limited dispersability. The best examples are probably relictual plant groups such as Thyrsoperidaceae and Lactoridaceae, known from fossils from various parts of South America, where they became extinct. Currently these two families are represented by a single species each on the recent volcanic Juan Fernández Islands (Stuessy, Crawford & Marticorena, 1990), but their earlier fossil distributions and those of their relatives appear to fit the vicariant hypothesis.

Another likely relict distribution can be found in Strelitziaceae, a family with a crown group that may be sufficiently old to be Gondwanan (stem and crown groups dated at 78 and 59 Mya, respectively; Janssen & Bremer, 2004), with Phaneropspermum guianense (Rich.) Miq. in northern South America, Ravenala madagascariensis Sonn. (and perhaps an additional undescribed species) in Madagascar, and the slightly more diverse genus Strelitzia Aiton in southern Africa. Fossils reported for the related families Heliconiaceae and Musaceae (Zingiberales) from the Arctic in the Tertiary (Boyd, 1992) increase the complexity of this hypothesis but do not rule Gondwana out as an explanation for the relict distribution of Strelitziaceae. It is possible this was once a more widespread group that became separated by drift of the continents and then suffered extensive extinction in most areas while its relatives in other families were more widely distributed.

Nevertheless, there are plant families in the Southern Hemisphere that were once considered to be distributed via plate tectonics but do not have sufficient age for their current distribution to be explained by breakup of Gondwana, such as Berberidopsidaceae, Nothofagaceae, Restionaceae and Proteaceae. The stem group of Nothofagaceae, for instance, is certainly old enough to have been widespread before the break up of Gondwana (up to 95 Mya), but Cook & Crisp (2005) estimated the crown group to be too recent, and the sequence of break up of continental areas does not fit relationships of the clades in Nothofagus Blume.

Other groups, such as Araucariaceae, cycads, Gnetaceae and several fern families, have crown group nodes that are certainly old enough, but extant genera and species have been shown to have only recently radiated (e.g. Pryer et al., 2004; Nagalingum et al., 2011), and general patterns observed in these families do not fit well in a tectonic framework (i.e. clades within these families do not reflect the known sequence of Gondwanan disintegration). Although not satisfying from a plate tectonic perspective, most groups that have been purported to exhibit vicariant
patterns have turned out to be too young by molecular
clock estimates to be around at the appropriate time,
and when the phylogenetic patterns have been clari-
fied the expected area relationships have not been
realized (as in the case of Nothofagus above). Disper-
sal is stochastic in nature and related to factors such
as niche conservation and dispersal capabilities
(Crisp et al., 2009), although some authors have cited
dispersal as unpredictable, which, if true, would
justify the critique of Nelson & Platnick (1981). If
dispersal is stochastic in nature, then it can be mod-
elled (as in the unified neutral theory of biodiversity
and biogeography; Hubbell, 2001), and dispersal is
then clearly in the ascendency as the preferred expla-
nation for most groups of plants in the study of
historical biogeography.

LONG-DISTANCE DISPERsal
In the case of intercontinental distributions, dispersal-
ist biogeography considers long-distance dispersal
across oceans to South America (mainly from Africa
and, to a lesser extent, from Australasia simply
because of the greater distances involved) to be com-
monplace, something that has been disputed often in
the past, due to the lack of evidence for dispersal
vectors for the seeds or spores in question. Plants
with these types of distributions have often been
assumed to be species with great dispersability,
usually by wind, water or migratory birds, and often
are plants that are opportunistic and highly competi-
tive. However, these sorts of assumptions do not take
into consideration the long periods of evolutionary
time involved, and this even out what appear to be
different capacities for dispersal. Dispersal events
may be rare, but given enough time, then most groups
of plants demonstrate the capacity to travel over
great distances, regardless of their seed or spore
characteristics (Dick, Abdul-Salim & Berringham,
2003), probably through non-standard means of dis-
persal (e.g. by methods of transport for which they
appear not to be adapted; Richardon et al., 2001;
Higgins, Nathan & Cain, 2003; Pennington, Richard-
son & Lavin, 2006).

