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# REVIEW ARTICLE

# Neotropical Plant Evolution: Assembling the Big Picture

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This paper and this issue attempt to address how, when and why the phenomenal *c*. 100,000 species of seed plants in tropical America (the Neotropics) arose. It is increasingly clear that an approach focusing on individual major biomes rather than a single aggregate view is useful because of evidence for differing diversification histories among biomes. Phylogenetic evidence suggests that Neotropical-scale diversification patterns are structured more ecologically than geographically, with a key role for phylogenetic niche or biome conservatism. Lower geographical structure reflects the fact that long-distance dispersal, inferred from dated phylogenetic trees, has overcome many supposed dispersal barriers. Overall, high rates of species turnover as inferred from palaeontological and molecular data have been the hallmark of plant evolutionary dynamics in the Neotropics throughout the Cenozoic, with most extant species diversity post-dating the Mid- to Late Miocene, perhaps reflecting the conjunction of both global climatic changes and geological upheavals such as the Neogene uplift of the tropical Andes. Future studies of Neotropical diversification will be facilitated by taxonomically and genetically better sampled phylogenetic analyses, their integration with palaeontological, geological and ecological data, and improved methods to estimate biogeographic history and diversification dynamics at different spatial and temporal scales. Future biome-focused approaches would benefit greatly from better delimitation and mapping of Neotropical biomes. 

ADDITIONAL KEYWORDS: biogeography – biome evolution – botany – biodiversity hotspots – ecology – phylogenetics – systematics.

Perhaps the most salient question concerning Neotropical plant evolution is why are there so many plant species there? The 90 000–110 000 species of seed plants in the Neotropics make up around 37% of the world's total, and potentially as many as, or more than, the whole of the Palaeotropics combined (Antonelli & Sanmartín, 2011). This is reflected in the imbalance in species diversity between the Neotropics and the Palaeotropics for many of the clades investigated in this issue [e.g. Solanaceae, Bignoniaceae, Verbenaceae (Olmstead, 2012); Melastomeae (Michelangeli *et al*., 2012); and perhaps most strikingly in Chrysobalanaceae in which 80% of the 531 species in the family are found in the Neotropics (Bardon *et al*., 2012)]. The reasons for Neotropical hyperdiversity have inspired and intrigued biogeographers, plant evolutionary biologists and systematists ever since Humboldt set foot in the Andes and first documented the exceptional plant diversity there nearly 200 years ago (Humboldt, 1820). Many theories and explanations for this phenomenon have been proposed (e.g. Gentry, 1982; Antonelli & Sanmartín, 2011), but a satisfying synthesis remains elusive.

The Neotropics harbour exceptional physiographic (topographic and habitat) heterogeneity spanning all major tropical biomes including lowland rain and seasonally dry forests, savannas, deserts,

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mid-elevation montane forests and high elevation grasslands (Fig. 1). The Neotropics also present a set of prominent tectonic and other geohistorical events (Burnham & Graham, 1999; Potter & Szatmari, 2009; Hoorn *et al*., 2010) that have shaped geographical dispersal opportunities and barriers through time, both large continental-scale ones separating South America from Africa and North America throughout much of the last 100 million years (Simpson, 1980; Stehli & Webb, 1985; Cody *et al*., 2010) and more regional ones, such as the rising Andes and the mega-wetlands in western Amazonia (Hoorn *et al*., 2010; Antonelli & Sanmartín, 2011). Even if South America may not have been under the 'splendid isolation' envisioned by Simpson (1980) throughout much of its history (see, e.g., new evidence summarized by Bacon *et al*., 2012), the comparative lack of historically highly complex connections that characterize many other global biodiversity hotpots (e.g. the Mediterranean or tropical Australasia) appears to offer important advantages for studying large-scale biogeographical questions. These features combined with the very uneven distribution of diversity, with several biodiversity hotspots located across the Neotropics (Myers *et al.,* 2000) and a flora that is made up of the full span of species-rich and species-poor lineages, mean that the Neotropics provide an intriguing setting – an 'evolutionary laboratory' – for addressing key questions in evolution and biogeography. These might include fundamental questions in evolutionary biology, such as: Is Neotropical hyperdiversity attributable to greater time for diversification, lower extinction rates or higher speciation rates? What are the geotemporal patterns and the evolutionary dynamics of diversification? Is diversification mainly recent or old, or a mixture of the two, and what does this imply for rates of species turnover? Do different lineages follow similar or different patterns and why? What are the extrinsic and intrinsic factors driving diversification and how do they interact? What are the roles of ecology and geography and the prevalence of phylogenetic niche or biome conservatism vs. biome or niche shifting, and their possible interplay, in shaping and structuring geohistorical patterns of diversity? Do these patterns differ on different continents and across biomes and among biodiversity hotspots in the Neotropics, and if so, can this be attributed to unique features of regional- and continental-scale geohistory or other factors at different spatial and temporal scales?

Over the last decade or more, critical new insights into geotemporal patterns of Neotropical plant diversification have come from both palaeontology (e.g. Jaramillo *et al*., 2006; Graham, 2010, 2011; Hoorn *et al*., 2010) and phylogenetics (e.g. Richardson *et al*., 2001; Hughes & Eastwood, 2006; Pennington *et al*., 2006b, 2010; Antonelli *et al*., 2009; Simon *et al*., 2009; Arakaki *et al*., 2011; Nagalingum *et al*., 2011; Kissling *et al*., 2012), shedding new light on the underlying causes of hyperdiversity in the Neotropics and laying important foundations for answering many fundamental questions that lie at the heart of plant biogeography and the evolutionary dynamics of tropical plant diversity today.

The 16 papers in this issue represent the proceedings of a two-day symposium entitled *Neotropical Plant Evolution: Assembling the Big Picture*, at the XVIII International Botanical Congress held in July 2011 in Melbourne, Australia. They provide a valuable and significant injection of new primary data, evidence and insights into questions about the historical assembly and evolution of Neotropical species diversity. The contributions survey diverse plant groups with a wide range of life history strategies (lianas, epiphytes, herbs, shrubs and trees); they span plant groups originating and diversifying mainly in the Neotropics and immigrant lineages from elsewhere; they span family, species and population levels and older and more recent timespans, including recent radiations; they cover broad trans-continental, regional and more local community geographical scales and they encompass almost all the major Neotropical biomes and regions. In other words, they provide a snapshot of the state-of-play in this important arena.

In this introduction we attempt to provide an overview and synthesis of what these contributions tell us about Neotropical plant evolution. The majority of papers in this issue use phylogenetic approaches to gain insights into large-scale biogeographical questions and historical assembly of species diversity. This introduction mirrors that emphasis in providing a

**Figure 1.** Neotropical biomes. A, tropical rain forest, Rio Negro, Amazonia, Brazil; B, tropical rain forest, Mata Atlántica, Rio de Janeiro, Brazil; C, tropical wetlands, Pantanal, Mato Grosso do Sul, Brazil; D, savanna, cerrado, São Paulo, Brazil; E, campos rupestres, Serrania de Santiago, Bolivia; F, mid-elevation grassland, Campos de Cima da Serra with *Araucaria* forest, Rio Grande do Sul, Brazil; G, seasonally dry tropical forest, Pacific coastal Oaxaca, Mexico; H, seasonally dry tropical forest, Loja, southern Ecuador; I, seasonally dry tropical forest, Baja California, Mexico; J, mid-elevation montane forest, Grand Etang forest reserve, Granada; K, high elevation Andean grasslands, páramo, Las Cajas National Park, Ecuador; L, tropical pine savanna, Petén, Guatemala. Photos A-D & K, Alexandre Antonelli; E, G, I, J & L, Colin Hughes; F, Toby Pennington; H, Gwilym Lewis.

