

Odd man out: why are there fewer plant species in African rain forests?

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Abstract Although tropical rain forests represent the most species-rich terrestrial ecosystem on the planet, the three main rain forest regions (Neotropics, South-East Asia and continental Africa) are not equally diverse. Africa has been labeled the “odd man out” because of its perceived lower species diversity when compared to the Neotropics or South-East Asia. Understanding why, within a biome, certain regions have higher or lower species diversity provides important insights into the evolution of biodiversity. I review the evidence in favor of an “odd man out” pattern and the different hypotheses that have been advanced to explain and test this pattern using recent ecological, biogeographical and diversification studies. The “odd man out” pattern has yet to be formally tested using extensive inventory plot data (including non woody species) between all three major rain forest regions based on appropriate statistics in an area controlled manner. The lower species diversity is not the result of a single cause, but is probably linked to numerous intricate causes related to present and past events. Future comparative studies should combine numerous variables including novel ones such as plant functional diversity. Finally, though more extinction in Africa is apparent from the fossil record, it is still hard to precisely quantify to what degree extinction varied between the three major regions. Diversification studies of important tropical plant lineages

tend to support higher speciation rates in the Neotropics and South-East Asia instead of higher extinction in Africa as the main cause explaining the differences in species diversity. The lower species diversity of African rain forests remains an understudied question with numerous preconceived and largely untested ideas for which we are still far from having a synthetic explanation. This review highlights that there are still very little intercontinental rain forest comparisons of plant species diversity hindering any solid conclusions. To better address this, an integrative approach involving archeologists, climatologists and biologists coupled with data from all three regions should be privileged.

Keywords Odd man out · Neotropics · South-East Asia · Diversification rates · Extinction · Fossil record · Biogeography · Palms

Introduction

Explaining differences in species diversity between regions is a central aim for ecologists and biogeographers (Gaston 2000). Biomes are defined as geographically widespread (and generally disjunct) natural communities occurring under similar climatic conditions (Olson et al. 2001). Understanding why, within a same biome, certain regions have higher or lower species diversity provides important insights into the evolution of biodiversity (e.g., Sauquet et al. 2009; Wiens 2011). In addition, understanding how the same biome has responded to past climate change in different regions will provide interesting data towards better conservation planning of biodiversity in the future. Differences in species richness between regions are the result of ecological, geological and/or biogeographical processes ultimately influencing one or several of three

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fundamental mechanisms influencing species diversity: speciation, extinction and dispersal (Ricklefs 1987; Wiens 2011).

Tropical rain forests (TRF) are the most species-rich terrestrial biome of the planet (Gentry 1992) and are represented in three main forest blocks: continental Africa, the Neotropics and South-East Asia (Richards 1996). Rain forests also occur in smaller regions such as Madagascar, the Western Ghats in India and North eastern Australia (Morley 2000) and will not be directly discussed here. In continental Africa (i.e., excluding Madagascar), rain forests extend from West Africa into the Congo basin and in smaller patches along the East African coast and Eastern Arc Mountains (Fig. 1). Locally, these forests show high levels of plant species diversity and endemism (e.g., Kenfack et al. 2007; Linder 2001; Linder et al. 2012; Wasser and Lovett 1993). For example, the coastal and montane rain forests of eastern Africa have an exceptional density of endemic plants, which is one of the highest on the planet (Myers et al. 2000). However, at a continental scale, African rain forests have been labeled as the “odd man out” in terms of vascular plant species richness when compared to the Neotropics or South-East Asia (Richards 1973, but see below). Explanations for the “odd man out” pattern have been numerous including differences between regions in climate or geological history, biogeography and even human disturbance. Yet over the years, a single hypothesis has mainly prevailed and is generally cited in literature as the only explanation: TRF of Africa underwent higher extinction rates than other TRFs (Raven and

Axelrod 1974). Here, I review different hypotheses advanced to explain this patterns and recent studies that have tested them. As indicated above, three main mechanisms will influence species diversity (speciation, extinction and migration), and the ideas and hypotheses about the “odd man out” pattern have either focused on the processes influencing these mechanisms (climate, geology etc.) or on the mechanism themselves (differences in diversification and migration).

