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The Amazon drainage basin (Amazonia) contains the largest continuous area of tropical rainforest in the world and is the most species-rich terrestrial ecosystem on Earth. In biogeographical terms, the Amazon rainforest is still somewhat of a mystery, beset by data shortfalls in many taxonomic groups, lacking systematic surveys and faced with the challenge of collecting and collating data over a vast area. Nevertheless, considerable progress has been made over the last 20 years, leading to new insights from diverse fields of study. One of the most exciting developments has been the creation of large international research networks which are collating and synthesizing information from widely scattered permanent botanical plots. Data from these networks and other



studies are providing valuable new insights on contemporary biodiversity patterns and processes in Amazonia. Here we review the major findings of these networks and discuss the factors that correlate with and may explain the spatial distribution of Amazonian tree species and the factors that may underpin the emergent patterns of functional traits and diversity across the Amazon Basin.

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The ecological biogeography of Amazonia

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Abstract. The Amazon drainage basin (Amazonia) contains the largest continuous area of tropical rainforest in the world and is the most species-rich terrestrial ecosystem on Earth. In biogeographical terms, the Amazon rainforest is still somewhat of a mystery, beset by data shortfalls in many taxonomic groups, lacking systematic surveys and faced with the challenge of collecting and collating data over a vast area. Nevertheless, considerable progress has been made over the last 20 years, leading to new insights from diverse fields of study. One of the most exciting developments has been the creation of large international research networks which are collating and synthesizing information from widely scattered permanent botanical plots. Data from these networks and other studies are providing valuable new insights on contemporary biodiversity patterns and processes in Amazonia. Here we review the major findings of these networks and discuss the factors that correlate with and may explain the spatial distribution of Amazonian tree species and the factors that may underpin the emergent patterns of functional traits and diversity across the Amazon Basin.

Keywords. Amazonian flora, origins, paleoecology, Amazon, contemporary diversity

Introduction

Biogeography is a broad and complex discipline with many facets, traditions, and schools of thought. However, the core task of biogeographers is to describe, explain and predict patterns of distribution and diversity at a variety of taxonomic levels (Whittaker and Ladle 2011). This is a daunting task, especially for relatively poorly explored regions of the world such as the Amazon drainage basin (hereafter Amazonia), where there are enormous shortfalls in biological knowledge (Hopkins 2007, Milliken et al. 2011).

Nevertheless, recent years have seen major advances in our knowledge of the biogeography of Amazonia, with new insights coming from fields such as (but not limited to) geology, palaeontology, phylogeography (e.g., Fernandes et al. 2012), paleoecology (reviewed by Colinvaux 2007, Hoorn et al. 2010), and from the data synthesized from networks of permanent botanical plots such as

Amazon Forest Inventory Network (RAINFOR; Peacock et al. 2007) and the Amazon Tree Diversity Network (ATDN; ter Steege et al. 2003, 2006, Stropp et al. 2009). In this review we focus on the factors responsible for contemporary biodiversity patterns and processes in Amazonia. By adopting such an ecological biogeography perspective we largely omit a discussion of deep time processes and Amazonian paleoecology—these fascinating, complex and sometimes controversial areas have been extensively covered elsewhere (e.g., Colinvaux 2007, Hoorn et al. 2010).

Our review is not intended to be comprehensive or exhaustive—this would be impossible within the limitations of the format. Rather, we provide a broad overview of the contemporary processes contributing to current diversity patterns and highlight emerging patterns, new understandings and insights. Moreover, we unashamedly focus on the biogeography of Amazonian tree

species for two good reasons. First, the trees clearly have a pre-eminent role in structuring the Amazonian biological community and may therefore act as a surrogate for understanding the diversity patterns of other taxonomic groups. Second, many of the most recent and exciting developments in Amazonian biogeography have come about through the synthesis of data on tree diversity, structure and dynamics by recently formed research and data collection networks.