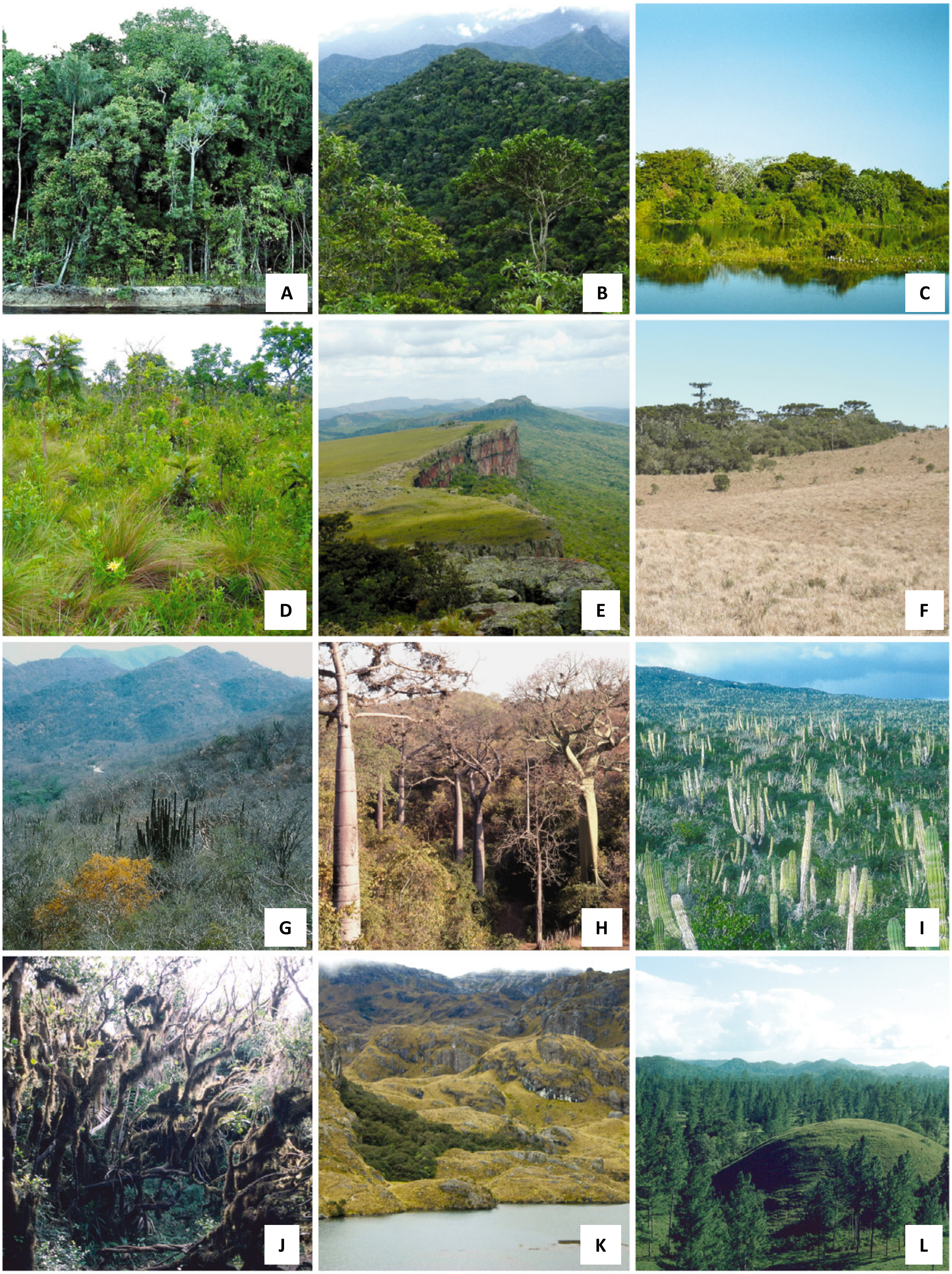


**Figure 1.** See caption on previous page.

largely phylogenetic perspective that sets these papers in the wider context of what is known about the historical assembly of the most diverse flora on the planet. We also briefly look to the future to foresee what research is needed and what new research developments can bring to these questions.

## GEOTEMPORAL TRAJECTORIES OF PLANT EVOLUTION AND DIVERSIFICATION IN THE NEOTROPICS

Much of the discussion in the last few decades about historical species assembly and geotemporal trajectories of plant diversification in the Neotropics has revolved around two extreme models. First, the museum hypothesis suggests that an ancient history of steady accumulation of diversity with low extinction under favourable and relatively stable environments has underpinned the assembly of high extant species diversity (Stebbins, 1974; Richardson *et al.*, 2001). The alternative cradle model favours more recent diversification, high speciation rates and potentially high species turnover to account for high levels of extant diversity (Haffer, 1969; Richardson *et al.*, 2001). An extreme example of the latter is Haffer's (1969) refuge theory that suggested recent Pleistocene diversification as a result of the impacts of glacial/interglacial climate change. This dichotomy between ancient and recent, and especially Haffer's refuge theory, has now been largely abandoned. More heterogeneous models that combine elements of older and more recent diversification (McKenna & Farrell, 2006) and episodes of rapid and slower diversification are suggested by several recent meta-analyses of dated phylogenetic trees for Neotropical plants (Rull, 2008, 2011; Hoorn *et al.*, 2010; Antonelli & Sanmartín, 2011; Särkinen *et al.*, 2012a) and palaeontological data (Jaramillo *et al.*, 2006; Hoorn *et al.*, 2010). Furthermore, there is now plenty of evidence to suggest that a single aggregate view of Neotropical plant diversification ignores critical differences in how diversification may have proceeded in different Neotropical biomes occurring in diverse regions and climates (e.g. rain forest, seasonally dry tropical forests, savannas, montane forests, high elevation grasslands (Pennington *et al.*, 2006b, 2009, 2010; Särkinen *et al.*, 2012a), prompting a more nuanced biome-by-biome approach to synthesizing overall patterns of Neotropical plant evolution. These insights have been based largely on phylogenetic data, albeit until recently for just a small number of lineages representing a subset of Neotropical biomes. The new data in this issue provide new phylogenetic hypotheses for additional lineages, many of which corroborate emerging ideas for several of the better-studied Neotropical biomes – high elevation grasslands, seasonally dry tropical forests and savannas (see below) – and new data for what remain somewhat more neglected and less well understood biomes, including Amazonian and Mata Atlántica rain forests (Bardon *et al.*, 2012; Michelangeli *et al.*, 2012; Perret *et al.*, 2012; Roncal *et al.*, 2012), campos rupestres (Trovó *et al.*, 2012) and pampas (Fregonezi *et al.*, 2012).