First I review the evidence supporting the lower plant species diversity of African rain forests. I then go over the hypotheses that focus on the processes that might have influenced speciation, extinction and/or dispersal leading such as climate, time or area. Finally, I review recent data to tease apart the contribution of the three fundamental mechanisms cited above in explaining lower diversity in Africa when compared to South America or South-East Asia.

Are African rain forests really less species rich?

Richards (1973) was the first to coin the term “odd man out” for Africa relating to its perceived lower species diversity when compared to the two other tropical regions: the Neotropics and South-East Asia. His arguments were based on comparisons at floristic levels or by looking at differences between species richness of numerous pan tropical plant families. For example, he underlined that numerous tropical lineages have higher species diversity in

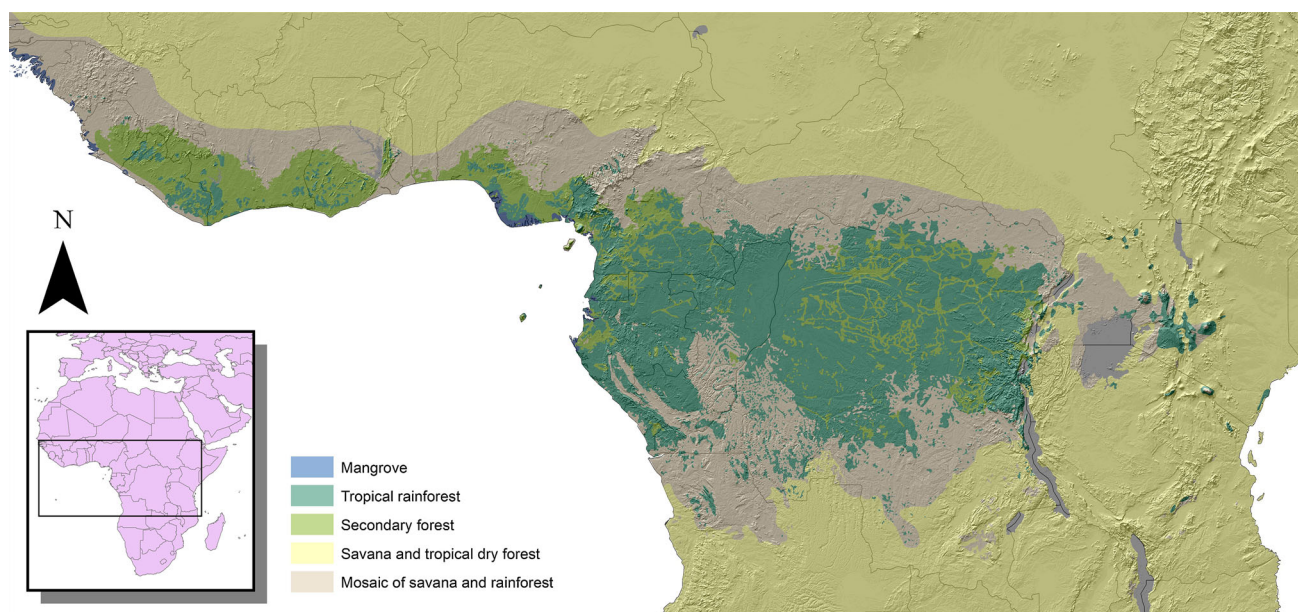


Fig. 1 Distribution of tropical rain forests, secondary forests, mangroves and savannas in equatorial Africa. Map taken from Guillaumet et al. (2009)