Coastal species being dispersed over long distances
by sea currents is the most easily believed scenario,
and many cases of seeds of such plants remaining
viable after prolonged periods in seawater exist.
Darwin (1856) immersed various seeds in seawater
to determine their viability, and the fact that coconuts
occasionally wash ashore in Europe (e.g. Cadée &
Rühland, 2010) also shows that distance is no
problem for these sea-dispersers. However, it is
becoming clear that such over-water dispersal is not
limited to species with seeds resistant to the effects
of seawater. Even massive seeds, such as those of Sym-
phonisia globulifera L.f. (Clusiaceae sensu Dick et al.,
2003; APG III, 2009), seem to move as easily as those
that clearly have characteristics that suggest they
can be dispersed effectively.

The difference between truly long-distance disper-
sal and stepping-stone dispersal (or short- to medium-
distance dispersal) is only a matter of distance, one
factor in the probability of dispersal. Usually, disper-
sal over longer distances has been considered to be
influenced by the degree of vagility of the dissem-
Inules (e.g. size, resistance, shape, viability and
physical characteristics) and time. Because long-
distance dispersal is potentially continuously occur-
ing, it is implied that it could have occurred recently,
as can be observed by the dispersal to new or recent
distant oceanic islands in the Caribbean, Mascarenes
and Polynesia. However, one has to be careful about
assuming probabilities of long-distance dispersal
simply based on current distribution and vagility of
disseminules.

The almost exclusively New World family Cacta-
ceae occurs from Canada to Chile, but, as is often the
case, is most diverse in the tropical areas between
these two. They have their greatest diversity in
deserts and seasonally dry tropical forests/woodlands
(e.g. Brazilian caatinga) and in the Old World their
niche is (mostly) filled by species of Aloë L. (Xan-
thorhoeaeaceae) and succulent species of Euphorbia
L. (Euphorbiaceae). Fruits of Cactaceae are small
bird-distributed berries, and a number of species have
become worldwide invasives, indicating the degree to
which they could occupy suitable habitats anywhere.
Only one species, Rhipsalis baccata (J.S.Muell.)
Stearn, an epiphyte in the canopy of rainforests (but
also found on city trees) that occurs throughout tropi-
cal South America, is also native in Africa, Madagascar,
Sri Lanka and the Mascarenes. It has been
generally assumed that R. baccata in Africa is the
result of long-distance dispersal, probably by birds,
but Maxwell (http://www.rhipsalis.com/maxwell.htm)
and others find this unlikely (because questions
remain as to why only this species has made the leap
and which, if any, bird frequents coastal rainforests
and flies across the Atlantic) and thus stated that it
must be old and its distribution due to vicariance.
This hypothesis, however, would make Rhipsalis
Gaertn an ancient genus (older than the break-up of
Gondwana), but recent molecular analyses have
placed it in the crown group, subfamily Cactoideae,
which is dated to c. 21 Mya (Arakaki et al., 2011) and
therefore decidedly not Gondwanan; of course, Rhip-
salis is undoubtedly much younger than the crown
age of Cactoideae. Also there are many older groups
of cacti that are not in Africa. Additionally, berries of
Rhipsalis are sticky so they must have hitched a ride
from its centre of diversity in coastal eastern Brazil to
West Africa. Such rare single occurrences must be anticipated in groups that are otherwise poorly adapted for long-distance dispersal, although it appears to have happened only for a single species of Cactaceae (which then radiated with polyploidy in the Indian Ocean). If viewed in the context of the stochastic nature of dispersal, then a wet-forest species is the most likely to establish after long-distance dispersal not because it can more easily disperse (due to its seed structure), but rather because its ecology makes it better able to tolerate such disturbance. The relatively recent dispersal of another species, Pitcairnia felicina (A.Chev.) Harms & Mildbr. (Bromeliaceae), is a similar such instance and is estimated to have occurred about 9 Mya (Givnish et al., 2008).

