Tansley review

Plant phylogeny as a window on the evolution of hyperdiversity in the tropical rainforest biome

Wolf L. Eiserhardt[1], Thomas L. P. Couvreur[2] and William J. Baker[1]

[1]Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AE, UK; [2]Institut de Recherche pour le Développement (IRD), UMR

DIADE, F-34394 Montpellier, France

Author for correspondence:
Wolf L. Eiserhardt
Tel: +44 20 8332 5247
Email: w.eiserhardt@kew.org

Contents

Summary

Tropical rainforest (TRF) is the most species-rich terrestrial biome on Earth, harbouring just under half of the world's plant species in *c.* 7% of the land surface. Phylogenetic trees provide important insights into mechanisms underpinning TRF hyperdiversity that are complementary to those obtained from the fossil record. Phylogenetic studies of TRF plant diversity have mainly focused on whether this biome is an evolutionary 'cradle' or 'museum', emphasizing speciation and extinction rates. However, other explanations, such as biome age, immigration and ecological limits, must also be considered. We present a conceptual framework for addressing the drivers of TRF diversity, and review plant studies that have tested them with phylogenetic data. Although surprisingly few in number, these studies point to old age of TRF, low extinction and high speciation rates as credible drivers of TRF hyperdiversity. There is less evidence for immigration and ecological limits, but these cannot be dismissed owing to the limited number of studies. Rapid methodological developments in DNA sequencing, macroevolutionary analysis and the integration of phylogenetics with other disciplines may improve our grasp of TRF hyperdiversity in the future. However, such advances are critically dependent on fundamental systematic research, yielding numerous, additional, well-sampled phylogenies of TRF lineages.

I. Introduction

Tropical rainforests (TRFs) are widely celebrated as the most species-rich terrestrial biome on Earth (Wilson, 1988; Hill & Hill, 2001; Turner, 2001; Lomolino *et al.*, 2010; Corlett & Primack, 2011). They are estimated to harbour around half of all vascular plant species (Box 1) and are therefore of primary interest to plant ecology and evolution. Since the early days of biological exploration in the tropics, naturalists have speculated about the origins of this outstanding diversity (e.g. Wallace, 1878) and a number of testable hypotheses have been proposed (e.g. Stebbins, 1974; Hill & Hill, 2001). However, these

Tropical rainforest (TRF) is undoubtedly the most biologically diverse terrestrial biome on Earth, but this extreme richness makes it hard to estimate the percentage of global terrestrial biodiversity that occurs in this biome. Across all organisms, a ballpark estimate of 50% is often used (e.g. Lomolino *et al.*, 2010) – but do plants reflect this overall pattern? Turner (2001) estimated that TRF harbours 175 200 species of vascular plants. Combined with a recent estimate of 391 000 species for global vascular plant diversity (RBG Kew, 2016), this suggests that *c.* 45% of global plant diversity occurs in TRF. We derived an independent estimate from the World Checklist of Selected Plant Families, a global yet still incomplete resource on plant species names, distributions and morphology. Using a dataset consisting of 128 913 published checklist records (WCSP, 2017) and 75 249 as yet unpublished records (R. Govaerts, unpublished), we calculated that *c.* 43% of all listed species occur in TRF. Although species are not added to the list at random, there is no apparent bias towards, or against, TRF species. Based on those two estimates, it seems safe to say that just under half of all vascular plant species are found in TRF.

hypotheses have received differing degrees of empirical scrutiny. Phylogenetic trees now serve as a crucial and increasingly robust framework for testing them.

The term 'biome' has a varied history of changing and sometimes controversial definitions (cf. Pennington *et al.*, 2004a). However, recent usage has converged on a biome concept referring to global biotic units of similar vegetation physiognomy (Olson *et al.*, 2001; Moncrieff *et al.*, 2015). As such, in contrast to biogeographic realms (e.g. Holt *et al.*, 2013; Vilhena & Antonelli, 2015), biomes are defined irrespective of their constituent species or clades (Moncrieff *et al.*, 2015), and the same biome on different continents will usually harbour different lineages as a result of long-term dispersal constraints. At the same time, species rarely cross biome boundaries, and phylogenetic diversification is thought to happen more often within than across biomes ('phylogenetic biome conservatism'; Crisp *et al.*, 2009). Although biomes are by no means absolute units and their exact boundaries are often blurred and controversial, they are meaningful broad-scale evolutionary arenas with distinctive histories, environmental and biotic characteristics (Crisp *et al.*, 2009; Jetz & Fine, 2012; Hughes *et al.*, 2013; Fine, 2015; Pennington & Lavin, 2016). Thus, they constitute both appropriate and practical units for studying the evolutionary processes underpinning large-scale biodiversity patterns.

The TRF biome forms a belt around the equator in Africa, the Neotropics and the Indo-Pacific region (Fig. 1), naturally covering *c.* 7% of the Earth's surface (Hill & Hill, 2001). While TRF is highly characteristic in its physiognomy, developing globally consistent criteria to define it is difficult owing to regional variation in the factors determining the distribution of TRF (Corlett & Primack, 2011; Moncrieff *et al.*, 2015). Thus, numerous criteria and definitions have been suggested (Fig. 2), usually including a combination of both climatic and biotic factors (Turner, 2001). TRFs occupy warm-humid climates, with 2000 mm of annual precipitation and mean monthly temperatures of 18°C commonly

used as lower boundaries (e.g. Morley, 2000; Hill & Hill, 2001). Moreover, TRF is characterized by the absence of a pronounced dry season (e.g. < 4 months with < 100 mm of precipitation in two years out of three; Morley, 2000). Biotically, TRF is characterized by a closed, multi-layered, angiosperm-dominated canopy (Gentry, 1992), with an abundance of vines and epiphytes. Other biotic criteria, such as frost-intolerance and low proportions of drought-deciduous species, are also in use (Turner, 2001).

The TRF biome stands out by its biological richness across spatial scales from local to global. Almost 1000 different species of vascular plants have been counted in just one hectare of TRF (Balslev *et al.*, 1998), and at the regional scale, the five areas of highest plant species richness on Earth all fall within TRF (Barthlott *et al.*, 2005). Globally, TRF is the most biodiverse terrestrial biome on earth (Turner, 2001). Evolutionary explanations for this diversity date back to the time of Wallace (1878), but have been challenged by alternative explanations focusing on ecological carrying capacities (cf. Rabosky & Hurlbert, 2015). Most of the proposed mechanisms are not mutually exclusive, but their relative contributions to high TRF diversity remain unclear.

New opportunities for studying the diversity of TRF have recently opened up as a result of the growing availability of phylogenetic trees. Previously, explanations involving long-term processes (e.g. speciation, extinction, niche evolution) were based mainly on fossils, morphology and the distribution of extant taxa (e.g. Takhtajan, 1969; Morley, 2000, 2003). Phylogenetic trees provide a fundamental evolutionary framework that complements these sources of evidence on the past (Pennington *et al.*, 2006; Hughes *et al.*, 2013). This is particularly useful in fossil-poor biomes, such as TRF (cf. Wing *et al.*, 2009). Usually inferred from DNA sequences of extant taxa, phylogenetic trees contain information on the evolutionary relationships of taxa (order of lineage divergence, 'topology') as well as the amount of molecular change between reconstructed speciation events ('branch lengths'). Combined with other data, phylogenetic information can be used to infer the age, distribution and diversification processes of ancestral lineages, allowing evolutionary hypotheses to be tested. Phylogenies are not a panacea, having a number of limitations. For example, typically extant taxa alone are included in phylogenetic trees, which means that a substantial proportion of past biodiversity is unrepresented. However, the information that can be gleaned from phylogenetic trees has already yielded important insights into the generation of TRF hyperdiversity (e.g. Couvreur & Baker, 2013; Koenen *et al.*, 2015; Pennington *et al.*, 2015).

Here, we review the role of phylogenetic methods in unravelling the origin and evolutionary history of TRF. We highlight the main controversies regarding the origins of high TRF diversity, extracting the main hypotheses and suggesting a framework for addressing them. We underpin our discussion with a review of cases where phylogenetic evidence has helped answer questions about the evolution of TRF diversity, and discuss the extent to which sufficient phylogenetic data have accumulated to allow meaningful tests of processes hypothesized to underpin TRF diversity. Although we focus on TRF plants, the methodological considerations are general, and a similar approach could be applied to other groups of organisms, or indeed other biomes.