the Neotropics and/or South-East Asia and lower species diversity in Africa (reviewed in Thorne 1973). Palms, which are an important ecological component in TRF (Couvreur and Baker 2013), provide a case in point with ~800 species in the Neotropics, ~1,200 in South-East Asia, ~200 in Madagascar and just 65 species in Africa (Dransfield et al. 2008). However, other plant groups do not follow this pattern being for example as diverse in Africa than in South America (e.g., dalbergioid legumes, Lavin et al. 2000). In general, studies that discuss differences of diversity between the three main TRF areas provide rough estimates of species diversity without controlling for area. Thus, it is generally acknowledged that there are 90,000 plant species for the Neotropics (Thomas 1999), of which ~16,000 tree species for the Amazon basin alone (ter Steege et al. 2013) and more than 50,000 plant species for South-East Asia (Whitmore 1998). The African Plant Checklist and Database (Klopper et al. 2007) indicates a total of ~32,000 native and accepted species names registered for tropical Africa (excluding the region considered in the Flora of Southern Africa) with other estimates ranging between 30,000 to 35,000 species. The “odd man out” pattern is also visible at the family level with fewer plant families in Africa (Francis and Currie 2003) although family diversity might not be a good indicator to demonstrate regional effects (Qian and Ricklefs 2004). One would be tempted to compare overall species diversity values, however, properly assessing species richness differences especially at large continental scales needs to be undertaken in a controlled manner to avoid area effects confounding the conclusions (Whittaker et al. 2001). For example, area size should be maintained constant and diversity metrics well defined (Whittaker et al. 2001). Interestingly, to date very few studies have been carried out to formally quantify plant diversity differences between Africa and the other tropical regions (De Cáceres et al. 2012). Parmentier et al. (2007) were the first to provide a formal analysis of tree diversity between the TRFs of the Amazon basin and Central Africa. They used over 1,500 tree plots (1,000 for Central Africa and 500 for the Amazon, trees inventoried with diameter larger than 10 cm) located across both regions and showed that mean α -diversity (measured using Fisher’s α , an index that does not depend on sample size) in Amazonia is up to threefold more diverse than in Central Africa and this stood true when controlling for area. Because these plots draw species diversity from a regional pool which is theoretically a good indicator of overall regional diversity (Stropp et al. 2009) the Parmentier et al. (2007) study suggests that, at least compared to the Amazon basin, African rain forests are indeed less diverse. Interestingly, the study also suggested that for plots under similar climatic conditions (medium precipitation and temperatures, see below), Africa

contained similar or higher levels of diversity than the Amazon basin. Thus, overall African TRFs appear less diverse at least for tree species, but certain areas in Africa can be as diverse as those encountered in the Amazon basin (Parmentier et al. 2007). It is important to underline that these studies (e.g., Parmentier et al. 2007; ter Steege et al. 2013) focus on tree species with a diameter at breast height (DBH) greater than 10 cm. However, non-tree species such as herbs, epiphytes, shrubs and non-epiphytic climbers contribute significantly to TRF species richness (Gentry and Dodson 1987). In addition, a study showed that more than 92 % of individuals and 38 % of species within a 50-Ha plot in Cameroon had a DBH less than 10 cm (Kenfack et al. 2007). This underlines that estimates of species richness based on inventorying individuals with DBH higher than 10 cm can largely underestimate the true diversity of TRFs, even for tree species (Gentry and Dodson 1987). The Parmentier et al. (2007) study certainly supports lower tree diversity for central African rain forests overall when compared to the Amazon, but we have little insight into knowing if this pattern is also valid when looking at total plant species richness.

This lower species diversity is probably not the result of insufficient taxonomic knowledge (Richards 1973). Indeed, Africa has one of the best explored tropical floras with numerous regional floras completed (Flora of Tropical West Africa; Flora of Tropical East Africa, Beentje, pers. com.) or nearing completion (Flora of Gabon, Sosef pers. com.). Thus, one cannot justify Africa’s lower diversity based on poorer floristic knowledge alone even though new species and genera are described regularly and some areas remain to be botanically explored (Küper et al. 2006).

Contemporary versus historical climate

Climate has played a central role in explaining differences in species diversity between regions and is referred to as richness–climate patterns (Francis and Currie 2003). The impact of climate can be divided into two main categories (Araújo et al. 2008): energy-diversity hypotheses where higher levels of available energy (water, temperature, evapotranspiration) lead to less competition between species/individuals favoring co-existence of more species or, historical climate stability hypotheses where climatically stable areas favor speciation and persistence of species over time.

Can present-day climate differences explain plant species diversity?