Another taxon traditionally associated with the Neotropics is the papaya family Caricaceae. The stem lineage of Caricaceae split from its Afromadagascan/Indian sister family Moringaceae around 58–60 Mya (Wikström, Savolainen & Chase, 2001). In Africa, Caricaceae include only Cylicomorpha Urb., with two species of disjunct distribution: one, C. solmsii (Urb.) Urb., in West Africa and another, C. parviflora Urb., in East Africa. In contrast, there are four Neotropical genera: Carica L., Jaccaratia A.DC., Jarilla Rusby and Vasconcellea A.St.-Hil., the last having the greatest diversity with c. 20 species. The African species of Cylicomorpha are sister to the rest of the family (Kyndt et al., 2005), which, together with the knowledge that Moringaceae are sister to Caricaceae, indicates that the family probably evolved in Africa. A much more recent long-distance dispersal from Africa to America led to a Neotropical radiation. Based purely on their distribution and without a molecular clock, one could argue for a tectonic (vicariant) explanation, but this has obviously not been the case. These examples show that long-distance dispersal is not unidirectional and species-richness is not necessarily an indication of taxon origin.

A different example in which plate tectonics was assumed to have played a role is the genus Nicotiana L., which has the greatest number of species in the Americas (49 species) but is also represented by the allotetraploid N. section Suaveolentes in Australia (25 species) and Africa (one species in Namibia). Molecular studies have demonstrated that the Old World species are allotetraploids approximately 10 Myr old and derived from parental lineages now restricted to the Americas (Chase et al., 2003; Clarkson et al., 2004). The seeds of Nicotiana are small, but not wind-dispersed, and the age of section Suaveolentes definitely rules out other explanations; it seems clear that long distances across oceans are being covered by taxa without any clear adaptations for travelling such distances. Explanations such as the boreotropics hypothesis cannot be invoked in these cases. Other groups also demonstrate dispersal over great distances in the Pacific and Indian Oceans, such as Melastomataceae (Renner & Meyer, 2001; Renner, Clausing & Meyer, 2001).

There are many other groups for which vicariance through plate tectonics was assumed to play the major role in explaining the distribution patterns, but long-distance dispersal is actually more important in explaining their current distribution. Good examples are found in Araceae (Cabrera et al., 2008), Arecales (Couvreur, Forest & Baker, 2011), Ebenaceae (Daugjai et al., 2006), Ericales (Sytsma et al., 2006), Euphorbiaceae (Wurdack et al., 2004), Lauraceae (Chanderbali, van der Werff & Renner, 2001), Sapindaceae (Buerki et al., 2011) and Phyllanthaceae (Wurdack, Hoffmann & Chase, 2005), all families with relatively large seeds, but in which all major clades have representatives on several major landmasses and are thought to have dispersed across the oceans several times during their evolutionary history. These sorts of examples are becoming so frequent that it is rare to observe families in which major clades isolated by continents occur.

**BOREOTROPICS HYPOTHESIS**

Long-distance movement from Africa and Eurasia to the Neotropics (including South America) does not in all cases have to involve dispersal across water. An excellent alternative is reflected in the boreotropics hypothesis of Wolfe (1975), Tiffney (1985a, b) and Tiffney & Manchester (2001). This was based on fossil taxa that were shared by North America and Europe during the Eocene, but also had relatives in Central America/Caribbean and the Asian tropics. With greater distances between Europe and North America and decreasing global temperatures in the early Oligocene, this tropical connection was lost, and the taxa involved were pushed further south, including into South America. Thus, relationships of these lineages in South America are not directly linked to African taxa, but rather to species further north in the Americas and southern Europe; they also date from much more recent times (30–40 Mya rather than > 65 Mya).