Contemporary biodiversity patterns in Amazonia

The combination of the vast size of Amazonia, high levels of primary productivity, spatial variability in edaphic and climatic conditions and the relative stability of the ecosystem over a long time period has turned Amazonia into one of the most species-rich areas on Earth. Indeed, a single hectare (1 hectare (ha) = 10^4 m²) of Amazonian rainforest can in places support more than 350 tree species with diameter at breast height >10 cm (Valencia et al. 1994, De Oliveira and Mori 1999, Stropp et al. 2009). This represents the highest alpha diversity of any rainforest community. Most of the tree species in Amazonia are thought to belong to lineages that evolved after the break-up of West Gondwana (ca. 100 mya [million years ago] Gentry 1982), although recent molecular studies found that approximately 20% of species in a sample of Ecuadorian rainforest were derived from taxa that dispersed from Africa and North America during the late Cretaceous and Cenozoic periods (Pennington and Dick 2004). Many lineages have split numerous times during the frequent periods of isolation and fragmentation imposed by the complex geomorphological and climatic history of the region over this time span. A good example of a lineage that apparently colonized South America after the splitting of Gondwana is *Guatteria* (Annonaceae) which, with 265 species, is one of the largest genera of Neotropical trees after *Inga* (Fabaceae) and *Ocotea* (Lauraceae). The *Guatteria* lineage is thought to have reached South America by trans-oceanic migration in the Miocene prior to the formation of the Isthmus of Panama (Erkens et al. 2007). By

the time the Panamanian land-bridge had formed *Guatteria* had undergone an extensive adaptive radiation and several species have subsequently back-colonised into Central America (Erkens et al. 2007).

In their analysis of geographic ranges of trees in the region of Manaus (Brazil), De Oliveira and Daly (1999) analyzed the distribution of 364 species of *terra firme* forest (see Table 1 for a definition of major forest types). Of the 15 different types of distribution that were recognized, the most common type was of species (89.4%) that have continuous if somewhat restricted distributions. Only 9.6% of species showed broad distributions (Neotropical, Amazonia-central America or tropical South America), while 5.5% showed a distinct separation between Amazonia and Eastern Brazil. Furthermore, the region was one of the distribution limits for many of these species, leading the authors to suggest that this area may be a region of re-convergence among floras and faunas that diversified in isolated fragments during one of the periods of fragmentation during the Cenozoic. However, given the deficiencies in species distribution data (Hopkins 2007) this suggestion should probably be treated with caution. Recent phylogeographic analyses provide an alternative approach to raising and evaluating such hypotheses, based on various forms of clustering and coalescence analyses of genetic data to infer patterns of isolation, migration, and introgression between related species (e.g., Fine et al. 2013, Scotti-Saintagne et al. 2013).

Many of the 90,000 or so plant species of the Neotropics (Govaerts 2001, Antonelli and Sanmartín 2011) have relatively narrow distributions, and what seems like a continuous carpet of trees when viewed from a satellite image typically hides considerable geographical variation in species diversity and many other community or species characteristics. Another interesting feature of Amazon plant communities is that they are often dominated by a limited set of species (known as oligarchic dominance) (Pitman et al. 2001). Macia and Svenning (2005) assessed this by quantifying the abundance of the ten most common species, genera and families in 69 x 0.1 ha plots in two dis-

tant western Amazonian regions (Ecuador and Bolivia). Oligarchic dominance was identified at all spatial scales although dominance decreased with increasing scale (from site to sub-region to region). Species level dominance was stronger than that seen in families and was similarly strong for both canopy and understory trees. These findings also demonstrate that while some areas do have exceptionally high alpha diversity (see above), this is not the case for all parts of Amazonia.