*High-elevation Andean grasslands*. High-altitude grasslands (including páramo, puna and jalca) occur above *c.* 3000 m in the tropical Andes (Fig. 1K) (Luteyn, 1999; Hughes & Eastwood 2006; Pennington *et al.*, 2010; Sklenář *et al.*, 2011). The páramo alone comprises an estimated 3500 species of vascular plants (Luteyn, 1999; Sklenář *et al.*, 2011). Perhaps one of the most consistent biome-specific patterns is the recency and rapidity of plant diversification in these high elevation Andean grasslands. The idea that the early explosive phase of species radiations, with exceptionally high rates of net species diversification and little evidence of extinction, has been confidently inferred in these geologically young habitats (Hughes & Eastwood 2006; Drummond *et al.*, 2012) and is reinforced by new studies of *Puya* Molina (Bromeliaceae; Jabaily & Sytsma, 2012) and *Lepechinia* Willd. (Lamiaceae; Drew & Sytsma, 2012) presented here. Both these studies reveal further examples of Andean clades that remain largely or completely unresolved and, in the case of *Lepechinia*, a recent divergence time estimate for the Andean clade and species within it (Drew & Sytsma, 2012). The extreme difficulties associated with obtaining robustly supported phylogenetic resolution for high elevation Andean clades prompted Jabaily & Sytsma (2012) to assemble an extensive amplified fragment length polymorphism (AFLP) data set in terms of the number of species analysed, to gain insights into how the large and apparently recent and rapidly diversifying cohort of *c.* 200 species of *Puya* in the Andes may have evolved. It seems clear that in these high elevation Andean habitats a high proportion of the diverse endemic flora has arisen in the last few million years, as deduced from meta-analyses of dated phylogenetic trees separating exclusively high elevation clades from others (Hoorn *et al.*, 2010; Särkinen *et al.*, 2012a). This recency fits remarkably well with geological reconstructions indicating that a major uplift of the central and northern Andes only took place in the last 10 Myr, and in several regions (such as the north-eastern Cordillera) considerably later (Garzione *et al.*, 2008; Hoorn *et al.*, 2010). It also seems that, although more phylogenetic focus has been given to northern immigrants in the Andes, the proportion of southern immigrant lineages in the páramos may be equally large (Sklenář *et al.*, 2011).

*Seasonally dry tropical forests*. Seasonally dry tropical forests (SDTF) are found on generally fertile soils in scattered areas throughout the lowland Neotropics (reaching *c*. 2500 m in some dry inter-Andean valleys) from Mexico to Argentina that receive a four- to six-month dry season that is too severe for rain forest species (Pennington *et al*., 2000, 2006a). SDTF are deciduous or semi-deciduous in the dry season, often rich in cacti and other succulents and with only a few grasses in the ground layer (Fig. 1G–I). Despite a history of neglect compared to the more charismatic and widely publicized lowland tropical rain forests, research on seasonally dry tropical forests has blossomed in the last decade, revealing not only the biological importance of these forests in terms of their highly endemic floras, but also important insights into the biogeography of this biome and the processes and factors that have apparently shaped the historical assembly of SDTF species diversity (Linares-Palomino *et al*., 2011; Prado, 2000; Lavin *et al*., 2004; Pennington *et al*., 2004a, 2006a, b, 2009, 2010; Lavin, 2006; Särkinen *et al*., 2011a, 2012a). A growing number of detailed and well-sampled phylogenetic analyses of SDTF lineages show high levels of dry forest niche conservatism (Pennington *et al*., 2009; Govindarajulu *et al*., 2011), high geographical phylogenetic structure (e.g. Olmstead, 2012), predominance of allopatry and allopatric speciation (e.g. Govindarajulu *et al*., 2011), pre-Pleistocene divergence time estimates for species and clade ages and well-supported monophyly of individual species in densely sampled gene trees. Taken together, this evidence points to a scenario of dispersal limitation across the highly fragmented, disjunct distribution of SDTFs, *in-situ* diversification of pairs or small clades of species in specific SDTF nuclei and long persistence and relative stasis of stable populations of SDTF species and lineages over the past two to ten or more million years (Lavin *et al*., 2004; Lavin 2006; Pennington *et al.,* 2006a, b, 2009, 2010).

*Savannas (cerrado) and campos rupestres*. Like SDTFs, Neotropical savannas are under seasonal rainfall conditions, with at least five to six months receiving <100 mm (Pennington *et al*., 2000). However, they tend to occur on poorer soils (Sarmiento, 1992) and, unlike the deciduous or semi-deciduous SDTFs, savanna trees frequently have sclerophyllous, evergreen leaves (Ratter *et al*., 1997). In contrast to SDTFs, savanna formations do not form closed canopies, even though they may have abundant trees, and they are defined by a xeromorphic, fire-tolerant grass layer (Fig. 1D) (Simon & Pennington, 2012). The largest area of Neotropical savanna, once covering more than two million square kilometres (Ratter *et al*., 1997) is the cerrado of central Brazil and eastern Bolivia. Within the cerrado, and especially along the hills (chapadas) of its eastern margin, are found the higher elevation, rockier, but still fire-prone 'campos rupestres' ('rocky fields') (Fig. 1E).

Several papers in this issue suggest divergence time estimates (Roncal *et al*., 2012) or at least phylogenetic topologies (Trovó *et al*., 2012) for cerrado clades in line with previous evidence for a Late Miocene/Pliocene origin of the diverse, fire-adapted, endemic flora of the cerrado (Simon *et al*., 2009; Simon & Pennington 2012). It is also apparent that for some of the most species-rich genera of the cerrado in the broad sense, such as *Mimosa* L. (Simon & Proença, 2000) and *Paepalanthus* Kunth. (Trovó *et al*., 2012)*,* levels of endemism are higher in the campos rupestres than in cerrado and that phylogenetic analyses of campos rupestres lineages may be geographically structured across several separate chapadas (Trovó *et al*., 2012). Based on their similar fire-prone ecologies and overall physiognomies and their inter-digitated geography, it seems likely that campos rupestres and cerrado lineages will be phylogenetically intermingled, but there are still few data to assess the extent to which campos rupestres species and lineages are derived from cerrado species or vice versa. Diversification of *Hoffmannseggella* H.Jones, an orchid genus restricted to campos rupestres, has been estimated to pre-date diversification of several cerrado lineages by a few million years (Antonelli *et al.,* 2010; Gustafsson *et al.,* 2010). This could indicate that the campos rupestres responded faster to the climate cooling that followed the Mid-Miocene Climatic Optimum, providing the first open habitats in eastern Brazil, followed later by the cerrado (Antonelli *et al*., 2010). Additional studies are clearly needed to shed further light on this topic.

*Lowland rain forests*. Rain forests (Fig. 1A–B) can grow where annual rainfall is *c*. 1500 mm or greater, but what is critical is the lack of extreme seasonality of rainfall (Malhi *et al*., 2009; who provide a detailed discussion of the effects of seasonality in rain forest – savanna/SDTF transition zones). As a rule of thumb, if seasonal drought occurs, the period with rainfall <100 mm per month is three months or less in rain forest regions (Burnham & Johnson, 2004). In contrast to the SDTF, lowland rain forests occupy a much more continuous distribution across the Neotropics, especially across the huge area of Amazonia and the Guianas. It is important to note, however, that these large areas of rain forest are seldom homogeneous. Amazonia encompasses a variety of soil and vegetation types, including high canopy forest on both poor and richer soils, scrub vegetation on white sand forming more or less open habitats (campinas and campinaranas) and forest along river floodplains that is seasonally inundated (várzea and igapó). Amazonia exhibits few obvious dispersal barriers to lowland terrestrial species other than the recently uplifted northern Andes and the many rivers that form the Amazon drainage basin, some of which are wide enough to be suggested as dispersal barriers for some birds (Bates *et al.*, 2004) and primates (Ayres & Clutton-Brock, 1992). However for plants, many rare tree species are apparently widespread, albeit occurring at low frequency. Many species previously thought to be narrow endemics have been shown to be more widely distributed as collecting efforts have gained momentum across the Amazon, suggesting that rivers are unlikely to present significant dispersal barriers for plants.