(a)

(b)   **(c)**   **(d)**
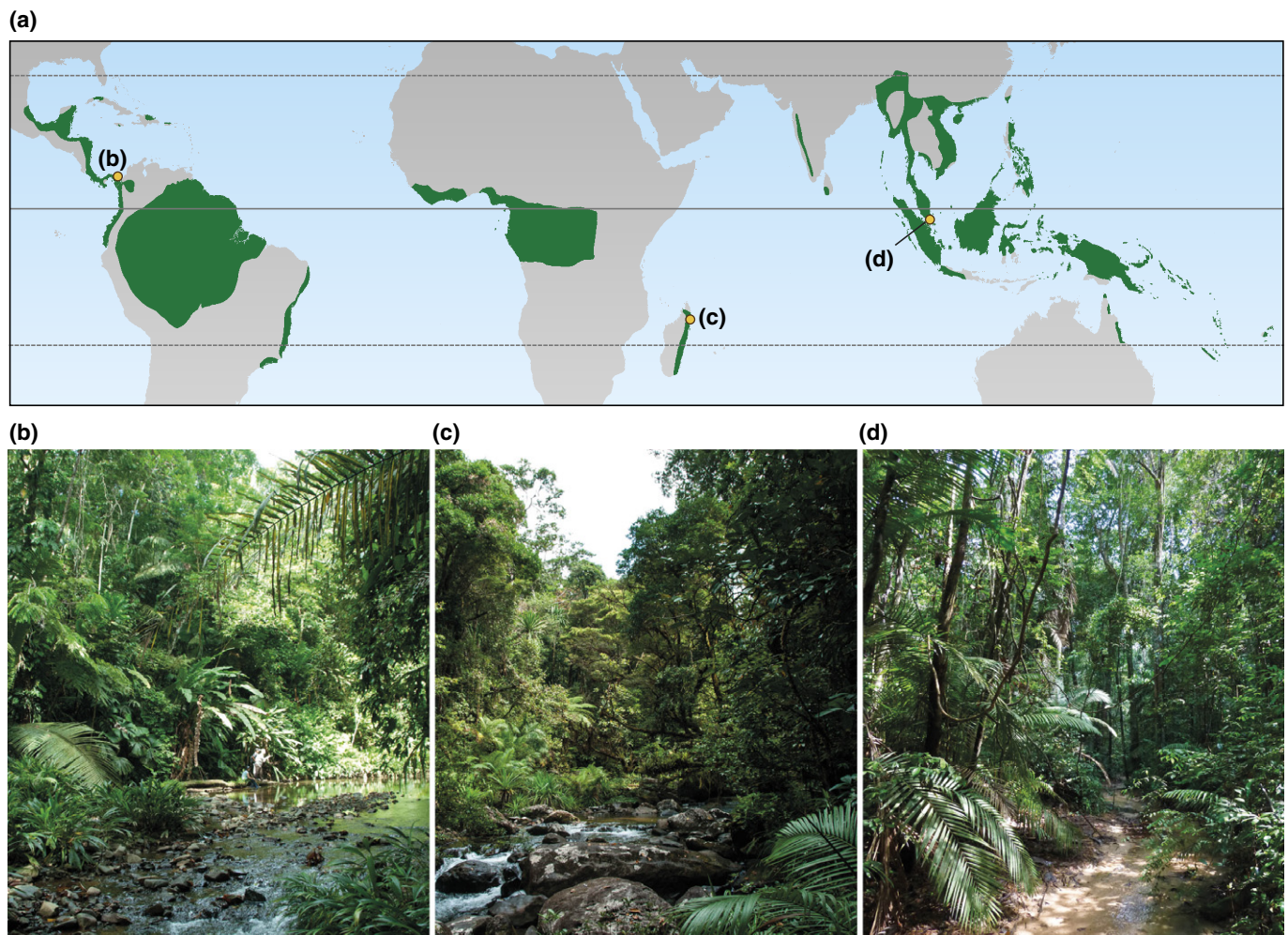
Photos: W. J. Baker

Fig. 1 (a) The global distribution of tropical rainforest following Corlett & Primack (2011). (b–d) Tropical rainforests in different parts of the world, illustrating the famously similar appearance of this vegetation throughout its distribution: (b) Serranía del Darién, Colombia; (c) Masoala peninsula, Madagascar; (d) Malaysian peninsula, Singapore.

II. A brief history of hypotheses

In spite of the outstanding biodiversity of TRF, the question, 'Why are there so many species in tropical rainforests?' is asked much more rarely than the broader question, 'Why are there so many species in the tropics?' (e.g. Jansson *et al.*, 2013; Brown, 2014). TRFs are located at the very peak of the well-known latitudinal diversity gradient (LDG) of biodiversity (e.g. Fischer, 1960; Mittelbach *et al.*, 2007; Fine, 2015). The LDG is a pervasive (though not universal, Brown, 2014) phenomenon begging a global explanation, and the richness of TRFs may thus simply be an extreme outcome of a global mechanism. However, there is reason to believe that high TRF diversity is not merely a manifestation of the LDG, at least in plants. First, the next most diverse biomes for plants are not tropical, but rather subtropical coniferous forests and Mediterranean ecosystems (Kier *et al.*, 2005). Thus, the LDG in plants breaks down at the continental level, with only the New World showing a 'classic' bell-shaped LDG (Mutke & Barthlott, 2005). Second, the plant diversity of other tropical biomes (such as dry forests and savannahs) lies, at least at the ecoregion scale, on

average below the global mean (data from Kier *et al.*, 2005). Third, within certain biomes it has been noted that diversity is highest away from the equator (e.g. tropical dry forest; Pennington *et al.*, 2009 and references therein). It thus seems that low latitude *per se* is not what characterizes species-rich areas, and plant diversity gradients need to be unpicked at a finer scale.

Much of the literature on TRF biodiversity has emphasized the question of whether TRFs are evolutionary 'cradles' or 'museums' (e.g. Stebbins, 1974; Richardson *et al.*, 2001; Couvreur *et al.*, 2011a; Koenen *et al.*, 2015; Pennington *et al.*, 2015). Those metaphors are used to describe two contrasting (though not necessarily mutually exclusive; Stebbins, 1974) evolutionary scenarios explaining the high species richness of today's TRF. While it is intuitively clear that this debate concerns the relative importance of species origination and persistence, the terms 'cradle' and 'museum' have not been applied consistently.