Richards (1973) suggested that lower African diversity could be related to the higher number of “dry” months,

defined as areas receiving less than 100 mm precipitation per month. Africa has very few regions lacking dry months (Fig. 2) and as a whole the African rain forest region is comparatively drier than other TRF regions (Malhi and Wright 2004). Areas of year round high monthly precipitation are localized, mainly along or near mountain regions such as the Kivu region (east Democratic Republic of Congo), Mount Cameroon, Cristal Mountains and the Chaillu Massif along the northern part of the Central African coasts (Fig. 2). These regions have been shown to harbor high levels of diversity in birds and plants (Fjeldså and Lovett 1997). In contrast, the Neotropics and South-East Asia contain widespread areas that lack dry months, with wet areas (more than 100 mm per month) covering entire regions such as the Malesian islands in South-East Asia and the Chocó and Western Amazon basin in the Neotropics (Fig. 2). In the Amazon, species diversity is highly correlated with rainfall and the length of the dry season is a limiting factor for α -diversity of tree species

(Bjorholm et al. 2005; Kreft et al. 2006; Parmentier et al. 2007; ter Steege et al. 2006). This is also true in Africa and appears to be a general pattern throughout the tropics (Barthlott et al. 2005). In fact, angiosperm species richness at global levels is strongly correlated with climate, notably with annual temperature and annual water deficit (Francis and Currie 2003) or water–energy variables (Kreft and Jetz 2007). There are thus clear current climate differences between the three regions that could potentially explain the differences in species richness. However, how energy can directly influence species richness remains debated beyond the observed correlations (Davies et al. 2004; Evans et al. 2005; Jansson and Davies 2008; McGlone 1996).

In a large-scale analysis of tree species richness between the Amazon and Central Africa, Parmentier et al. (2007) showed that for areas of medium precipitation and temperature values (from 1,500 to 2,500 mm and 22–25 °C), African and Amazonian α -diversity are equivalent or even higher for Africa. However, under higher values of