Neotropical rain forests are occupied by lineages that often show moderate or high levels of species sympatry at community and local scales (up to hundreds of square kilometres). This appears to be reflected in a lack of geographical phylogenetic structuring for several lowland rain forest clades compared to SDTF plant lineages (Lavin, 2006; Pennington *et al.*, 2009; Pennington & Dick, 2010) at geographical scales that correspond to the size of many of the isolated areas of Neotropical SDTF. This is in line with the idea that these forests are not as dispersal limited as SDTF. Genera largely lacking obvious large-scale phylogenetic geographic structure in Amazonia include *Inga* Miller (Lavin, 2006; Kursar *et al.*, 2009), *Clusia* L. (Gustafsson & Bittrich, 2003), *Guatteria* Ruíz & Pavón (Erkens *et al.*, 2007), *Renealmia* L.f. (Särkinen *et al.*, 2007; Pennington & Dick, 2010), *Ruellia* L. (Tripp, 2008) and *Swartzia* Schreber (Torke & Schaal, 2008). While current data suggest that this may indeed be a dominant pattern, well-resolved and densely-sampled phylogenetic analyses of more lineages are needed to test these ideas.

Although divergence time estimates for several lowland rain forest lineages are surrounded by uncertainties, there is growing evidence that many species-rich Amazonian clades have diversified within the last 10 million years and potentially even more recently (Richardson *et al.*, 2001; Lavin 2006; Roncal *et al.*, 2012), suggesting high rates of net species diversification. These patterns are exemplified by the large Neotropical rainforest genus *Inga* (Fabaceae) which shows a contiguous distribution across the wet lowland Neotropics (Pennington, 1997) and remarkable levels of sympatry (e.g. up to 50 species in single one degree latitude/longitude squares; Reynel & Pennington, 1997; Kursar *et al.*, 2009), recent crown-node age estimates (Richardson *et al.*, 2001; Lavin, 2006), lack of obvious large-scale geographical structure across the phylogenetic tree (Richardson *et al.*, 2001; Lavin, 2006) and rapid evolution of leaf defence chemistry as a possible driver of rapid recent speciation and maintenance of high levels of sympatric species diversity (Kursar *et al.*, 2009).

A potentially key factor in the evolution of Amazonian biodiversity is the Mid-Late Miocene dominance of vast wetlands, in western Amazonia, and most importantly the Pebas system (Wesselingh *et al.*, 2002, 2010; Antonelli *et al.,* 2009; Hoorn *et al.*, 2010; Antonelli & Sanmartín, 2011). An important question here is whether diversification of species-rich lowland rain forest clades post-dates the drainage of these systems such that they constrained colonization and inhibited *in-situ* species diversification, or whether most diversification took place elsewhere (e.g. along the margins of the wetlands or in patches of *terra firme* forests) prior to the drainage and subsequently colonized western Amazonia. The Pebas system may also have played a role as dispersal barrier for pre-Pebas clades that could account for the well-known (Gentry, 1982) pattern of Andean-centred vs. Amazonian-centred biodiversity (Antonelli & Sanmartín, 2011). To date, very few molecular phylogenetic or biogeographical studies have addressed the influence of the Pebas wetlands on the diversification dynamics and distribution patterns of Neotropical plant lineages. A notable exception in this issue points in the direction of post-Pebas, *in-situ* diversification for the palm genus *Astrocaryum* G.Meyer (e.g. Roncal *et al.*, 2012), in line with recent divergence time estimates for other lowland rain forest clades (Richardson *et al.*, 2001; Erkens *et al.*, 2007) and with ideas that diversification of western Amazonian lineages occurred after drainage of the Pebas system (Antonelli *et al.*, 2009; Hoorn *et al.*, 2010).

The post-Pebas recency, rapidity and lack of significant large-scale dispersal limitation, all point to other principally biotic factors as the most likely drivers of species diversification in Neotropical lowland rain forests. These might include fine-scale niche differentiation reflecting adaptations to local hydrological and soil variation (Fine *et al.*, 2005), much of which can be ultimately derived from geotectonic processes in the Neogene. It seems clear, for instance, that the huge input of Andean-derived nutrients deposited in western Amazonia during the Pebas and Acres systems has played a role in shaping the taxonomic composition and possibly diversification of Amazonian taxa (Hoorn *et al.*, 2010). Other important, but often overlooked and still poorly understood factors include biotic interactions between plants and their pollinators (Kay *et al.*, 2005), dispersal agents and herbivores (Kursar *et al.*, 2009). Here, Eiserhardt *et al.* (2012) provide evidence for the critical importance of environmental filtering caused by hydrological and edaphic variation in assembly and maintenance of palm diversity in Amazonian lowland rain forests. Importantly, all these mechanisms call into question the once dominant view that most speciation in Amazonia took place in allopatry, as dictated under the original refuge hypothesis (Haffer, 1969), and suggest that we should be examining other potential models of speciation that may not invoke geographical barriers (Fine *et al*., 2004, 2005; de Aguiar *et al*., 2009). More robustly supported phylogenetic resolution of species within rain forest clades, which has so far proved elusive using traditional DNA sequence loci, just as it has been for high elevation Andean clades is needed. Perhaps even more crucially, denser taxon sampling for groups where obtaining material for DNA extraction has been problematic up to now, will be a prerequisite for gaining insights into these questions.

## SPECIES TURNOVER AND THE NEOGENE ORIGIN OF MODERN NEOTROPICAL DIVERSITY

Whatever the detailed differences in timing and trajectories of species diversification and their underlying causes in different Neotropical biomes, combined evidence across all Neotropical plant lineages strongly suggests that high rates of species turnover may have been the hallmark of plant evolutionary dynamics in the Neotropics through much of the Cenozoic, and that a very high, but as yet unquantified, fraction of extant species diversity post-dates the Mid-Late Miocene. On the one hand there is startling evidence for repeated near-complete turnovers in species composition of fossil pollen from cores spanning the Cenozoic in north-western South America (Jaramillo *et al*., 2006; Hoorn *et al.,* 2010). On the other hand, several meta-analyses of plant phylogenies (e.g. Rull, 2008, 2011; Simon *et al*., 2009; Hoorn *et al*., 2010; Antonelli & Sanmartín 2011; Särkinen *et al*., 2012a) and several recently published phylogenetic analyses including important Neotropical plant clades (e.g. Arakaki *et al*., 2011; Nagalingum *et al*., 2011) have revealed the marked prevalence of species diversification across many lineages and different Neotropical biomes from the Late Miocene and relatively little to no evidence of extant clades sharing most recent common ancestors in Gondwanan times (i.e. prior to *c*. 90 million years ago) (Hoorn *et al*., 2010). Six of the seven papers in this issue that include time-calibrated phylogenetic trees include striking examples of species-rich Neotropical clades that originated in the Late Miocene or later, e.g. *Couepia* Aublet and *Hirtella* L. (Chrysobalanaceae) (Bardon *et al*., 2012); species-rich Andean and Mata Atlántica clades of Gesnerioideae (Gesneriaceae) (Perret *et al*., 2012); *Lepechinia* (Lamiaceae) (Drew & Sytsma, 2012); Trachycarpeae (Arecaceae) (Bacon *et al*., 2012); *Astrocaryum* (Arecaceae) (Roncal *et al*., 2012) and marked lack of phylogenetic resolution and short branch lengths are also suggestive of recent diversification for *Paepalanthus* (Eriocaulaceae) in campos rupestres (Trovó *et al*., 2012) and *Petunia* Juss. and *Calibrachoa* Cerv. (Solanaceae) in the pampas (Fregonezi *et al*., 2012).

There are still relatively few estimates of species diversification rates for Neotropical plant clades, let alone of the underlying speciation and extinction rates or diversification rate shifts, but the few that there are, including new data for Chrysobalanaceae (Bardon *et al*., 2012) presented here, provide further evidence for high species turnover. For Chrysobalanaceae, Bardon *et al*. (2012) suggest that higher speciation rates in the Neotropics may account for the much higher Neotropical vs. Palaeotropical species diversity in that family, but also show that higher Neotropical speciation was accompanied by high rates of extinction (despite overall net species diversification still being higher than in the Palaeotropics). Once again, these results provide intriguing pointers towards the idea of high species turnover and a preponderance of Mid to Late Miocene and later diversification of extant species diversity. The methodological advances in estimating speciation, extinction and net diversification rates from both the fossil record and phylogenies (see below) point the way to how these ideas can be thoroughly tested in coming years.