Stebbins (1974) was the first to use the terms 'cradle' and 'museum', defining them as communities with overall high speciation rates and low extinction rates, respectively. Stebbins' definition did not include any specific drivers: any community 'in
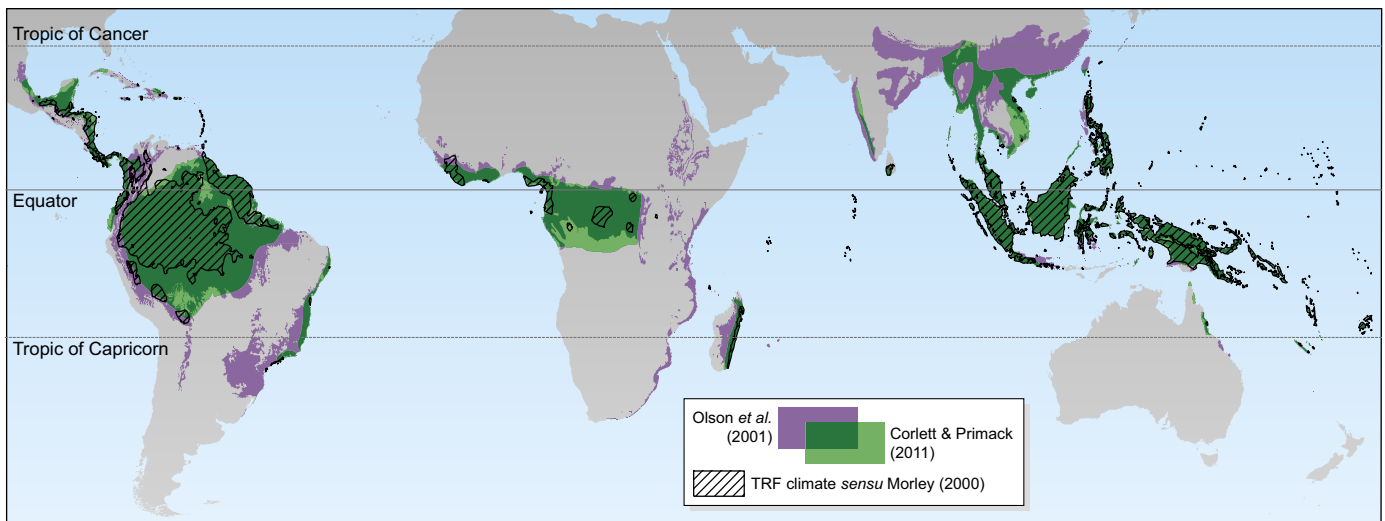
Fig. 2 Ambiguity in the definition of the tropical rainforest (TRF) biome. The 'tropical and subtropical moist broadleaf forest' biome of the World Wide Fund for Nature (Olson *et al.*, 2001) is often treated as TRF sensu lato, but includes nonTRF vegetation (e.g. the Madagascan high plateau). This becomes evident when compared with a recent expert-drawn map of TRF (Corlett & Primack, 2011) that reconciles biotic and climatic factors. Climatic definitions alone are insufficient; to illustrate this, we mapped a common climatic definition of TRF (annual precipitation > 2000 mm, less than four consecutive dry months (i.e. < 100 mm precipitation and mean monthly temperatures of ≥ 18°C); Morley, 2000) using Worldclim data (Hijmans *et al.*, 2005) at 5′ resolution. This climate covers only 46% of the TRF biome as defined by Corlett & Primack (2011), and 35% of the broadly defined biome of Olson *et al.* (2001), omitting some areas that are considered classical TRF, such as the Brazilian Mata Atlântica and large parts of the Congo Basin. Considering the lack of straightforward climatic correlates (Moncrieff *et al.*, 2015), it has even been suggested that biome definitions should be based entirely on plant traits (Moncrieff *et al.*, 2016).

which archaic forms are preserved' is a museum, and any community 'in which new adaptive complexes arise' is a cradle (Stebbins, 1974, p. 14). However, he used TRFs as an example of an evolutionary museum, arguing that their high diversity is a result of low extinction, which he attributed to environmental stability of TRF (Stebbins, 1974). This led some authors (e.g. Richardson *et al.*, 2001; Couvreur *et al.*, 2011a; Pennington *et al.*, 2015) to incorporate long-term environmental stability into the definition of the museum hypothesis as a whole, and broaden its predictions to include other putative effects of such stability, namely constant diversification rates and old clade age. Leading on from this, the term 'cradle' has been modified to refer to any system with diversification rates that are not constant (Couvreur *et al.*, 2011a), irrespective of whether the speciation rate is high or low. Thus, usage of the terms 'cradle' and 'museum' has now departed significantly from Stebbins' initial definitions, which focused purely on speciation and extinction, respectively.

The confusing usage of the 'museum' and 'cradle' hypotheses illustrates that these concepts inadequately account for the complexity of lineage diversification in TRF and should be used with great caution. Other factors, such as the age of the biome, rates of immigration and ecological limits (Wiens, 2011; Donoghue & Edwards, 2014; Rabosky & Hurlbert, 2015) must also be considered. These factors are not equal: speciation, extinction and immigration are the immediate building blocks of species richness (Wiens, 2011), jointly determined by rates and age. Meanwhile, ecological limits – together with other aspects of the biotic and abiotic environments – are one step further removed, determining the rates of speciation, extinction and immigration in a way that depends on organismal traits and their propensity for evolutionary change (Fig. 3). Below, we discuss how each element

of this framework has been addressed, or could be addressed, from a phylogenetic perspective.

III. Age of TRF biome and lineages

The hypothesis that TRF is species-rich because it is ancient was perhaps the first attempt to explain the diversity of this biome (Wallace, 1878). In principle, older biomes should have both more lineages and, on average, more species per lineage, as there has been more time for speciation as well as immigration. This hypothesis is intuitive, but demands some assumptions, for example that speciation exceeds extinction and that diversification rates are not affected by standing diversity (see Section VI). Two questions need to be addressed in testing whether the age of TRF plays a role in their diversity: how old are TRFs; and what is the contribution of old clades to TRF diversity?

1. How old are TRFs?

The exact age of a biome is difficult to pinpoint, as biomes do not appear at a precise moment, but rather assemble over a period of time through immigration and *in situ* diversification. Fossils provide the only direct way to assess the presence, distribution and composition of biomes through time (e.g. Stromberg, 2004; Kooyman *et al.*, 2014), notwithstanding inherent biases in preservation and detection, which are prevalent in species-rich floras in the humid tropics (Pennington *et al.*, 2004a). The fossil record most strongly supports an origin of TRF at equatorial latitudes around the Cretaceous-Palaeogene (K-Pg) mass extinction event *c.* 66 million years ago (Ma) (Jaramillo *et al.*, 2010; Couvreur *et al.*, 2011a; geological dates follow Cohen *et al.*, 2013).
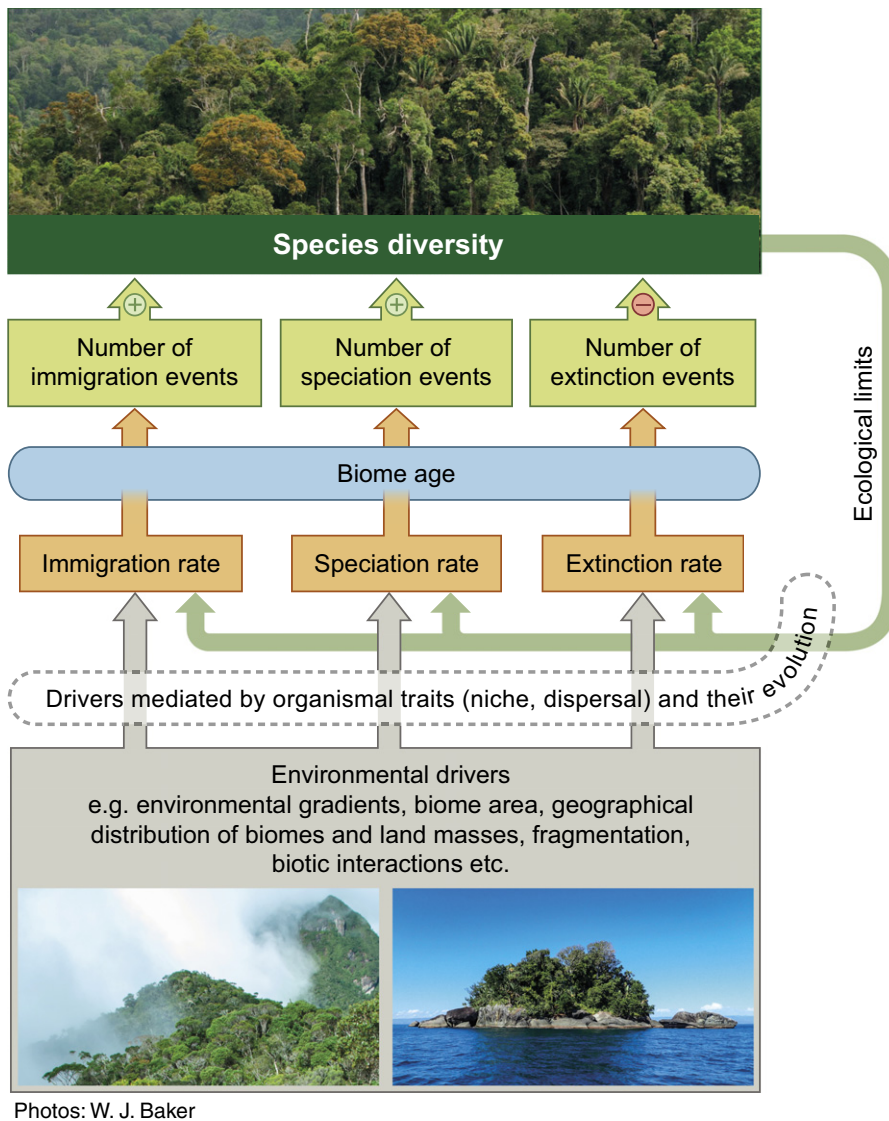
Fig. 3 A framework of hypotheses regarding the origin of tropical rainforest (TRF) species diversity. The immediate determinants of species diversity are events of speciation, extinction and immigration into a biome (green boxes). The number of those events depends on the age of the biome and its clades (blue), and the rates at which speciation, extinction and immigration happen (yellow). These rates may depend on the environment (grey, e.g. if the environmentally defined area of a biome is large, extinction is thought to be less frequent and speciation more frequent than in smaller biomes; Fine & Ree, 2006), and the way in which rates respond to the environment depends on the intrinsic properties of species. A special case of environmental determination of rates is 'ecological limits', where the outcome of the diversification process (i.e. species diversity itself) is thought to exert a feedback effect on rates, increasing extinction or decreasing speciation/immigration (dark green arrow).