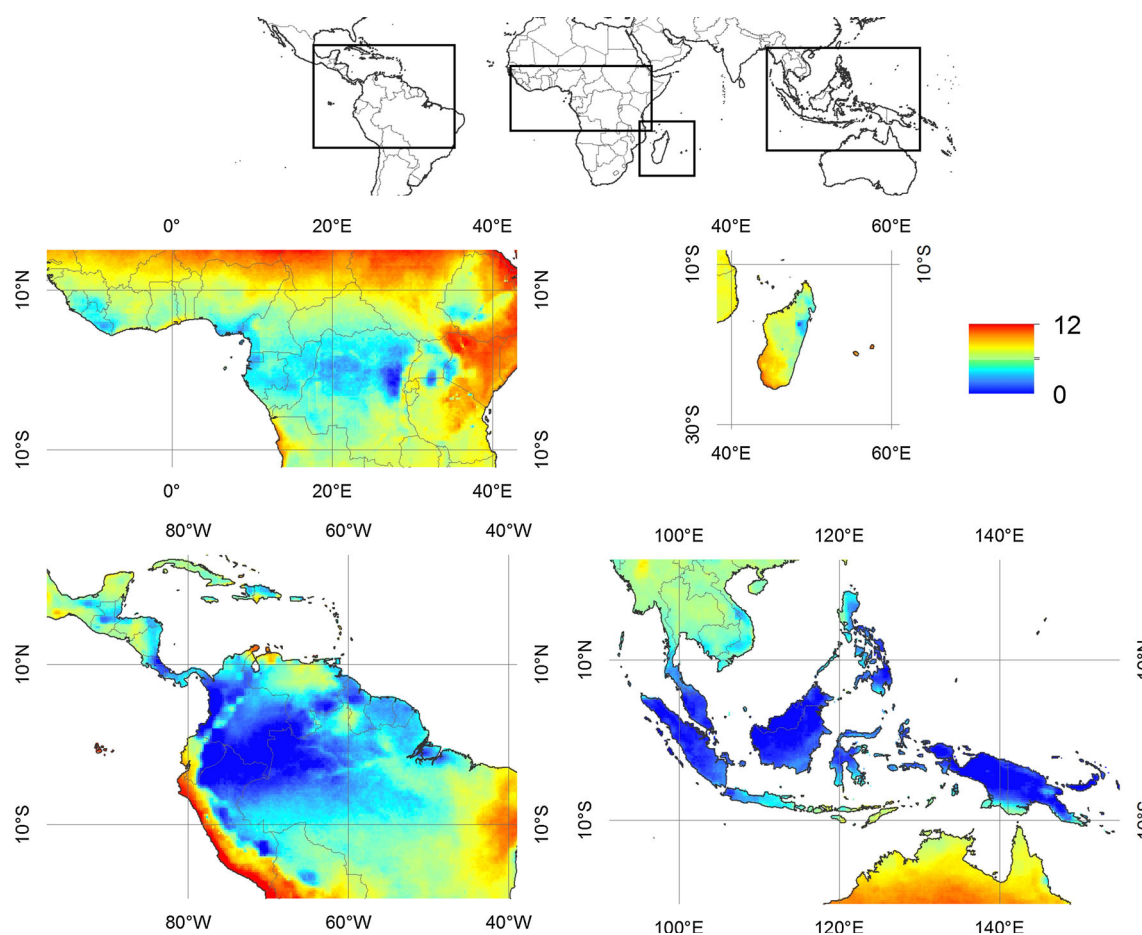


Fig. 2 Precipitation differences between the three major rain forests blocks in the Neotropics, Continental Africa, South-East Asia and Madagascar. The map represents the number of “dry” months per pixel. A dry month is defined as a month receiving less that

100 mm of rain. The data were taken from Tropical Rainfall Measuring Mission (TRMM), product 3B43 version 7 acquired from 1 January 1998 to 31 December 2013 and plotted using ArcGis 10.0 at $\frac{1}{4}$ of a degree/pixel

precipitation and temperature (between 2,500 and 4,000 mm; 25 and 28 °C), the Amazon is significantly more diverse. This led the authors to suggest that African rain forests had a lower species pool adapted to these higher precipitation and temperature values unable to fill up these niches. Interestingly, diversity between Africa and the Neotropics appears quite similar at familial and generic levels (Gentry 1993; Pennington and Dick 2004; Ricklefs and Renner 2012). Pennington and Dick (2004) suggested that these similarities were possibly the result of important recent dispersal events either via long-distance dispersal or selected migration routes (Christenhusz and Chase 2013). This is also supported by molecular dated biogeographical studies showing that long-range dispersal appears as a fundamental element in explaining present-day plant distributions (Renner 2005). Thus, explaining species differences in terms of different adaptation potential would seem unlikely given the important exchanges that have occurred between continents.

Climate stability and species range dynamics

In contrast to the energy–diversity hypotheses, it has long been suggested that climate stability over time is a better predictor of species richness and endemism (Araújo et al. 2008; Jansson and Dynesius 2002; McGlone 1996; Stropp et al. 2009; Wallace 1878). Regions knowing stable climates over time appear to harbor higher species richness and small ranged species (endemism). A recent study showed that for amphibians, mammals and birds, endemism was correlated with low climate-change velocity (climatically stable areas) at a global level (Sandel et al. 2011). In Africa, high levels of endemism (paleo and neo endemics) of bird and plant species were suggested to occur in climatically stable areas (Fjeldså and Lovett 1997). In palms, higher species diversity is correlated to areas with higher Pliocene precipitation in continental Africa (Blach-Overgaard et al. 2013) and higher last glacial maximum (LGM) precipitation compared to that present in Madagascar (Rakotoarinivo et al. 2013). Jansson & Dynesius (2002) introduced the “orbitally forced range dynamics” (ORD) hypothesis (Dynesius and Jansson 2000; Jansson 2003; Jansson and Dynesius 2002) whereby increased climate variability leads to shifts in the geographic distribution of species and gene pools negatively impacting diversity. Jansson (2003) showed a significant correlation between lower temperature change since the LGM and species endemism for birds, reptiles, amphibians, mammals and vascular plants at a global scale. This pattern has also been found in other studies for example amphibians and reptiles in Europe (Araújo et al. 2008). Thus, maybe South America and South-East Asia have known larger areas with more stable climates (i.e., lower ORD)

during the Pliocene or Pleistocene when compared to Africa? Although patterns of TRF plant diversity within continents have been studied in much detail, intercontinental comparisons to test these hypotheses between Africa and the other regions remain few.