## BIOME CONSERVATISM OR NOT?

Many of the studies in this issue also reinforce the idea that continental-scale patterns in Neotropical plant phylogenies are first and foremost ecologically rather than geographically structured, and that large-scale phylogenetic niche/biome conservatism (*sensu* Schrire *et al*., 2005; Donoghue, 2008; Crisp *et al*., 2009; Crisp & Cook, 2012) has played a significant role in shaping Neotropical plant evolution. The tropical-temperate divide as a major adaptive barrier and the prevalence of tropical niche conservatism have long been recognised (Wiens & Donoghue, 2004), but like most large-scale ecological adaptive barriers it has not been quantified in any detail. The comparative analysis of the latitudinal extents of 32 New World clades of Solanaceae, Bignoniaceae and Verbenaceae in North and South America presented by Olmstead (2012) provides a rare example of quantification of tropical niche conservatism, demonstrating striking consistency of the northern and southern distribution limits, the extent to which these clades have succeeded in colonizing both North and South America and the very low proportions of species in each family (1%, 5% and 7.5%, respectively) that occur outside the tropics. Olmstead's study also adds at least four more examples of large-scale New World amphitropical disjunctions, which share similar semi-arid or arid ecologies separated by thousands of kilometres in North and South America, again providing strong evidence of larger scale phylogenetic niche conservatism across drylands. Similarly, there are several other striking examples of clades confined to wet or dry biomes documented here (Olmstead, 2012; Lu-Irving & Olmstead, 2012; Michelangeli *et al*., 2012).

The potential importance of ecology in shaping patterns of co-existence and community assembly at smaller spatial scales has long been recognised, and new methods of analysing the phylogenetic structure of communities have been developed to help elucidate the importance of evolutionary process in the assembly of biological communities (Webb *et al*., 2002, Cavender-Bares *et al*., 2009). While first used for studies at small spatial scales (a few hectares), they can be co-opted for much larger, even continental, scales (e.g. Pennington *et al*., 2006b; Kissling *et al*., 2012). Here, Eiserhardt *et al.,* (2012) use community phylogenetic methods to show that environmental filtering, especially in relation to hydrological and soil features, is potentially critical in the assembly and maintenance of high species diversity in lowland rain forests and that niche conservatism appears to be a prominent feature of Amazonian flood-plain palms, probably due to the unique adaptations in phenology and tolerance of submergence required to live in inundated forests.

Several contributions presented here add to growing evidence that the distribution of plant diversity at all spatial scales can indeed be partitioned by strong adaptive barriers posed by, e.g., drought, cold and flooding tolerance. As documented by Crisp *et al*. (2009) for southern hemisphere temperate and subtropical biomes, at broad geographical scales in the Neotropics, the overall pattern that is emerging is one suggesting predominance of niche or biome conservatism. As documented by Perret *et al*. (2012) for Gesnerioideae, Michelangeli *et al*. (2012) for Melastomeae (Melastomataceae) and Olmstead (2012) for Verbenaceae and Lycieae (Solanaceae), numerous, often species-rich radiations (often encompassing genera or clades of several genera) show remarkable ecological and geographical integrity within biomes. This ecological stasis is apparently punctuated relatively infrequently by major ecological shifts, in many cases apparently associated with the recognition of different genera, such that all or most plant families occupy a wide range of, and in many cases all, Neotropical biomes (e.g. Olmstead, 2012). One prominent exception to this idea of large-scale ecological adaptive barriers shaping species diversification is the apparent ease of fire adaptation, whereby many plant lineages have been recruited to the cerrado from diverse and geographically adjacent dry, wet and pampas biomes (Simon *et al*., 2009; Simon & Pennington, 2012). A number of new studies in this issue also suggest recruitment of cerrado lineages from both adjacent dry and rain forest biomes [e.g. *Lippia* L./*Lantana* L. in Verbenaceae from dry adapted ancestors vs. *Stachytarpheta* Vahl. (Verbenaceae) from rain forest ancestors (Olmstead 2012)]. However, current taxon sampling is still too low to assess properly the monophyly and hence the numbers of transitions to cerrado for many of these large species flocks endemic to the cerrado (Olmstead, 2012; Trovó *et al*., 2012).

A second intriguing exception to this picture of widespread biome conservatism comes from the tribe Bignonieae (Bignoniaceae) study of Lohmann *et al*., (2012), showing that lianas tend to have wider geographical distributions and ecological amplitudes than many other plant groups, such that many liana species span several biomes, suggesting that liana life history could be less niche conserved than some other plant types. This study highlights the need for more phylogenetic analyses to ensure that all life forms are well sampled across all major biomes before general conclusions about the number of evolutionary shifts among biomes can be made.

## DISPERSAL LIMITATION

Although evidence for the significance of major adaptive (ecological) barriers for diversification appears ever more compelling, the same cannot perhaps be said for the major geographical dispersal barriers considered to have played critical roles in shaping the historical assembly of species in the Neotropics. Many of the papers in this issue present convincing evidence for frequent dispersal over oceans and between continents. Foremost among these are the numerous instances of Old World – New World post-Gondwanan dispersal newly documented here, e.g. at least five in Chrysobalanaceae (Bardon *et al*., 2012) and at least 15–17 in Solanaceae, five or six in Bignoniaceae and six in Verbenaceae (Olmstead, 2012; Christenhusz & Chase 2012), adding to the now overwhelming evidence that intercontinental dispersal is commonplace among flowering plants (e.g. Pennington *et al*., 2004b; Lavin *et al*., 2004; Renner, 2004; Pennington & Dick, 2004). Similarly prominent is the frequency of north-south and south-north dispersal between North and South America. Indeed several studies presented here suggest that the majority of large New World plant clades with ancestral areas in South America have succeeded in reaching North America (e.g. Bacon *et al*., 2012; Olmstead, 2012; Lohmann *et al*., 2012; Roncal *et al*., 2012), with a mix of several relatively old and many recent trans-Panama dispersals. Recent evidence for significantly earlier collision of the South American and Panamanian plates and closure of the Central American Seaway (Farris *et al*., 2011; Montes *et al*., 2012) is prompting re-evaluations of the timing and importance of overseas vs. overland/stepping-stone migration for the numerous Neotropical plant lineages that span North and South America, and of the difficulties of disentangling these two alternatives using time-calibrated phylogenetic trees (e.g. Bacon *et al*., 2012; Olmstead, 2012). We can see little evidence from the studies presented in this issue, or previous data (Cody *et al*., 2010), that over-water gaps prior to completion of the Panama land bridge presented a significant barrier for plants.

This apparent frequency and ubiquity of dispersal explanations for disjunctions across several of the most prominent dispersal barriers implicated in studies of Neotropical biogeography does not imply completely unfettered dispersal or that some Neotropical biomes or clades are not dispersal limited, but simply that what we need to be measuring and attempting to quantify is comparative dispersal limitation for different lineages and geographical barriers. For example, as mentioned above, there is growing evidence to suggest that diversification across the highly fragmented disjunct distribution of SDTFs across the Neotropics and beyond has been shaped by dispersal limitation (Lavin *et al*., 2004). It would appear that SDTFs of some inter-Andean valleys, such as the Marañon valley in northern Peru, may be among the most dispersal limited systems, mirroring the geographical isolation of oceanic islands (Pennington *et al*., 2010; Särkinen *et al*., 2012a). It thus seems that some Neotropical biomes are much more dispersal limited than others (Lavin 2006; Pennington *et al*., 2009).