Major modern angiosperm families typical of multilayered, closed-canopy TRF become dominant in Neotropical and Southeast Asian palaeofloras *c.* 66−60 Ma (Morley, 2000; Burnham & Johnson, 2004; Jacobs, 2004; Jaramillo *et al.*, 2006, 2010; Wing *et al.*, 2009; Jacobs *et al.*, 2010). This evidence is consistent with the appearance of typical TRF morphologies such as large seeds and 'dicotyledonous' wood structures at the start of the Cenozoic (Tiffney, 1984; Wheeler & Baas, 1993; Wing & Boucher, 1998).

An alternative scenario implies an earlier origin of TRF at mid-latitudes (Morley, 2000; Davis *et al.*, 2005). Fossil evidence from the mid-Cretaceous (*c.* 100 Ma) Dakota Formation of North America has been interpreted as resembling TRF in leaf charac-teristics (Upchurch & Wolfe, 1987; Wolfe & Upchurch, 1987). Climates suitable for TRF are thought to have extended to mid-latitudes during the mid-Cretaceous (Beerling & Woodward, 2001), while low latitudes may have been too dry (Wolfe & Upchurch, 1987; Morley, 2000). In addition, increases in leaf vein density observed in the plant fossil record around 100 Ma suggest

an early ecophysiological adaptation to more humid climates before the Cenozoic (Boyce *et al.*, 2009, 2010).

Dated molecular phylogenies of TRF restricted lineages provide an alternative way to study the origins of this biome (Pennington *et al.*, 2004a; Couvreur & Baker, 2013), and can provide crucial insights where the fossil record is incomplete. Focusing on clades that are diverse in TRF today, several studies suggest that the ancestral habitat of their focal groups was probably TRF, and this ancestor was present as early as the mid-Cretaceous (*c.* 100 Ma). The congruence of the results for Malpighiales (Davis *et al.*, 2005), Arecaceae (Couvreur *et al.*, 2011a) and Menispermaceae (Wang *et al.*, 2012) is striking, suggesting a common pattern of TRF-centred lineages starting to diversify sometime between the Aptian and Turonian (119−101 Ma for Malpighiales, 108−92 Ma for Arecaceae, and 102−115 Ma for Menispermaceae). This evidence is consistent with studies of other clades that are also diverse in TRF, but for which an ancestral association with TRF has not been statistically tested, e.g. Annonaceae (Couvreur *et al.*, 2011b; Pirie

& Doyle, 2012), Chrysobalanaceae (Bardon *et al.*, 2013), Sapotaceae (Richardson *et al.*, 2014) and Malvaceae (Richardson *et al.*, 2015).

How can we reconcile the fact that phylogenetic evidence supports the mid-Cretaceous TRF origin scenario, while strong fossil evidence for TRF is not found until the early Cenozoic? While in principle phylogenetic age estimates could be an artefact and change with improved methods (cf. Section VII), the congruence of results for several unrelated lineages suggests that a mid-Cretaceous origin must be taken seriously. TRF-like vegetation may have started to assemble during the mid-Cretaceous, with key lineages originating and archetypal TRF adaptations starting to accumulate. However, those forests may have been geographically restricted, leaving little fossil evidence. Also, it is unclear how strongly such forests may have resembled present-day TRF, as biomes themselves are subject to change via evolutionary turnover forced by variable environments and the evolution of key traits (Pennington *et al.*, 2004a). Perhaps phylogenetic evidence can guide future palaeobotanical research to seek evidence for earlier evidence of TRF or TRF-like vegetation, predating the widespread appearance of archetypal TRFs in the early Cenozoic (Couvreur & Baker, 2013).

2. What is the contribution of old clades to TRF diversity?

Old biomes can be expected to harbour high diversity because of the long time-frame for immigration from other biomes and subsequent diversification ('time-for-speciation effect', Stephens & Wiens, 2003). The effect depends on the age distribution and diversification rates of the clades that make up each biome. As lineage diversification is an exponential process, early immigrations into a biome can have a disproportionately large influence on its diversity later on. This is clearly visible in palms, for example, where the majority of Neotropical species diversity can be traced back to just four independent immigration events (Baker & Couvreur, 2013a,b). If most constituent lineages of TRF really are old, then time alone could account for much of the biome's high diversity.

As discussed earlier, phylogenetic evidence shows that at least some TRF lineages do indeed date back to the mid-Cretaceous (Davis *et al.*, 2005; Couvreur *et al.*, 2011a; Wang *et al.*, 2012), but the proportional contribution of old lineages to total modern TRF diversity remains to be fully surveyed and quantified. Also, temporal variation in diversification rate within those lineages determines the impact of their age. If the diversification rate is initially low, greater age may not lead to significant diversity gain. If diversification decreases with the diversity of a lineage (cf. Rabosky & Hurlbert, 2015), the effect of age could also be small or absent. Two old TRF clades, Annonaceae and palms, show a pattern of constant diversification rate for most of their history (Couvreur *et al.*, 2011a,b). Although these studies are limited by the lack of complete, species-level sampling (Koenen *et al.*, 2015), their results imply that early diversification has contributed significantly to the current species richness of these clades and thus, by extension, the overall richness of TRF. By contrast, Menispermaceae (Wang *et al.*, 2012) and Neotropical Protieae (Fine *et al.*, 2014) show initially high, but then decreasing diversification, potentially counteracting

a time-for-speciation effect. The prevalence of those patterns across TRF lineages and the occurrence of time-for-speciation in lineages with nonconstant diversification should be tested comparatively with phylogenetic evidence from a large set of representative lineages.

The relative contribution of old lineages to overall TRF diversity also depends on the contribution of younger lineages, which may attain high species diversity over strikingly short periods of time (e.g. Richardson *et al.*, 2001; Erkens *et al.*, 2007). Although it has been suggested that most immigration into TRF was early (Donoghue & Edwards, 2014), some phylogenetic evidence supports immigration into TRF from other biomes during the Neogene, e.g. in Meliaceae (Koenen *et al.*, 2015), Polygonaceae (Pennington *et al.*, 2004b; Chomicki *et al.*, 2015) and Cucurbitaceae (Holstein & Renner, 2011). The frequency of such later immigrations and their contribution to overall TRF diversity is unclear, but could be addressed by reconstructing biome shifts within further lineages that occur in TRF as well as other biomes. At present, studies addressing the diversification of TRF plants may be biased towards moderately large TRF-restricted lineages such as palms or Annonaceae, leading to a skewed reconstruction of the true patterns of immigration into TRF over time. Taken together, however, the available evidence suggests that age, and more specifically a combined time-for-immigration and time-for-speciation effect, may explain at least part of the species richness of TRF.

IV. Frequency of immigration from other biomes

Opportunity for immigration into a biome increases with its age, but frequency of immigration is independent of age. Is the TRF biome species-rich because it has been colonized often throughout its history? The frequency of immigration into a biome depends on a number of geographic and biotic factors, including biome size, its proximity to source areas, preadaptation of immigrant lineages to the recipient biome, and the biotic communities already present (Donoghue & Edwards, 2014). As TRF covers a large area (even larger areas in the past; Morley, 2000) with a complex boundary involving many other biomes, there should have been ample geographic opportunity for immigration from varied source pools. It has also been hypothesized that the TRF biome, at least in its more fertile and productive parts, is easy to colonize because no specialized adaptations to harsh environments are required (Honorio Coronado *et al.*, 2015). Moreover, as tropical environments are thought to be ancestral for most plant lineages (Donoghue, 2008), preadaptations to the TRF environment may be common in the floras of other biomes, facilitating colonization of TRF. On these grounds, relatively high immigration rates into TRF might be expected. Surprisingly, then, the prevailing view is that there is 'little evidence in plants of shifts into rainforests' (Donoghue & Edwards, 2014).