Accounting for these complex, overlapping and scale-dependent patterns is challenging. Ultimately, the presence of a particular species in a given study area is determined by an interaction between historical and contemporary ecological factors. Assuming that a species is present within the regional species pool (ultimately due to processes of speciation, adaptive radiation and persistence/extinction) and that there are no major biogeographical barriers preventing the species spreading into the study area, its presence will largely depend upon ecological factors (abiotic and biotic). It thus follows that the processes driving patterns of diversity and distributions must be strongly scale dependent (Whittaker et al. 2001, Willis and Whittaker 2002). For example, local distribution patterns may depend on fine-scale biotic and abiotic interactions adjusted over a time scale of less than a century. In contrast, landscape-scale distributions within Amazonia are more influenced by edaphic factors and environmental differences linked to elevation. If we consider diversity patterns over an entire region then we need to consider a suite of macrogeographic factors acting over millennia, most notably radiation budget, water availability and area of the ecosystem as well as the evolutionary constraints set by the available species pool at the regional scale (Willis and Whittaker 2002, Malhado et al. 2010; see also Fine and Ree 2006).

Soils

Soil chemistry is a key abiotic factor influencing the ecology of trees and the species associated with them (Pomara et al. 2012). Setting aside floodplain forests receiving contemporary alluvial inputs, Amazonian soils can be broadly split into

two main categories: those deriving from rocks of comparatively recent origin (<30 mya), and soils of the geologically old Amazonia (>300 mya). These two soil types have distinct distributions, with the young soils occurring in western Amazonia and the old soils in the central and eastern portions of the Basin (Jordan 1985, Sombroek 2000). The nutrient-poor eastern soils developed on the sediments produced by the erosion of the two cratons (= segments of the Earth's continents that have remained tectonically stable for long periods of time) and are of Proterozoic and Palaeozoic origin (Sombroek 2000, ter Steege et al. 2010). The more fertile soils of western Amazonia have developed on much younger Cenozoic sediments derived from the Andean orogeny (Sombroek 2000).

This difference in bedrock age between the West and the Central/East has had distinct consequences for forest dynamics. For instance, plant productivity on the older soils is much lower than on younger mineral-rich soils (Sombroek 2000), and turnover rates for large trees on younger soils are approximately twice those on older soils (Phillips et al. 2004). These relationships are not apparent in all Amazonian forest types. For example, seasonally flooded forests, which receive annual nutrient inputs, will be far less affected by bedrock age. More recently ter Steege et al. (2010), using data from Malhi et al. (2006), calculated that the division between 'old' and 'new' soils accounted for 42% of the variation in biomass productivity in the RAINFOR plots across Amazonia. Furthermore, tree alpha diversity in plots on the more fertile Cenozoic soils of Western Amazonia tends to be higher than that of older plots to the east (ter Steege et al. 2006, 2010; Figure 1a). ter Steege et al. (2010) explain this pattern by suggesting that western Amazonian species typically have a combination of higher turnover, faster regeneration and faster evolutionary rates, leading to observed patterns of species richness.

Soil characteristics may also influence tree assemblages at finer spatial scales. For example, Phillips et al. (2003) attempted to quantify the extent and pervasiveness of habitat association of trees within a 10,000 km² area of lowland rainfor-