It has been suggested that the dispersal limitation of Neotropical seasonally dry forests does not only reflect their disjunct distribution, but may also be reinforced by their ecology and how this influences the successful establishment of immigrants (Lavin, 2006; Pennington *et al*., 2009, 2010). This is partly another expression of the power of niche conservatism – the SDTF biome may only be open to immigration by lineages that already have drought adaptations allowing them to survive a seasonal environment (Schrire *et al*., 2005; Pennington *et al*., 2009), adaptations which are lacking in species from adjacent biomes that experience non-seasonal climates (e.g. rain forests). The resident plants in SDTF are resistant to drought (which causes mortality in rain forests), such that saturation of the woody plant community (*sensu* Hubbell, 2001) may further restrict immigration. Additionally, the SDTF biome is not prone to fire disturbance, which is widespread in savannas, in the absence of humans. Consideration of the intrinsic ecology of biomes and the plants that occupy them and how that affects the establishment phase of immigration, are thus likely to be an important and perhaps neglected factor to consider when assessing the power of dispersal as a biogeographic force. For example in this issue, Christenhusz & Chase (2012) point out that despite the great mobility of the dust-like seeds of orchids, the phylogeny of Orchidaceae is highly geographically structured, with major clades confined to continental areas. The probable explanation is complex mycorrhizal associations required for mature plants to establish (Christenhusz & Chase, 2012).

It is thus not so much a question of whether dispersal occurs, but rather about understanding and quantifying dispersal limitation and its impacts on patterns of diversification. Relative ease of dispersal (often over long distances) and subsequent successful establishment can be key for large-scale ecological structuring of lineages across biomes, whereby areas with comparable ecologies can be occupied by single lineages or sister lineages even if they are geographically highly disjunct. Several striking examples of this documented here and elsewhere suggest that, as proposed by Donoghue (2008), for many Neotropical plant lineages it has indeed been '*easier to move than to evolve*'. We anticipate that defining and quantifying more precisely and comprehensively the relative strengths of ecological adaptive barriers, coupled with similarly greater understanding of levels of dispersal limitation and the interplay and trade-offs between the two (see also Crisp & Cook, 2012), will be key to gaining a better understanding of large scale plant biogeography and evolution in the Neotropics and elsewhere. The knowledge acquired, especially if combined with experimental research (e.g. common garden experiments; cf. Fine *et al*., 2004), would not only teach us more about the evolutionary processes underlying biome and niche shifts. They might also offer tools for assessing how plant diversity may respond to climate change, e.g. by indicating the extent to which lowland plants might be able to survive at higher temperatures *in situ* or increase their altitudinal ranges to track their current climatic requirements and tolerances.

## WHAT'S NEXT?

*Defining and mapping areas and ecology.* Given the central importance of ecology and biomes in shaping biodiversity, how we delimit and map biomes is a critical issue for continental-scale macroevolutionary and biogeographical studies. However, for the Neotropics, especially at the continental scale, there is a striking lack of consistency and precision in how supposed phytogeographic regions, major biomes and vegetation types are partitioned, categorized and mapped. Even among recent studies, some authored by ourselves (e.g. Simon *et al.*, 2009; Antonelli & Sanmartín, 2011) and some in this issue, many different area/biome categories are used, a few large ones to much more narrowly defined small ones and at varying levels of spatial resolution. These inconsistencies not only generate confusion, but also greatly limit the scope for integration and comparison amongst studies of different plant groups. Currently available maps of major Neotropical biomes perform poorly due to either poor biome delimitation and/or poor spatial resolution (Pennington *et al.*, 2009; Särkinen *et al.*, 2011b; Oliveira-Filho *et al.*, in press). These problems perhaps reflect the lack of a widely accepted Neotropics-wide biome synthesis and map that mirror White's (1983, 1993) monumental Vegetation Map synthesis for Africa. Such a broad-scale synthesis can cut through three key problems. The first is the over-split vegetation types used at national levels, which often employ local names for vegetation and therefore make continental synthesis very difficult (e.g. the names caatinga, agreste, mata acatingada, mesotrophic, mesophilous or mesophytic forest, semideciduous or deciduous forest, bosque caducifolio, bosque espinoso, have all been used for the seasonally dry tropical forest biome; see Murphy & Lugo, 1986, 1995; Lugo *et al.*, 2006; Pennington *et al.,* 2006a). The second is the recognition that remote sensing approaches do not always reflect biological reality without ground-truthing and/or consideration of the effects of habitat alteration. An example of the importance of ground-truthing, highlighted by Särkinen *et al*. (2011b), is equating the woodlands of the Chaco, which have temperate floristic affinities, with seasonally dry tropical forests (Eva *et al*., 2004). For biogeography we need to understand the full distribution of biomes prior to extensive clearance and alteration, and this is difficult from remote sensing for biomes such as mid-elevation montane forest and seasonally dry tropical forest, which in many areas are nearly entirely destroyed.

Though it is beyond the scope of this paper, we see a clear and pragmatic need for greater consensus around a set of continental-scale biome and phytogeographical categories for the Neotropics with schematic maps that can be widely adopted for large scale biogeographic studies of the kind presented by many of the studies in this issue. There have been labyrinthine debates about vegetation definitions based upon subtleties of taxonomic composition and relative abundance of species (e.g. Poore, 1955; Mucina, 1997) which cannot be summarized here, and biomes are complex empirical realities that are hard to organize into fixed categories. However, to study evolution and ecology, definitions of biomes/phytogeographical regions that are biologically meaningful may be most useful (Särkinen *et al.,* 2011b). Historically, this has meant taking into account floristic similarity at different taxonomic levels (e.g. White, 1983, 1993), climatic factors and vegetation physiognomy. Extensive georeferenced specimen datasets can now be subjected to cluster and classification analyses to establish common biogeographic regionalisations for diverse groups at a continental scale (e.g. Kreft & Jetz 2010; Linder *et al*., 2012). Another promising approach for a single biome was recently outlined by Särkinen *et al*., (2011b), who refined the map of South American seasonally dry tropical forests using an extensive database of georeferenced herbarium records and bioclimatic data. In the context of considering similarity at different taxonomic levels, a far more nuanced view, moving beyond simple Linnean categories, is now possible by considering phylogenetic information, and there are suggestions that biomes could be defined as 'evolutionary metacommunities' (e.g. Pennington *et al*., 2009; Särkinen *et al*., 2012a) – separated in an evolutionary sense by niche conservatism. Community phylogenetic approaches may also prove useful in exploring biome definitions in this context (e.g. Oliveira-Filho *et al.,* in press, for cerrado and seasonally dry tropical forest). Whatever approach is followed for the categorisation of phytogeographic regions, biomes and vegetation types, it would be helpful that resulting maps are GIS-based layers or polygons, so that occurrence data can be unambiguously coded for purposes such as analyses of ancestral areas and phylogeographic structure.