To explain the scarcity of observed evidence for immigration into TRF, Donoghue & Edwards (2014) propose two explanations. First, TRF may have been so extensive in the past that there was little in the way of other biomes that could have contributed immigrants. Second, and maybe more importantly, the highly

diverse biota of TRF may have ecologically 'resisted' the immigration of competitively inferior immigrants. Interestingly, the relatively few documented cases of lineages entering TRF after the initial phase of colonization tend to be re-immigration from adjacent biomes, i.e. immigration of lineages with more or less distant TRF ancestors (Donoghue & Edwards, 2014 and references therein). Such re-immigration may have been facilitated by inherited pre-adaptations to the competitive environment of TRF, supporting the biotic resistance theory. However, a third explanation may be that immigration was indeed more frequent, but has gone undetected. As discussed above, cases of immigration into TRF are beginning to emerge from phylogenetic studies (e.g. Pennington *et al.*, 2004b; Holstein & Renner, 2011; Koenen *et al.*, 2015), and more putative cases remain to be tested phylogenetically. The frequency of lineage migration among biomes can be quantified phylogenetically (Crisp *et al.*, 2009), and it should be possible to settle this issue by analysing species-level phylogenies of a sufficient number of clades of mixed TRF and nonTRF distribution, such as Meliaceae (Koenen *et al.*, 2015) or Bignoniaceae (Lohmann *et al.*, 2013).
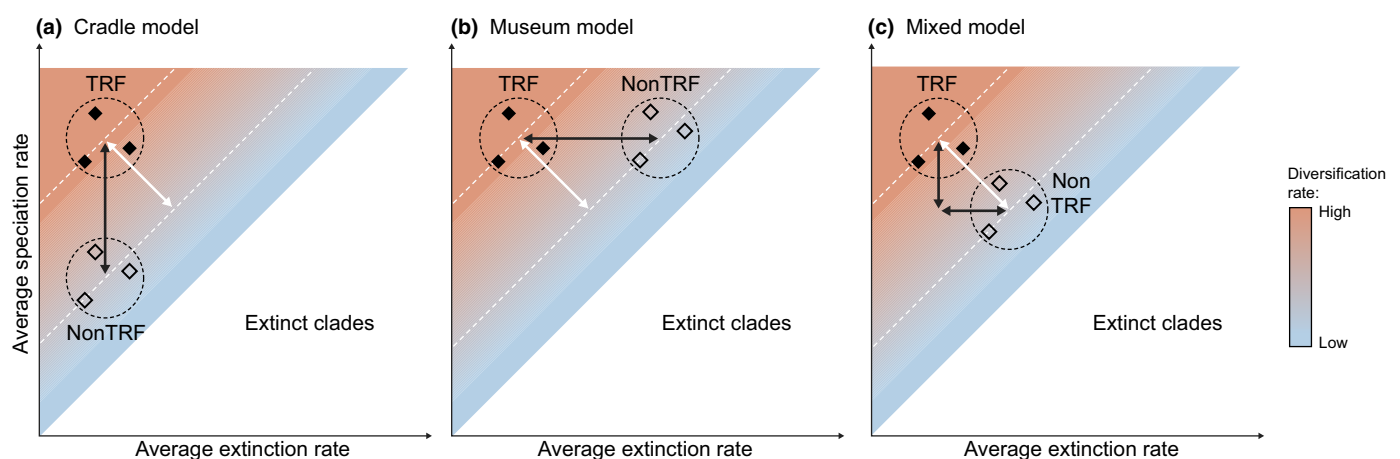
V. Speciation and extinction

Provided that movement of lineages among biomes is generally limited (Crisp *et al.*, 2009), the species richness of biomes should depend strongly on within-biome speciation and extinction. If rates of speciation and/or extinction vary among biomes, they should accumulate different numbers of species in a given time period. Speciation and extinction rates are likely to vary among biomes to the extent that they depend on abiotic (e.g. climate, Currie *et al.*, 2004) and biotic (e.g. coevolution; Suchan & Alvarez, 2015) factors, which themselves vary among biomes. Here, we focus on the detection of variation in speciation and extinction rates, a necessary first step before the underlying drivers can be addressed.

1. Overall speciation and extinction rates

Diversification is a cumulative process: whenever the speciation rate exceeds the extinction rate, i.e. the diversification rate (speciation rate minus extinction rate) is positive, a clade accumulates species. Whenever diversification rate is negative, the clade loses species. Those gains or losses will be reflected in the clade's diversity indefinitely. The diversity of a clade at any time after its origin is therefore determined by the average diversification rate that it has experienced throughout its history. Thus, high diversity of TRF clades compared with clades from other biomes may suggest that TRF was, at least at some point, characterized by exceptionally high diversification rates, either through high speciation rates and/or low extinction rates.

Whether high speciation or low extinction is driving this pattern is at the heart of the cradle vs museum debate (see Section II). While diversification rates can be easily calculated, requiring in their simplest form only clade age and diversity (Magallón & Sanderson, 2001), it is much more difficult to disentangle the effects of speciation and extinction (Rabosky, 2010). However, given the right data, it is possible (Pyron & Burbrink, 2013; Beaulieu & O'Meara, 2015; de Vos *et al.*, 2015). Because extinction only leaves very subtle evidence in phylogenetic trees (Pyron & Burbrink, 2013), our power to detect and quantify it depends on the amount and quality of phylogenetic evidence at hand.

While the quantification of extinction for individual clades at specific points in time is highly unreliable, its overall magnitude can be estimated for a set of clades, albeit with considerable uncertainty (de Vos *et al.*, 2015). Thus, for studies that aim to contrast the 'cradle' and 'museum' models despite the ambiguity of these terms (discussed in Section II), the best way of doing so may be comparing the average diversification, speciation and extinction rates of TRF clades to the average diversification, speciation and extinction rates of nonTRF clades (Fig. 4). If diversification rates are, on average, higher in TRF clades and associated with higher average speciation

Fig. 4 Separating the roles of extinction and speciation in the evolution of tropical rainforest (TRF) species diversity requires a large sample of TRF (closed diamonds) and nonTRF (open diamonds) clades. Using well-sampled species-level phylogenies, overall speciation rate and extinction rate can be estimated for each clade, and analysed across clades (de Vos *et al.*, 2015). Assuming that TRF clades have a higher diversification rate than nonTRF clades (white arrows and lines), i.e. high TRF species richness is not exclusively a result of age or immigration, three scenarios are possible. In (a), only speciation rates (*y*-axis), but not extinction rates (*x*-axis), are significantly different; this corresponds to the 'cradle' scenario of Stebbins (1974) (see Section II). In (b), only extinction rates are significantly different, corresponding to Stebbins' 'museum'. However, high diversification rates may also be a result of a combination of higher speciation and lower extinction (mixed model, c).

rates, but not lower average extinction rates, 'cradle' dynamics *sensu* Stebbins (1974) are supported (Fig. 4a). Conversely, if higher diversification rates are caused by lower average extinction rates but not higher average speciation rates, the 'museum' model is supported (Fig. 4b). Importantly, a combination of those patterns may occur (Fig. 4c). This test requires a large sample of TRF and nonTRF clades with phylogenetic trees that satisfy a range of criteria regarding species-level sampling and age estimation, among others (cf. de Vos *et al.*, 2015). Such a dataset is not currently available, but may soon come about as a result of the growing body of species-level phylogenetic evidence in public repositories, ideally augmented with data from the fossil record (Quental & Marshall, 2010).

2. Variation in diversification rates over time

Analyses of average diversification rate may reveal whether a biome has been, overall, a 'cradle' or a 'museum' of biodiversity. However, this focus on overall diversification overlooks the variation in speciation rates that can occur in space, time and among clades. Stebbins (1974) already acknowledged that a biome can be a 'cradle' for one clade while being a 'museum' for another (Fig. 4c). However, rate variation among lineages within TRF clades remains invisible if only net diversification is estimated. Such variation could easily arise through trait or environment dependent diversification (Vamosi & Vamosi, 2011). For example, speciation and extinction rates may vary within and among TRF lineages as a result of certain traits (e.g. Baker *et al.*, 2014; Couvreur *et al.*, 2015). However, the interacting effects of traits and environments on lineage diversification cannot yet be fully modelled with available techniques.