Such patterns of relationships have been demonstrated for several families, in particular Fabaceae (Lavin & Luckow, 1993), based on cladistic analysis of morphological data. Later, molecular data (Wojciechowski, Lavin & Sanderson, 2004), to which rates and age estimates were added by Lavin et al. (2004), supported this hypothesis for legumes (Lavin, Herendeen & Wojciechowski, 2005).

Another example in which a tectonic explanation was expected but another set of relationships emerged with molecular analyses was Amaryllidoideae (Amaryllidaceae; Meerow et al., 1999). In this
analysis, South American genera were not sister to the South African clades, but rather to those from further north in the Americas and then to Eurasian genera. Given later information about molecular clocks and ages of clades in the monocots, this also supports a boreotropics explanation for the tropical American and Andean taxa in Amaryllidoideae. Other examples of a boreotropics explanation include genera of Annonaceae (Scharaschkin & Doyle, 2005; Erkens, Maas & Couvreur, 2009; Couvreur et al., 2011; Erkens, Chatrou & Couvreur, 2012), Lauraceae (Chanderbali et al., 2001) and Malpighiaceae (Davis et al., 2002, 2004).

SURPRISING VICARIANT PATTERNS OF RELATIONSHIPS

Two families for which geographical patterns reflecting tectonic movements predominate are Marattiaceae and Orchidaceae, both of which have diaspores that could potentially be dispersed effectively over great distances. As for angiosperms, it is clear that some ferns do disperse over great distances and some have done so only recently (Rouhan et al., 2012). Others are clearly doing something different. Marattiaceae are an ancient fern family with a fossil history dating back to the Carboniferous (Christenhusz, 2007). The extant genera are of somewhat more recent descent, but they are restricted to either the Palaeotropics (Angiopteris Hoffm., Christensenia Maxon and Ptisana Murdock) or the Neotropics (Danaea Sm., Eupodium J.Sm. and Marattia Sw.). Although their spores are relatively large among ferns, dispersability in these genera does not appear to be a limiting factor: Neotropical Danaea has occupied all the wet Caribbean islands and reached Cocos Island in the Pacific (Christenhusz, 2010), Marattia has reached as far as Hawaii, with its closest relative in Jamaica (Murdock, 2008), Palaeotropical Ptisana is represented on Ascension Island in the mid-Atlantic, New Zealand and New Caledonia, and Angiopteris is widespread in the Indian and Pacific Oceans, with outliers in Madagascar, the Seychelles, Polynesia and Pitcairn Island. Despite this ability to establish on isolated oceanic islands, Danaea and Marattia are not found in the Palaeotropics and Angiopteris and Ptisana are absent from the Neotropics. It has been shown that when brought as plants by humans Angiopteris can successfully invade Neotropical areas (Christenhusz & Toivonen, 2008), but they are not able to do this on their own accord.

In Orchidaceae, seeds are nearly always wind-dispersed, but there are only a few cosmopolitan genera, e.g. only Bulbophyllum Thouars (Smidt et al., 2011) and Polystachya Hook. (Russell et al., 2010b). In the case of Bulbophyllum, there are major clades confined to continental areas (Gravendeel et al., 2004; Fischer et al., 2007; Smidt et al., 2011), so, although the genus as a whole is cosmopolitan, its internal structure reflects more limited dispersability. In Polystachya, one clade has managed recently to migrate from Africa to both the New World and the Asian tropics (Russell et al., 2010a, 2011), a situation again of a wet-forest species, much akin to the situation with Rhipsalis (see above), becoming successfully established after long-distance dispersal. Despite these examples of long-distance dispersal, major clades in Orchidaceae are confined to single continents (Cameron et al., 1999; Górmik, Paun & Chase, 2010). For example, at the subtribal level (sensu Chase et al., 2003) Catasetinae, Laeliinae, Maxillariinae, Oncidiinae, Pleurothallidinae, Stanhopeinae and Zygopetalinae are all exclusively New World, whereas Coelogymini, Collabini, dendrobini, Eriinae and Podochilinae are Asian except for one species of Calanthe R.Br. (Collabini). Angraecinae and Aerangidae are all African/Madagascan except for one group of genera that has recently reached the New World tropics (Carlsward, Whitten & Williams, 2003). At the subfamily and tribal levels, such restricted distributions are much rarer, but at these taxonomic levels older tectonic explanations become feasible; the orchids diverged from their sister clade about 110 Mya, and all five subfamilies (the orchid crown group) existed before the end of the Cretaceous (Chase, 2001; Ramírez et al., 2007; Gustafsson, Verola & Antonelli, 2010), so we could expect that the oldest clades would be likely to have evolved at a time when the continents were amalgamated and thus these groups have broader distributions dissected by plate tectonics. This is in fact the pattern that would have been expected in other old families, such as Lauraceae, but has not been observed.