*Neglected biomes.* Lack of data and understanding persists for several major Neotropical biomes, including the woodlands of the Chaco (defined by Prado, 1993a, b), the southern grasslands (see Iganci *et al*., 2011), campos rupestres (see above), the Mata Atlántica and mid-elevation montane forests, especially in the Andes, Central America and southern Mexico (defined for the Andes by Pennington *et al*., 2010 and Särkinen *et al*., 2012a) (Fig. 1). In some cases, the exact nature and distinctiveness of these biomes needs to be clarified. A recent study of the grasslands of southern Brazil and neighbouring countries by Iganci *et al*. (2011) is an example of the kind of study that is needed. They showed that subtropical grasslands in southern Brazil (Campos de Cima da Serra – Fig. 1F) are distinctive in terms of species composition and high species endemism when compared with tropical (e.g. the cerrado) and temperate grasslands (e.g. the pampas of Argentina and Uruguay). In addition, we still know rather little about the history and development of these biomes. In this context, several contributions in this issue are most welcome, such as the new phylogenetic analyses for lineages from pampas (Fregonezi *et al*., 2012), Amazonian (Bardon *et al*., 2012; Roncal *et al*., 2012), Mata Atlántica (Lohmann *et al*., 2012; Perret *et al*., 2012) rain forests and campos rupestres (Trovó *et al*., 2012). Of particular interest are the hyperdiverse mid-elevation montane rain forests of the Andes. Very few phylogenetic analyses are available for the many species-rich groups in these forests, and none of them is well-sampled compared to those for clades in lower Andean dry forests and high elevation Andean grasslands (Särkinen *et al*., 2012a).

*Enhanced and mega phylogenies using genome-scale data.* In a previous symposium entitled *Plant Phylogeny and the Origin of Major Biomes* (Pennington *et al*., 2004b), the power of phylogenetic approaches to provide potent insights into geotemporal patterns of species diversification was highlighted and an expansion of phylogenetic evidence predicted. This has indeed been the case. Fourteen of the 16 papers in this issue use phylogenetic evidence to infer patterns of diversification, and many other new phylogenetic analyses published in the last eight years have provided insights into geotemporal patterns of Neotropical plant diversification (e.g. Hughes & Eastwood, 2006; Antonelli *et al*., 2009; Simon *et al*., 2009; Nagalingum *et al*., 2011; Arakaki *et al*., 2011; Kissling *et al*., 2012; Pennington *et al*., 2006b, 2010). While the many wider and deeper insights into geotemporal patterns of diversification, the prevalence of niche conservatism and the differential impacts of dispersal limitation in different biomes discussed above are all compelling, they are still based on just a small number of pieces of what is clearly a big and complicated puzzle.

Compared to eight years ago, perhaps what is most striking is that we now have basic phylogenetic analyses for many more plant groups, providing scope to test early biogeographical insights that were based on just a handful of analyses with larger and more representative samples of lineages. However, it is also clear that the quality of plant phylogenetic trees has perhaps not improved as rapidly as might have been expected. With notable exceptions, current phylogenetic analyses are still in the main based on a small number of standard DNA sequence loci, often mostly from the plastid genome and rarely amounting to > 10kb, generally 4–5kb, of aligned sequence, and often even less. In some cases, even at species and subspecific levels, this can result in well-resolved, well-supported topologies (e.g. Pennington *et al*., 2010; Särkinen *et al*., 2012a). However, lack of resolution and support, as well as incomplete taxon sampling, remain significant issues when it comes to interpretation of many trees in terms of ancestral areas and ecologies or temporal trajectories of diversification. While the holy grail of complete, well-resolved and robustly supported phylogenies is easy to imagine, such trees are less easy to achieve in practice and have proved largely elusive so far. Such studies are difficult because they need to sample all described species (e.g. possibly a minimum of 80% taxon sampling to estimate diversification rates confidently; Cusimano & Renner, 2010) and, ideally, should sample multiple individuals per species to encompass intra- as well as interspecific diversity and assist in uncovering potential cryptic species (e.g. Govindarajulu *et al*., 2011; Särkinen *et al*., 2011a). More difficulties arise because a potentially significant proportion of the actual species diversity is yet to be discovered or, even worse, because many species may have already gone extinct by human activity (disrupting the background extinction rate).

The reconstruction of time-calibrated trees has seen much wider adoption and methodological advances; seven of the papers in this issue present time-calibrated phylogenetic trees, all of them using the program BEAST (Drummond & Rambaut, 2007), although lack of fossils means that calibration remains an issue for many lineages. Optimization of ancestral areas and ecologies onto phylogenetic trees remains somewhat uncertain methodologically, with little consensus as to the best of the several newly emerging approaches to use, although this is also a reflection of the large differences in data used and hypotheses to be tested (Ree & Sanmartín, 2009; Pirie *et al*., 2012). There is also a need to apply and test the new and increasingly sophisticated methods more widely to estimate rates of diversification, detect shifts in diversification rates and potentially tease apart whether these are attributable to changes in speciation or extinction rates or both (Alfaro *et al*., 2009; Silvestro *et al*., 2011; Morlon *et al*., 2011; Stadler, 2011); only two of the studies in this issue (Bardon *et al*., 2012; Roncal *et al*., 2012) estimate diversification rates.

These limitations of many current phylogenetic analyses suggest that the full potential of such approaches to track evolution and diversification has yet to be realized. We foresee great scope for larger and more completely sampled (all, or nearly all, species, plus sampling of intraspecific diversity) studies that can integrate information across different taxonomic, geographical and temporal levels and with scope for potentially powerful new insights into evolutionary diversification processes (Barraclough, 2010). More rigorous quantitative analyses (e.g. Crisp *et al*., 2009; Kissling *et al*., 2012) using enhanced, well-resolved, robustly supported and densely sampled mega phylogenies of much larger clades, and ultimately all plants, will be needed to reveal the balance between biome switching and phylogenetic biome conservatism in shaping geotemporal patterns of plant species diversification and the evolutionary dynamics of diversification across time and space. Bigger and better phylogenetic trees using next generation sequencing technologies (see below) offer excellent prospects for answering many of these questions across a range of spatial and temporal scales in the next few years. Cross-taxonomic comparisons, e.g. including not only plants but also seemingly disparate organismic groups such as metazoans and fungi, would also provide new insights into the ecological and evolutionary interactions that have formed the Neotropical biodiversity we see today.

New, enhanced and much bigger phylogenetic trees will depend on effective use of the recent biodiversity genomics revolution and rapidly advancing and ever-cheaper next generation sequencing technologies that permit ready access to genome-scale data for any plant group and open up massive new opportunities in phylogenetics (Harrison & Kidner, 2011). Most immediately this means easier access to many low-copy nuclear genes and a much wider selection of more informative DNA sequence loci for any group of taxa, something that has been difficult up to now. More widely, these technologies mean that there is no longer a need to choose between taxon and gene sampling in phylogeny reconstruction, especially given the constantly decreasing sequencing costs, options for targeted enrichment sequence capture (Cronn *et al.*, 2012; Grover *et al.*, 2012) and deep multiplexing (Rohland & Reich, 2012), and the potential of these methods to use partially degraded DNA (Mason *et al.*, 2011; Straub *et al.*, 2012; Särkinen *et al.*, 2012b), thereby opening more possibilities to use DNA extracted from even relatively old herbarium specimens. At the same time, inclusion of at least a subset of standard loci across all plant lineages [e.g. the standard barcoding loci *rbcL* and *matK* (Hollingsworth, 2011)] will be highly desirable to provide the sort of robust scaffold that is potentially required for supermatrix approaches to build mega-phylogenies (e.g. Sanderson *et al.*, 2010). All these developments hold the promise of much enhanced, more robust, more completely sampled and bigger phylogenies. This will open the way for more sophisticated and accurate, quantitative analyses of biogeography and niche conservatism and estimation of divergence times and dynamics of diversification in the next few years.