As environments change, different traits may favour speciation and/or reduce extinction, leading to a fluctuating occurrence of 'cradle-like' and 'museum-like' lineages within broader TRF clades. In this vein, it has been suggested that TRF are a museum for higher taxa, within which 'cradles' arise and perish periodically as changing environmental conditions favour the diversification of different groups at different times (Koenen *et al.*, 2015; Pennington *et al.*, 2015). More generally, the idea that TRF may have been a 'cradle' at certain times in the past, and a 'museum' at others, for the same clade is supported by phylogenetic evidence showing widespread temporal variation in diversification rates (Couvreur *et al.*, 2011a). Theoretically, this may even be the case for clades that appear to have diversified at a constant rate over time, as the same diversification rate may arise from different combinations of speciation and extinction. Overall, it appears that although analyses of average speciation and extinction may reveal which mechanism has dominated in TRF, the underlying dynamics are complex and unlikely to be fully understood until better data (including phylogenies and fossils) and more realistic models become available.

VI. Ecological limits

The role of ecology in setting upper limits to species coexistence is hotly debated (Rabosky, 2009; Wiens, 2011; Harmon & Harrison, 2015; Rabosky & Hurlbert, 2015). Investigations of geographical patterns of species richness usually start with a search for environmental correlates, emphasizing ecology (e.g. Kissling

et al., 2012a). Once environmental correlates have been identified, it follows that their influence on the direct determinants of species richness (speciation, extinction and migration; Fig. 3) should be tested. However, this is rarely done (but see, e.g. Svenning *et al.*, 2008).

Ecological limits imply that speciation and/or immigration decrease, or extinction increases, as the number of species increases (negative diversity dependence; Donoghue & Edwards, 2014; Rabosky & Hurlbert, 2015). Impacts of species richness on ecological opportunity, competition, and population sizes are thought to cause this diversity dependence (Rabosky, 2009). At some equilibrium species richness (the 'ecological limit'), speciation and extinction rates are thought to become equal, causing species richness to remain roughly constant, although individual species still originate and disappear. However, this model is essentially neutral (i.e. assuming that all species interact equally), while in reality niche differences may lead to more complex dynamics that cannot be captured by simple species counts. Importantly, assemblages are often dominated by few abundant species (e.g. ter Steege *et al.*, 2013) that may also dominate ecological limits. Also, the way in which species richness imposes ecological limits may depend on the environment (e.g. climate, soils), potentially explaining correlations between species richness and environmental conditions. For example, the Neotropical pollen record shows a good correlation between species diversity and climate during the Palaeogene (but not the Neogene; Jaramillo *et al.*, 2006; Hoorn *et al.*, 2010).

The inference of ecological limits from phylogenetic data has been controversial (Wiens, 2011), and additional evidence from the fossil record and ecological studies is needed. None of these sources of evidence clearly supports ecological limits for TRF plant diversity at the biome scale. A better fit of a diversity-dependent diversification model to phylogenetic data compared with other models (e.g. constant rates, time-dependent rates) may indicate ecological limits, although other reasons have been suggested (Quental & Marshall, 2010; Moen & Morlon, 2014). This pattern was found in Protieae, a clade of 140 species almost entirely confined to TRF (Fine *et al.*, 2014). Menispermaceae also show a pattern of diversification slowdown, but the study does not identify which diversification model fits the pattern best (Wang *et al.*, 2012). In palms and Annonaceae, diversity-dependent models have been formally tested, but were outcompeted by a model of constant speciation and no extinction (Couvreur *et al.*, 2011a,b). This indicates that at least in some clades, diversification is unrestrained, suggesting that high TRF plant diversity may be possible because ecological limits are absent or very high. However, whether TRF plant diversity appears high because the diversity of other biomes is constrained by ecological limits requires broader, cross-biome analyses. Importantly, clade-level tests are not necessarily conclusive as diversity dependence should act at the community level, across multiple clades (Wiens, 2011).

The fossil record of TRF is currently too incomplete to perform diversity-through-time analyses, which could reveal ecological limits, and while ecological studies indicate that at least some local TRF plant communities are not saturated (i.e. their species richness

is not determined by an ecological limit; Kristiansen *et al.*, 2011), ecological limits cannot be ruled out at other spatial and taxonomic scales. Phylogenetic analyses could help to resolve this issue once they can be applied at a community scale where negative diversity dependence can be meaningfully hypothesized. Ultimately, the role of ecological limits will only be clarified once a mechanism for negative diversity dependence has been convincingly demonstrated (Moen & Morlon, 2014).

VII. Key methodological challenges

The validity of the case studies discussed earlier rests on the realism and accuracy of the models used to infer past conditions and events from phylogenetic trees. Although increasingly complex macroevolutionary models are being developed (reviewed in O'Meara, 2012; Pennell & Harmon, 2013; Stadler, 2013; Lawing & Matzke, 2014; Morlon, 2014), many fundamental issues remain. In the following, we discuss three methodological challenges that we consider particularly important to the study of TRF diversity using phylogenetic data.

1. Challenge 1: is the 'molecular clock' fit for purpose?

Molecular age estimation (or 'dating') has become a vital method for testing hypotheses about the evolution of biodiversity. However, its validity is not universally accepted (e.g. Wilf & Escapa, 2015). The core assumption of molecular dating is that DNA substitutions are proportional to time ('molecular clock'). This assumption is usually violated to some extent by variation of DNA substitution rates across the branches of a phylogeny ('rate heterogeneity'). Models that accommodate rate heterogeneity have been developed ('relaxed clock' models; Sanderson, 2003; Drummond & Rambaut, 2007), but these can still lead to biased age estimates (Wertheim *et al.*, 2012; Magallón, 2014; Wilf & Escapa, 2015). The extent to which those biases preclude meaningful inferences remains controversial and needs to be addressed on a case-by-case basis. For example, in the tropical plant family Annonaceae, two major subfamilies show starkly different substitution rates in the plastome (Richardson *et al.*, 2004), and different models of rate heterogeneity lead to different age estimates (Pirie & Doyle, 2012; Chatrou *et al.*, 2014). To date, no method is able to properly cope with this drastic rate change (Chatrou *et al.*, 2014). However, problems like this may be solvable with improved models of rate heterogeneity, especially if deterministic variation can be accounted for. It has been shown that molecular rates may depend on traits and/or environments (e.g. Lanfear *et al.*, 2013; Bromham *et al.*, 2015), and relaxed clock models that incorporate these drivers could yield much improved age estimates.

A second major challenge of molecular dating is calibration, i.e. fitting phylogenetic trees to an absolute timescale using age constraints, often obtained from fossils. The placement of fossil age constraints is notoriously difficult (e.g. Sauquet *et al.*, 2012; Wilf & Escapa, 2015). It has been emphasized that age estimates are most reliable in the vicinity of calibrated nodes (e.g. Wilf & Escapa, 2015), highlighting the paramount importance of ample calibration with well-dated and correctly assigned fossils. However, just

how dense calibration needs to be to accommodate rate heterogeneity remains unclear, and densely calibrated studies are often complicated by conflict among fossils (e.g. Battistuzzi *et al.*, 2015). Calibration may be significantly improved by the development of methods that directly integrate fossils into phylogenetic analysis (e.g. Zhang *et al.*, 2016). Also, some questions can be addressed without an absolute timescale, using relative ages (e.g. Loader *et al.*, 2007). For example, very low molecular divergence in the Neotropical tree genus *Inga* strongly suggests rapid diversification independent of absolute timescales (Richardson *et al.*, 2001; Nicholls *et al.*, 2015). Notwithstanding these complexities, dated phylogenies will continue to be a core part of the macroevolutionary toolkit, but their implications must always be considered in light of the issues outlined here.