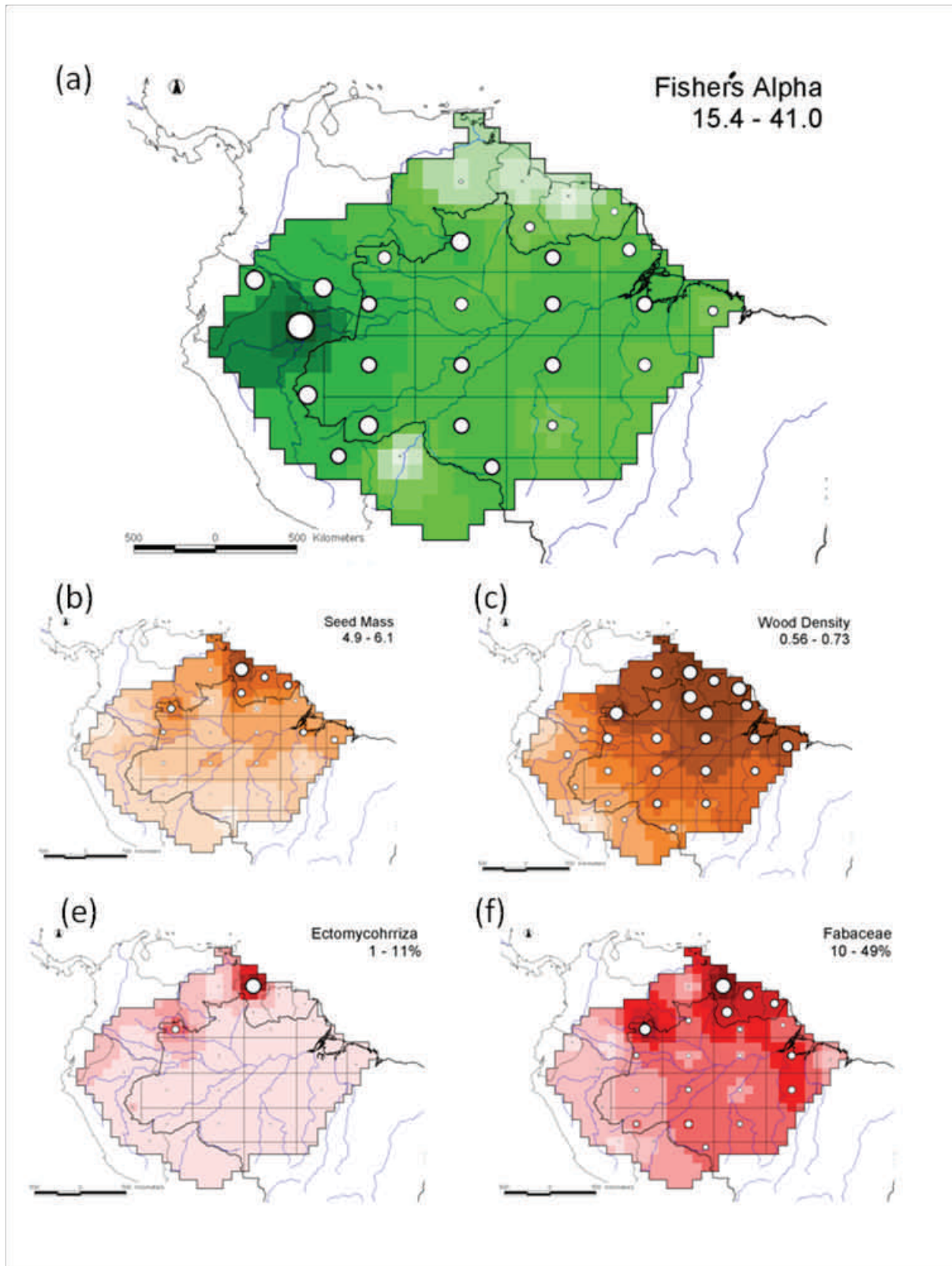


Figure 1. Geographic variation in some community characteristics of South American tree communities (after ter Steege et al. 2006). Values in each region are illustrated by the sizes of the open circles and are based on all individuals in that region. Numbers in the top right corners indicate minimum and maximum values. Colours represent an interpolation of the same data by inverse distance weighting; darker colours indicate higher values. (a) Large tree diversity, calculated with Fisher's α index from the number of individuals and number of genera in each region. (b) Community-weighted seed mass in logarithmic classes. (c) Community-weighted wood density (oven-dried weight divided by green volume). (d) Proportion of all trees belonging to ectomycorrhizal genera. (e) Proportion of all trees belonging to Fabaceae. Legend details from source paper: see ter Steege et al. (2006) for further details of methods.