For groups in which the phylogenetic patterns do not reflect what we expect through long-distance dispersal, even though they are capable of it (e.g. groups are restricted to continents), we have to look at factors of their life-history strategies that would limit their successful establishment elsewhere; their dispersal is taken for granted, given the successful long-distance dispersals that characterize families more poorly adapted to transoceanic migration, such as Ebenaceae, Fabaceae and Lauraceae. In the cases of both Orchidaceae and Marattiaceae it is possible that mycorrhizal relationships are behind their inability to establish following intercontinental dispersal, although this would also be expected to prevent their artificial introduction and subsequent invasiveness. Perhaps in these cases, their mycorrhizal associates have also been introduced when the mother plants were transplanted.
Another possible explanation is that old herbaceous families (palaeoherbs) do not exhibit the same propensity for establishment as woody families once dispersal occurs. We examined this topic by looking at other old tropical herbaceous families and found evidence to the contrary. Araceae (Cabrera et al., 2008) and Aristolochiaceae (particularly Aristolochia L.; Ohi-Toma et al., 2006) exhibit relationships indicating frequent long-distance dispersal, just as in the tropical woody families. The situation in Piperaceae (Jaramillo & Manos, 2001; Wanke et al., 2006) is less clear, but the sampling of species is highly skewed and not particularly suitable to address this question. It may also be that the particular ecological preferences of orchid and marattiod fern species are at least partly responsible for their apparent lack of successful dispersal and establishment and this possibility should be examined.

SURPRISING BIOGEOGRAPHICAL PATTERNS OF UNEXPECTED LINEAGES

Families that exhibit widely disjunct distributions could fall into one of the above categories (although we admit that they are not really distinct), depending on their age. For example, Coriariaceae have about 30 species in the single genus Coriaria Niss. ex L., disjunctly distributed in Central and South America, the Mediterranean, East Asia, some Pacific Islands and New Zealand. To achieve such a distribution must have required long-distance dispersal, but that they were related was obvious from the start of their recognition as a genus. Lardizabalaceae, a family disjunctly distributed in eastern Asia and southern South America (Qin, 1997; Christenhusz, 2012) is another such potential case. There are fossils known from the Oligocene of Europe and the Late Cretaceous of North America (Page, 1970; Mai, 1980), but the age of the South American lineage is probably not old enough to explain its occurrence there by vicariance.

Other cases have only come to light since the widespread use of molecular systematics to look at relationships within and between families. For example, the APG III classification (APG III, 2009) contains two orders that no one had recognized before the advent of molecular systematics: Crossosomatales and Huerteales.