2. Challenge 2: how well can we estimate ancestral biomes?

Most, if not all, phylogenetic studies of TRF diversification rely (explicitly or implicitly) on accurate reconstructions of the biome associations of ancestral lineages. Currently, ancestral biome reconstruction relies heavily on the distributions of extant species and simple models of biome switching (time-constant and symmetric probability of switching; Davis *et al.*, 2005; Couvreur *et al.*, 2011a; Wang *et al.*, 2012). In the absence of other information on the evolution of biome association, this is a reasonable assumption, but it may not reflect actual past events. Reconstructions of ancestral traits that are based exclusively on extant taxa fail if probabilities of switching between states were asymmetric in the past, e.g. as a result of directional selection (Fritz *et al.*, 2013). This problem applies to ancestral biomes, as rates of biome switching are not necessarily symmetric (Donoghue & Edwards, 2014). Moreover, probabilities of biome-switching may have varied over time (cf. Section IV). For example, immigration rates may have changed with the area and distribution of TRF-supporting environments. Also, the biotic resistance of TRF communities to immigration from other biomes may have been variable (cf. ecological limits discussed in Section VI). A hypothetical example of how simple models of biome switching may fail to capture such dynamics is shown in Fig. 5. The only way to solve this issue is including fossil constraints, drawing, for example, on the palaeoflora associations or functional traits of fossil taxa.

Besides asymmetric and time-variable probabilities of biome switching, an association between biome membership and diversification rates could potentially bias ancestral biome estimation (FitzJohn, 2010). A family of models recently developed to deal with this issue (Maddison *et al.*, 2007; FitzJohn, 2010; Goldberg *et al.*, 2011) has gained high popularity, but significance tests based on these models have been found to be unacceptably prone to type I error (Rabosky & Goldberg, 2015). If higher or lower rates in certain biomes are among the hypotheses being tested (see Section V), it is obviously problematic if the test is based on an analysis (ancestral biome reconstruction) which may be biased by the phenomenon being tested (rate variation). This is an area of active methodological research (e.g. Rabosky & Huang, 2016) and further developments addressing these issues are keenly anticipated.
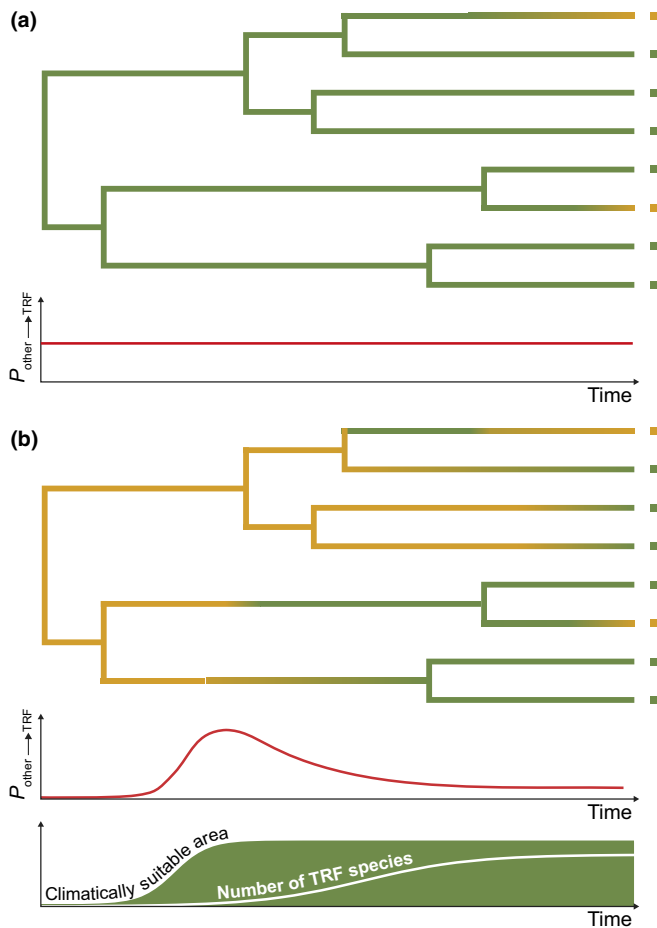
Fig. 5 Reconstructions of the biome in which ancestral lineages occurred is highly sensitive to the probability of biome shifts (*P*). This hypothetical example illustrates how erroneous assumptions regarding the immigration probability of lineages into tropical rainforest ($P_{other \to TRF}$) may bias reconstructions that are entirely based on the biome in which taxa occur at present (squares; green, tropical rainforest (TRF); yellow, other biomes). In (a), the immigration probability $P_{other \to TRF}$ is assumed to be constant (as is common practice), resulting in ancestral lineages to be reconstructed as occurring in TRF. In reality, the immigration probability may have been variable, e.g. high during the initial formation of TRF, and then decreasing as competition prevented further immigration (b; see Section IV for a rationale). Under such circumstances, the ancestral lineages would be reconstructed as occurring outside TRF. As the real $P_{other \to TRF}$ is unknown, ancestral biome reconstructions must therefore be interpreted with caution.

3. Challenge 3: can speciation and extinction rates be separated?

Our ability to infer the biological mechanisms underpinning diversification rate variation depends on methods for separating speciation and extinction rates. Whether or not this is actually possible based on phylogenetic information is controversial (Ricklefs, 2007; Rabosky, 2010; Pyron & Burbrink, 2013; de Vos *et al.*, 2015). In theory, a comprehensively sampled species-level phylogeny can be used to infer extinction rate in clades that have undergone constant-rate birth–death diversification (Ricklefs, 2007). This inference is based on the so-called 'pull of the present', an apparent upturn in diversification rate towards the present. The pull of the present is an ephemeral phenomenon that is observed

because species that are much younger than the average lifetime of a species seem to diversify without extinction: they have not yet had time to become extinct. Because this phenomenon is only ever observed for the recent past, it cannot be used to infer extinction rates that prevailed during the deeper past of a clade if rates have been time-variable.

Interestingly, a few TRF clades seem to have diversified with constant rates, thus allowing extinction rate to be estimated for their whole history, at least theoretically (Couvreur *et al.*, 2011a, b). However, these studies were based on generic level phylogenies, and not complete species-level sampling, leading to two distinct issues: relatively recent rate-shifts cannot be ruled out; and the magnitude and shape of the 'pull of the present' cannot be estimated. Other TRF clades show time-variable diversification, thus ruling out exact estimates of extinction rate (Wang *et al.*, 2012). It has been shown that estimation of extinction rates is, within an order of magnitude, robust to violations of the constant-rates assumption when estimated across a large number of clades (de Vos *et al.*, 2015). This means that an overall estimate of extinction rate in TRF clades may be possible, but it would necessarily reflect recent diversification regimes more accurately than diversification in the distant past. Approaches for estimating deep-time extinction rates must incorporate other kinds of information in addition to phylogenetic trees based on extant taxa. Such approaches are essential for the resolution of the cradle vs museum debate. The fossil record is also crucial in this context (Quental & Marshall, 2010), but, in the case of TRF, it may continue to be too sparse to allow reliable reconstructions of extinction in the distant past.

VIII. Perspectives

Phylogenetic data have already significantly improved our understanding of the origin and evolution of TRF plant diversity, but the full potential of this approach is yet to be realized. To this end, progress is needed in four major areas.

1. Comparative studies of TRF diversification

Studies of model TRF groups such as palms (Couvreur & Baker, 2013), Annonaceae (Couvreur *et al.*, 2011b; Erkens *et al.*, 2012) or Protieae (Fine *et al.*, 2014) can provide invaluable insights, but the extent to which their findings are applicable to the entire biome usually remains a matter of discussion. This problem can be amended by synthesizing findings from multiple groups. However, as we found in preparing this review, the number of TRF lineages for which diversification has been analysed statistically is surprisingly limited, and the choice of different methods limits comparability (e.g., different diversification models being tested). So far, meta-analyses have only been possible for simple metrics (e.g. crown age of clades; Hoorn *et al.*, 2010), and these are still fraught with uncertainty. Ideally, multiple clades should be analysed using the same methods in a joint statistical framework for hypothesis testing (as suggested for diversification rates in Section V; Fig. 4). By substantially increasing the sampled diversity, a comparative approach will also add to the power of methods that are otherwise

considered indecisive, such as the estimation of extinction rates (de Vos *et al.*, 2015).