est in south-west Amazonia. This area is subject to a relatively uniform climate, thus removing one of the factors that could contribute to the observed patterns of diversity and habitat associations. Up to 849 tree species were inventoried in two non-flooded landscape units (representing Holocene and Pleistocene surfaces) using 88 floristic plots. Remarkably, only 5 out of 230 species found in more than 10 localities were restricted to one landscape unit or the other, although many species showed a tendency towards habitat association—the distributions of 26 of the 34 most numerically dominant species were significantly associated with habitat (e.g., forest type). More generally, community-level floristic variation across the whole region was associated with a set of 14 physical and chemical soil properties and to the geographical distances between samples. Similar findings have emerged from recent phylogeographic analyses of tree species of the genus *Protium*, which have linked patterns of diversification to edaphic variation across Amazonia (Fine et al. 2013).

Despite strong associations between floristic characteristics and soil chemistry at a variety of spatial scales in Amazonia, it may be imprudent to assume direct causal relationships. ter Steege et al. (2000) suggest that the lower diversity in eastern Amazonia is not a product of the predominance of nutrient poor white-sand soils, but can be better explained by the isolated and often fragmentary nature of rainforest in eastern Amazonia. Moreover, the high diversity in western Amazonia may be the result of relatively stable history in the Cenozoic and high turn-over, leading to faster rates of evolution (ter Steege et al. 2010). ter Steege further elaborated upon these findings in a study of tree inventories from seven of the nine Amazonian countries (ter Steege et al. 2006). The inventories revealed two dominant gradients in tree composition and function across Amazonia, one paralleling a major gradient in soil fertility and the other paralleling a gradient in dry season length. The former gradient is congruent with parallel gradients in community-averaged wood density and seed mass and was hypothesized to be driven by the fact that, at the Guiana (eastern

Amazonia) shield end of the gradient, soils are poorer, wood is denser, and seeds are larger. This gradient probably predates the Quaternary (2.6 mya) because soil fertility is a reflection of the differences between the slow weathering quartz-rich Pre-Cambrian rocks of the Guianan and Brazilian massifs and the more rapidly weathering rocks of the western Andes (see above). The second gradient correlated with dry season length is more recent in origin and probably reflects tree species tracking changes in the Cenozoic climate (ter Steege et al. 2006). This is closely linked with the argument above, i.e. east Amazonia: slow growing species on poor soils, slow evolution, West Amazonia: fast growing species on rich soil, high turn-over, fast evolution.

Wittmann et al. (2006) recently performed a similar analysis but concentrated on the less widespread floodplain forests of Amazonia. They used data from 16 permanent várzea forest plots (definition of forest type in Table 1) of approximately 1 ha each and an additional 28 várzea forest inventories from across Amazonia. They concluded that species distribution and diversity (as measured by Fisher's alpha) showed three distinct trends. First, there was a distinct separation between tree communities in low-várzea forests and high-várzea forests. Second, species diversity was clearly related to the stage in the succession, with species-poor forests being associated with early stages of succession and species-rich forests in later stages. Finally, they observed a geographical trend of increasing species diversity from east to west and from the southern part of western Amazonia to equatorial western Amazonia.

Climate

Current climate is another abiotic factor that may have some predictive power in explaining patterns in Amazonian tree characteristics, especially at the local scale. Indeed, current climate was found to explain 37% of the variation in tree alpha diversity by ter Steege et al. (2010). Likewise, hydrology and soil characteristics were identified as the key factors driving palm species assemblages in Amazonia (Kristiansen et al. 2012). However, it should be remembered that the climate of Amazonia has

Table 1. Principal vegetation types of Amazonia (after Meirelles 2006). Note: percentages are approximate.