Of course it is also likely that denser sampling of genes, taxa and intraspecific diversity will continue to reveal ever more clearly the full intricacies, complexities and potential intractabilities of disentangling gene and species histories close to the species boundary, as illustrated by new studies in this issue (Drew & Sytsma, 2012; Lu-Irving & Olmstead, 2012). While coalescence of sequences of nuclear loci and resultant monophyly of species clades comprising multiple accessions of species have been found, and can be expected for older clades [e.g. seasonally dry tropical forest lineages where long persistence of populations in evolutionary persistent dry forest patches has prevailed (Lavin, 2006; Pennington *et al.*, 2011; Govindarajulu *et al.*, 2011)], for more recent and rapidly evolving clades, even much larger data sets comprising sequences of tens or hundreds of loci may still not reveal unequivocal hypotheses of species relationships. There is little doubt that disentangling divergent species relationships for the many examples of recent species radiations found across different Neotropical biomes is likely to remain a challenging endeavour for those interested in understanding how such radiations have evolved.

*Fossils.* Despite the fact that before modern molecular phylogenetics the fossil record provided the only source of evidence about diversification through time, the lack of papers focused on the fossil record in this issue is perhaps a disappointing omission, especially as there appear to be prospects and a real need for renewed focus on fossil evidence, as presented, for example, by Pirie & Doyle (2012) for Annonaceae. New palaeobotanical research as well as deeper and wider synthesis, verification and integration of existing fossil data in online databases to maximise what can be gleaned from the plant fossil record in the Neotropics are needed. This will allow us: to discover the most appropriate fossils to use for calibrating phylogenies; to generate ‘complete’ phylogenies, i.e. those that include all extant taxa plus fossils; to quantify origination and extinction rates through time for groups with especially rich fossil records; to attempt to integrate and reconcile fossil-based geotemporal diversification trajectories with what are often discordant phylogeny-based trajectories (Etienne *et al.*, 2012; Morlon *et al.*, 2011; Stadler, 2011); and to track the appearance of different biomes through time (e.g. Burnham & Johnson, 2004; Jacobs, 2004).

## CONCLUSIONS – TOWARDS A NEW SYNTHESIS

The coincidence of diverse global geological and climatic events in the Neogene was instrumental in establishing the modern world and much of the landscape as we know it today (Potter & Szatmari, 2009). Foremost among these changes was the Late Miocene global cooling and drying and consequent greater seasonality and expansion of dry and open habitats that caused the dramatic diversification of many dry-adapted plant lineages (Antonelli *et al*., 2010; Arakaki *et al*., 2011; Nagalingum *et al*., 2011) and contributed to the expansion of C4 grasslands (Edwards & Smith 2010; Edwards *et al*., 2010; Arakaki *et al*., 2011) and subsequent establishment of the savanna biome, including the cerrado biodiversity hotspot in the Neotropics (Simon *et al*., 2009; Simon & Pennington, 2012). In addition to global-scale change in the Late Miocene, several previously poorly understood or misunderstood Neotropical geological events are now thought to have also occurred in the Mid-Late Miocene including: the nearly complete formation of the Panama landbridge (Farris *et al*., 2011; Montes *et al*., 2012; Bacon *et al*., 2012); the massive Pebas system of shallow lakes and swamps that prevailed across much of western Amazonia in the Mid Miocene, and which dried up during the Late Miocene (Hoorn *et al*., 2010; Roncal *et al*., 2012); and a critical phase of particularly rapid Andean uplift starting *c*. 9–10 million years ago (Garzione *et al*., 2008; Hoorn *et al.,* 2010) which finally established the Andes as a prominent and continuous barrier to moisture and plant dispersal (Särkinen *et al*., 2012a), and led to the emergence of the high elevation Andean grassland biomes with many spectacular examples of rapid plant species diversification (Hughes & Eastwood, 2006), several of which are documented here (Drew & Sytsma, 2012; Jabaily & Sytsma, 2012), as well as the deeper isolation of inter-Andean SDTFs (Pennington *et al*., 2010; Särkinen *et al*., 2012a). The congruence of these events and the preponderance of Mid to Late-Miocene or younger crown ages for species-rich Neotropical plant clades (e.g. Rull 2008, 2011; Simon *et al*., 2009; Hoorn *et al*., 2010; Antonelli & Sanmartín 2011; Arakaki *et al*., 2011; Nagalingum *et al*., 2011; Särkinen *et al*., 2012a) is striking. Equally striking is the lack of lineages sharing ancient (Gondwanan) most recent common ancestors among the Neotropical biota (Hoorn *et al*., 2010; Antonelli & Sanmartín 2011) and the evidence of repeated near-complete species turnover across much of the Cenozoic (Jaramillo *et al*., 2006; Hoorn *et al.,* 2010). All these strands of evidence suggest that the Neogene, perhaps especially the Late Miocene, was a pivotal time for establishment and diversification of the modern Neotropical flora and that a very large fraction of extant Neotropical plant species diversity has arisen within the last 10 million years.

A second strand of emerging consensus, at least from a phylogenetic perspective, is that different geotemporal patterns and processes underlie the historical assembly of species diversity in different Neotropical biomes, for example in the patterns of geographic structure in rain forest and seasonally dry tropical forest clades (Lavin, 2006). It seems a fruitful approach to investigate patterns of diversification separately in different biomes because they may be shaped by the ecology of the biomes and by the intrinsic ecological attributes of the plants inhabiting them as much as, or potentially more than, by specific geological or climatic events. Such a synthesis of ecology and history is neatly encapsulated in the recent studies showing how broad-scale niche conservatism, operating over evolutionary timescales, has shaped patterns of diversification. In addition, closer consideration of ecology is clearly needed to understand diversification at least in some major biomes, e.g. that driven by narrow-scale biotic (hydrological, soil, plant-non-plant interactions) niche differentiation. At both continental and local spatial scales, co-opting community phylogenetic methods seems a worthwhile approach to understand the effects of ecological factors operating over evolutionary timescales (e.g. Eiserhardt *et al*., 2012).

One of the greatest botanists of the 20th Century, Alwyn H. Gentry, addressed the question of Neotropical hyperdiversity in a seminal paper with the title: 'Neotropical floristic diversity: phytogeographical connections between Central and South America, Pleistocene climatic fluctations, or an accident of the Andean orogeny?' (Gentry, 1982). Three decades later, we are nearer to understanding why there are so many plant species in the Neotropics and, as often happens, Gentry's conclusions were prescient. As Gentry concluded in his paper, Neotropical diversity has arisen from a complex interplay of factors, rather than due to a single, overarching cause. In addition, it seems that although the large abiotic (geological and climatic) events he outlined were crucial for 'setting the stage' for species diversification, the exceptional diversification in the Neotropics may have taken place at finer scales and have been regulated by ecological and biotic processes (Antonelli & Sanmartín 2011).

Gentry (1982, 1989) also speculated that the reason for Neotropical hyperdiversity of species lay in elevated diversification rates in the Neotropics (as compared at least to Africa). In terms of broad patterns, Gentry's ideas once again appear to be borne out by more recent research. Evidence is accumulating that suggests that high species turnover has prevailed throughout much or all of the Cenozoic, and that higher speciation, rather than low extinction, may have been instrumental in the assembly of Neotropical biodiversity (e.g. Kissling *et al*., 2012; Bardon *et al*., 2012). Global-scale analyses of pantropical lineages that have high Neotropical diversity provide the most obvious way to test these ideas properly. If higher speciation rates, rather than low extinction rates, have fundamentally underpinned Neotropical diversification, this at least narrows the focus to one of understanding the underlying causes of high speciation rates especially since the Mid to Late Miocene.

Botanical and especially plant evolutionary research in the Neotropics is gaining new momentum in important ways, not least in the wonderful blossoming of research and associated resources and infrastructure in plant systematics and evolution across Latin America itself, that is strongly reflected in the contributions in this issue. We hope that some of the questions and pointers highlighted here and in other papers in this issue will provide further motivation and inspiration for what promises to be an exciting next decade of research in Neotropical plant evolution.

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