The comparative approach will only succeed if new phylogenetic data for more TRF taxa are generated. Greater coordination among researchers studying the phylogeny of different key lineages would speed up this process greatly. Phylogenetic research has gained new momentum thanks to the increasing affordability of high-throughput DNA sequencing (Buerki & Baker, 2016). However, a more methodical approach to lineage selection is required to address TRF evolution more completely. Here, it is important to ensure that all major plant lineages occurring in TRF are represented. Covering different growth forms and ecological roles (trees, lianas, herbs etc.) is crucial for understanding the history of TRF diversity in its entirety (Pennington *et al.*, 2004a), and ecological importance in terms of diversity and/or estimated abundance (e.g. ter Steege *et al.*, 2013) may further guide lineage choice. Finally, Pennington *et al.* (2004a) noted a clear geographic bias in the availability of phylogenies, and this situation still persists for rainforests, with data being relatively scarce for Asian and African rainforests. Taxon sampling remains a real limitation, especially for biomes like TRF that occur in remote and inaccessible parts of the world where many species remain unsampled or even unknown (ter Steege *et al.*, 2013). However, this bottleneck may soon be removed by unlocking natural history collections (e.g. herbaria) for genomic research (Bakker *et al.*, 2016; Buerki & Baker, 2016; Hart *et al.*, 2016).

2. Tackling the challenge of mixed clades

Clades that are unequivocally TRF-restricted or TRF-centred are convenient models for studying TRF plant evolution, but provide only part of the picture. First, these studies are inherently biased towards lineages with limited biome shifting, and thus likely to underestimate immigration and overestimate the age of immigration events. Second, since a lineage needs to be reasonably diverse to be analysed statistically, but old and diverse lineages are rarely restricted to single biomes, studied TRF lineages are likely to be biased towards lineages of a certain intermediate age and/or exceptionally high diversification rates. To overcome such biases, it will be important to study lineages that contain TRF species or small TRF clades, while not being TRF-centred. A recent analysis of Meliaceae is an excellent example (Koenen *et al.*, 2015), but such studies are still rare, although there are many groups that lend themselves to this approach (e.g. legumes).

Analysing mixed clades is vital, but is complicated by the daunting task of ascertaining the biome association of a large number of species. Analytically, including evolving biome associations (or other traits) into diversification models is a young and controversial field (Rabosky & Goldberg, 2015), but new models are constantly being developed (e.g. Rabosky & Huang, 2016; Sukumaran *et al.*, 2016), and we believe that cross-biome analyses of diversification, including TRF species/ clades, among others, will soon be a viable alternative to the analysis of TRF-restricted lineages. In time, it should be possible to analyse TRF plant diversification across the entire plant tree of life.

3. Closing the knowledge gap in Neogene TRF diversification

Somewhat paradoxically, ancient diversification is more readily studied using phylogenies than more recent dynamics. This is because even incompletely sampled phylogenies tend to include all ancient nodes with extant descendants, while more recent nodes – unless specifically targeted based on prior knowledge – are less likely to be represented in sparsely sampled phylogenies. Thus, Davis *et al.* (2005) were able to infer Cretaceous dynamics from a phylogeny sampled at the family level, and Couvreur *et al.* (2011a) felt confident to analyse diversification up until the late Oligocene using a genus-level phylogeny of palms. To get insights into more recent dynamics, denser sampling is required. A push towards species-level phylogenies is essential to reach an understanding of what is arguably one of the most important periods in TRF history. TRFs have been highly dynamic during the geologically recent past (e.g. an estimated ~ 60% reduction in area during the past 30 Myr; Kissling *et al.*, 2012b), indisputably leading to significant evolutionary dynamics. To infer these dynamics, we need phylogenies that recover all or most branching events within the Neogene and Quaternary.

To date, densely sampled species-level studies of TRF lineages have been restricted to relatively small lineages. For example, in palms, numerous species-level studies have already been conducted in specific genera, often yielding useful insights into the diversification history of certain TRF areas (e.g. Neotropics, Roncal *et al.*, 2011, 2013; Freitas *et al.*, 2016; Afrotropics, Faye *et al.*, 2016; Asian tropics, Bacon *et al.*, 2016). However, genera or similarly sized clades are usually geographically restricted, limiting the generality of such studies. Comparative studies of multiple small clades are one possible solution (see earlier), but we believe that densely sampled species-level phylogenies of larger clades have the potential to provide crucial insights into Neogene diversification dynamics while accounting for regional variation and other idiosyncrasies of smaller lineages. Building large, species-level trees is a significant challenge that must be confronted. Synthesizing existing molecular data mined from public repositories is one option that has been explored, for example, in palms (Antonelli *et al.*, 2016; Faurby *et al.*, 2016), but the limitations of such patchy datasets are not always fully acknowledged. For example, molecular information is available for less than half of all palm species, and this information is distributed highly unevenly across the tree (i.e. concentrated in clades that have been subject to detailed phylogenetic analysis, while other clades are almost absent). The impact of this bias on diversification studies is not readily apparent, highlighting that the systematic generation of new data remains essential.

4. Traits and processes

Organismal traits are central to all aspects of TRF diversification dynamics, and including them into diversification models could substantially improve our understanding of underlying processes. First, the biome association of species is mediated by their traits; this link has in fact been used widely to reconstruct the past occurrence of TRF and other biomes from fossils (e.g. Upchurch &

Wolfe, 1987; Wolfe & Upchurch, 1987). Modelling the evolution of traits that are characteristic for TRF (e.g. leaf shape, seed size) on a phylogenetic tree could greatly improve the reconstruction of ancestral biome association, which is not a heritable trait in itself and thus, in principle, not amenable to evolutionary modelling. Using traits may also open up opportunities for incorporating fossil data, which can make a large difference in ancestral state reconstruction (Fritz et al., 2013). If individual traits are insufficiently characteristic of TRF, suites of independently evolving traits may help to identify ancestral lineages that were probably TRF-adapted. Such improved reconstructions could lead to much better estimates of the age of TRF and its constituent clades, as well as rates of immigration from other biomes. Second, as discussed earlier, traits could also help to account for molecular rate variation and thus lead to better age estimates using molecular clocks. Here, including morphological traits as simple as plant size (Lanfear et al., 2013) may improve models; life-history and demographic traits such as generation time (e.g. Baker et al., 2014) should also be explored, but are much harder to obtain across many species. Third, traits are instrumental in understanding the variation of speciation and extinction rates across clades and through time, potentially leading to much more realistic diversification models. Here, numerous traits have been implicated (e.g. habit, Couvreur et al., 2015; leaf traits, Onstein et al., 2016; seed traits, Willis et al., 2014), but dispersal traits play a special role as a result of their importance in allopatric speciation. Fourth, traits are thought to mediate species interactions such as competition, and are thus a vital component of more sophisticated models of ecological limits. Here, both traits related to the use of limiting resources and traits reflecting competitive ability (e.g. growth rate) would be of special interest (Mayfield & Levine, 2010). To pinpoint the traits that are relevant in this context, close collaboration with community ecologists seems inevitable. Last but not least, in addition to allowing an improved understanding of TRF plant diversification, traits are also essential for understanding the effects of this diversification in terms of ecosystem processes and services. Thus, the development of large trait databases (e.g. Kattge et al., 2011) and macroevolutionary models that link trait evolution and other processes opens up exciting new research directions that will continue to produce novel insights into the evolution of TRF as datasets grow and methods improve.

IX. Conclusions

In preparing this review, we have been surprised by how few studies have focused specifically on plant diversification in the TRF biome, and how biased they are towards the polarized classification of museums and cradles. Moreover, museum and cradle hypotheses in the strict sense are currently difficult to test as a result of the challenge of estimating extinction from single or few phylogenies. Nevertheless, the existing studies have provided important insights, indicating that the age of TRFs, low extinction and high speciation (at least in some groups) appear to play an important role in their high current plant diversity. The absence of ecological limits may also be important, while frequent immigration from other biomes is unsupported as a major driver of high TRF diversity. These conclusions show that TRF plant diversification is much more complex than a simple 'cradle' or 'museum'.

Ultimately, phylogenetic evidence on its own will not resolve the mystery of TRF hyperdiversity. Much greater integration with other disciplines is needed. It is often argued that phylogenetic data and methods benefit other disciplines (e.g. Webb et al., 2002; Lawing & Matzke, 2014), but the reverse is also true (Fritz et al., 2013; Pennell & Harmon, 2013). The full potential of phylogenetic trees can only be realized by combining them with other data sources (e.g. fossils, traits, environment). We believe that the development of total-evidence analytical approaches will revolutionize the study of diversification in TRF and other biomes. Phylogenetic trees are set to provide the unifying framework in the future development of this important field.

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