Type of Vegetation	% of Amazonia
Semi-arid forest on sandy soil (Campina or Caatinga)	4.10%
i. Dense forest	
ii. Open forest	
iii. Shrubs and low lying vegetation	
iv. Grassland	
Seasonal Deciduous or Semi-deciduous forest	4.67%
i. Alluvial forest	
ii. Lowland forest	
iii. Sub-montane forest	
iv. Montane forest	
Open Ombrophilous forest	25.48%
i. Alluvial forest	
ii. Lowland forest	
iii. Sub-montane forest	
iv. Montane forest	
Dense Ombrophilous forest	53.63%
i. Alluvial forest	
ii. Lowland forest	
iii. Sub-montane forest	
iv. Montane forest	
v. High montane forest	
Pioneer forests (influenced by riverine or marine environment)	1.70%
Refugial montane vegetation	0.03%
Savannahs	6.07%
Other forms of vegetation	4.15%

been very variable over ecological and evolutionary time and for this reason current climatic conditions may not always be a good indicator of those under which trees in a given region evolved (ter Steege et al. 2010). Furthermore, there is extreme annual and decadal variability in hydrological variables such as precipitation, partly driven by El Niño-Southern Oscillation and other ocean-atmosphere teleconnections (Costa and Foley 1999, Marengo 2004).

Climate may be responsible for some of the strong ecological trends that have been reported at macrogeographic scales (between landscapes). ter Steege et al. (2000) used data from 268 botanical plots across Amazonia to determine family-level floristic patterns in wet tropical South America. Plots in western and central Amazonia tended to have higher alpha diversity (as measured by Fisher's alpha) than those in eastern areas (Guiana Shield region; as per Wittmann et al. 2006, above). Surprisingly, annual rainfall was not

strongly correlated with tree species diversity as had previously been shown for plots in Western Amazonia (Gentry 1988) or for epiphyte species in Amazonia (Kreft et al. 2004). This finding is also somewhat inconsistent with work reported by Parmentier et al. (2007), who found a correlation between a range of climate variables including precipitation and alpha diversity in Amazonian plots (also using 1 ha plots). It is important to note that Gentry used plots that varied considerably in size (between 0.25–2.0 ha) while nearly all the plots in ter Steege's network had a standard size (1 ha). Furthermore, unlike ter Steege's survey Gentry used a crude measure of tree species richness rather than an appropriate metric of alpha diversity. For these reasons the studies may not be directly comparable.

Clearly further studies with more extensive databases are desirable to determine how these relationships may vary with system extent and grain of analysis (*sensu* Whittaker et al. 2001). It

should also be noted that although current climate correlates well with some measures of diversity, it is not necessarily the causal mechanism. Many species originated before current climatic conditions established and diversity may therefore not be in equilibrium with the biota. Moreover, changes in climate and forest cover have also shaped alpha diversity patterns and may be largely responsible for the lower diversity at the edges of Amazonia.

Functional Traits

There have been fewer studies that seek to describe and explain the distribution of functional traits within Amazonian trees. Among the first papers to address these issues for Amazonia were ter Steege and Hammond (2001) and ter Steege et al. (2006), which assessed average community traits such as wood density, seed mass (Figure 1b,c), and nitrogen-fixing mycorrhizae across the Amazon soil fertility gradient. More recently, macrogeographic analyses of the distribution of tree phenotypic traits (Malhado et al. 2009a,b, 2010, 2012) have provided new biogeographical perspectives on the complex ecological and evolutionary dynamics between the forest and the biophysical environment. For example, Malhado et al. (2009a) observed that the Amazon forest has a higher proportion of trees with large leaves in the northwest of the region and weak correlations between the proportion of large-leaved species and metrics of water availability. Malhado et al. (2009b) found little support for the hypothesis that narrow leaves are an adaptation to dryer conditions, but they did find strong regional patterns in leaf lamina length–width ratios and several significant correlations with precipitation variables, suggesting that water availability may be exerting an as yet unrecognised selective pressure on leaf shape of rainforest trees.