Crossosomatales are composed of seven families (Aphloiaceae, Crossosomataceae, Geissolomataceae, Guamatelaceae, Stachyuraceae, Staphyleaceae, Strasburgeriaceae), all of which are monogeneric except for Crossosomataceae (four genera) and Strasburgeriaceae (two genera). Most genera are also monospecific, so this order is really composed of an odd set of taxa, formerly included by previous authors in other families such as Flacourtiaceae [Aphloia (DC.) Benn.], Ochnaceae [Strasburgeria Baill.], Rosaceae [Guamatela Donn.Sm.] and Saxifragaceae [Iserba A.Cunn.] from a diverse set of orders. Only seed anatomy seems to be a clear synapomorphy for the order (Matthews & Endress, 2005). Guamatela, in particular, was only recently recognized as a member of Crossosomatales (Oh & Potter, 2006), but as far as it has been studied it appears to fit reasonably well there, although it is not morphologically similar enough to be accommodated into one of the pre-existing families of the order. Crossosomatales are split into two major clades, a Southern and a Northern Hemisphere clade. Wikström et al. (2001) dated the age of stem Crossosomatales at 91 Ma, but Magallón & Castillo (2009) came to an earlier age of 106 Ma. This is clearly old enough for plate tectonics to have played a role in their current distribution, and the crown groups were estimated to have evolved about 30 Myr later, so there is probably an overlay of some long-distance dispersal as well. For example, Staphyleaceae are now found throughout the North Temperate zone as well as into tropical Southeast Asia and the Americas, and this radiation occurred too recently to be an effect of tectonics; however, a primary influence of plate tectonics seems most obvious, and their now largely disjunct distribution appears to us likely to have been caused by a mixture of vicariance and long-distance dispersal, some of it occurring within the last 20 Myr.

Huerteales were only described as an order with three families by Worberg et al. (2009). The order was subsequently accepted in APG III (2009) and then a fourth family was added (Peteneaceae; Christenhusz et al., 2010). Similar to Crossosomatales, only characters of seed anatomy that link these four small families [Dipentodontaceae (two genera), Gerrardinae (one genus), Peteneae (one genus) and Tapisciaceae (two genera)] have been identified (Christenhusz et al., 2010). As for Crossosomatales, most of these genera were previously placed in other families: Celastraceae (Perrottetia Kunth), Elaeocarpaceae (Petenea Lundell), Flacourtiaceae (Gerrardina Oliv.) and Staphyleaceae (Huerta Ruiz & Pav. and Tapisea Oliv.), and ordinal placements were likewise diverse. Peteneaceae were found to be related to the recently described South African family Gerrardinae (Christenhusz et al., 2010). The distribution of a Central American species distantly related to an African genus follows the pattern in other families of Huerteales, e.g. Tapisciaceae, with Tapiscia restricted to central China, whereas Huerta is from Neotropical mountains. Unlike Crossosomatales, there is no clear split into northern and southern clades for Huerteales. The age of the overall clade is more recent than Crossosomatales (Wikström et al., 2010).
2001), and thus relationships in Huerteales seem less likely to be relictual and more likely to have resulted from dispersal rather than vicariance, although a boreotropics hypothesis with extinction in the higher latitudes is also a possible scenario; probably, a combination of the two is responsible for the overall pattern.

CONCLUSIONS

We can now state without hesitation that the flora of the Neotropics, and of the Americas in general, has many more shared relationships with the Palaeotropics than ever before imagined (Pennington & Dick, 2004; Pennington, Cronk & Richardson, 2004; Renner, 2004; Sammartin & Ronquist, 2004; Sanmartin, Wanntorp & Winkworth, 2007). Most families of land plants have more easily dispersed across the oceans than many ever thought possible, especially given the lack of vagility of their propagules and their apparent inability to survive long periods in seawater. Phytogeographical distributions appear to be mostly explainable through dispersal, although in a few rare cases an underlying effect of vicariance through plate tectonics can be observed. Many Neotropical connections are with plants that have a decidedly temperate nature (e.g. Amaryllidaceae), so it is also possible that some dispersal took place via land routes (e.g. the boreotropical route). Plants appear to have gone back and forth between the continents frequently and can successfully become established on a new continent when the ancestral ecology is preserved in their new home (e.g. when metacommunity processes are at work; Lavin et al., 2004; Crisp et al., 2009). Given the timescales involved, rare events begin to loom large, and in the results of molecular phylogenetic analyses combined with molecular clocks we now find evidence for relationships of which we were previously not cognizant due to the lack of obvious morphological synapomorphies for the taxa involved.

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