Malhado et al. (2012) observed that trees and species with drip-tips were significantly more prevalent in Central-East Amazonia than the other regions. They also found that the occurrence of species and individuals with drip-tips were more strongly correlated with precipitation of the wettest trimester than with total annual precipitation

or length of the dry season, supporting both existing hypotheses for the functional benefit of possessing a drip-tip. Significantly, they also uncovered new macrogeographic associations between the frequency of drip-tips in trees of the tropical forest understory and areas of heavy precipitation, suggesting an as yet unrecognised function for this trait (Malhado et al. 2012).

Wood density represents another functional trait with a strong geographic distribution within Amazonia. Baker et al. (2004) reported that stand-level wood specific gravity, on a per stem basis, was 15.8% higher in central and eastern forests than those of north-western Amazonia. They attribute this pattern to the higher diversity and abundance of taxa with high specific gravity values in central and eastern Amazonia, and the greater diversity and abundance of taxa with low specific gravity values in western Amazonia. It is likely that many functional traits co-vary, reflecting suites of adaptations to environmental conditions. For example, coordinated structural and physiological adaptations can be associated with light acquisition/shade tolerance strategies reflecting different ecological strategies (Patiño et al. 2012). Malhado et al. (2010) provide evidence that compound leaf structure is one of a suite of traits and life history strategies that promote rapid growth in rain forest trees.

Functional groups have also recently been the focus of various studies. Most notably, Michalski et al. (2007) attempted to assess the influence of forest disturbance on floristic composition and the abundance of tree functional groups in 21 separate forest fragments and two continuous forest sites in Brazilian Amazonia. As anticipated, patch size explained a high degree of the variation in composition and abundance. Perhaps more interesting was the fact that large fragments appeared to retain more hardwood species while small-seeded softwood ‘pioneer’ species were favoured in smaller fragments.

Conclusions

Among the greatest challenges facing biogeographers in Amazonia are the enormous shortfalls in information about the identity, distribution, ecol-

ogy and phylogeny of animal and plant species (Milliken et al. 2011, Riddle et al. 2011). The paucity of information is particularly associated with smaller, less intensively researched groups such as insects and other invertebrates. However, even plant and tree species are, in global terms, poorly known and existing knowledge is extremely geographically biased, with good information only available for a small number of well-collected areas (Hopkins 2007). Indeed, we arguably lack accurate and complete information on the geographical distribution of every Amazonian plant species (Bush and Lovejoy 2007). The situation is slowly improving, facilitated by global taxonomic initiatives and new regionally-based biodiversity information systems (e.g., Malhado and Ladle 2010), but it will be several years or even decades before sampling coverage will be adequate for detailed biogeographic analysis.

Even given the huge knowledge shortfalls, progress is being made in uncovering patterns of species diversity and distributions in Amazonia, promoted by efforts to collate existing data, develop international research networks and the increasing scientific capacity within the region. Although barely mentioned in this review, there is a large and expanding literature in Amazonian phylogeography (e.g., Lynch Alfaro et al. 2012, Naka et al. 2012, Fine et al. 2013, Scotti-Saintagne et al. 2013) that is providing fascinating insights into the evolution and biogeography of diverse taxonomic groups. Indeed, molecular phylogenetic analyses have the potential to provide insights into some of the key themes of this article such as the migration patterns and responses to climate change of Amazonian organisms

In closing, it should be mentioned that contemporary biogeographical research in Amazonia is becoming more applied, with a focus on either the conservation of biodiversity, climate change, or frequently both (Bush and Lovejoy 2007). Indeed, one of the key challenges facing Amazonian scientists during the current century is to collect enough baseline data to make meaningful comparisons in a time of extraordinary environmental change and habitat conversion (Milliken et al. 2011). Beyond this, many of the most fundamen-

tal questions remain: how many species does the Amazon rainforest contain? Why is the forest so diverse? What are the relative contributions of historical factors such as riverine barriers, climate change, sea level variation and geomorphological changes associated with mountain building to contemporary biodiversity?

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