The importance of time and area

Time-to-speciation effect

Early on it was recognized (Wallace 1876) that time is an important factor in explaining species diversity patterns (Fine and Ree 2006; Rabosky et al. 2012; Stebbins 1974; Stephens and Wiens 2003). This has been termed the “time-to-speciation” effect (Stephens and Wiens 2003), which suggests that species richness patterns are related to how long clades have persisted in a given region leading to more diversification. The importance of clade age as a factor explaining biodiversity patterns remains debated with some studies providing evidence for (McPeck and Brown 2007; Wiens 2011) and against (Rabosky et al. 2012). Have lineages persisted longer in the Neotropics and South-East Asia than in tropical Africa? Biogeographic evidence suggests that numerous important TRF lineages originated outside of the Neotropics (see Table 1) implying that South America is, at least initially, composed of “immigrant” plant lineages (Pennington and Dick 2004, see below). In addition, fossil data also support the idea that numerous plant lineages originated in Africa and dispersed into South-East Asia after the Paleocene–Eocene collision of the Indian plate with Asia (Morley 1998, 2012). A review of the biogeographical origins of numerous important pantropical plant lineages returns an equivocal pattern (Table 1). Whereas several families have an African origin (“out of Africa”; Muellner et al. 2006) with dispersal into South America and/or South-East Asia followed by diversification (e.g., Hughes and Eastwood 2006), numerous other studies also suggest either Neotropical or South-East Asia origins. In Annonaceae, the origin of the family is ambiguous between South America and Africa mainly because of the sister relationship of the genus *Anaxagorea* distributed in South America and South-East Asia. However, when looking at the origin of the two subfamilies that sustain most of the diversity within Annonaceae (Table 1), Africa is reconstructed as ancestral in both cases (Couvreur et al. 2011b). A similar situation is found in Sapotaceae which is inferred as having a South-East Asian origin because of the sister relationship of two small Asian genera to the rest of the family. However, subfamilies and most tribes are reconstructed as being African in origin (Richardson et al. 2014). Thus, for both these families, Africa can be considered as the origin of

Table 1 Synthesis of the geographic origins and species richness of several important tropical plant families

Family	Infra familiar	Inferred origin	Ancestral area method	Estimated species richness	References
Annonaceae		South America/Africa	ML-DEC	2,500	Couvreur et al. (2011b)
	Annonoideae	Africa	ML-DEC	1,250	Couvreur et al. (2011b)
	Malmeoideae	Africa	ML-DEC	750	Couvreur et al. (2011b)
Apocynaceae	Asclepiadoideae	Africa	Dated phylogeny	3,000	Rapini et al. (2007)
Arecaceae		Laurasia	ML-DEC	2,500	Baker and Couvreur (2013a)
	Arecoideae	North America	ML-DEC	1300	Baker and Couvreur (2013a)
Chrysobalanaceae		Paleotropics/Africa	BiSSE	530	Bardon et al. (2013)
Sapotaceae		Asia	BBM	1200	Richardson et al. (2014)
	Tribe Isonandreae	Africa	BBM	200	Richardson et al. (2014)
	Chrysophylloideae	Africa	ML-DEC/MP	600	Bartish et al. (2011)
Rubiaceae		Africa/Australasia	DIVA	13,000	Antonelli et al. (2009)
Rubiaceae		Asia/South America	DIVA	13,000	Manns et al. (2012)
Malpighiaceae		South American	Dated phylogeny	1,300	Davis et al. (2002)
Lauraceae		Laurasia	Dated phylogeny	3,000	Chanderbali et al. (2001)
Maranthaceae		Africa/Tropical America	DIVA	630	Kress and Specht (2006)
Menispermaceae		Indo Malayan	DIVA	450	Wang et al. (2012)
Melastomataceae		Africa	Dated phylogeny	4,500	Morley and Dick (2003)
Melastomataceae		Laurasia	Dated phylogeny	4,500	Renner et al. (2001)
Meliaceae		Africa	DIVA	565	Muellner et al. (2006)
Moraceae		Eurasian	Dated phylogeny	1,100	Zerega et al. (2005)
Sapindaceae		Laurasia	ML-DEC	1,900	Buerki et al. (2013)
Zingiberaceae		Africa/India	DIVA	1,300	Kress and Specht (2006)

BMM Bayesian binary MCMC model, *ML-DEC* maximum likelihood dispersal extinction cladogenesis model, *BiSSE* binary state speciation and extinction model, *MP* maximum parsimony, *DIVA* dispersal and vicariance analysis

most of their diversity. In some cases, the origin of the family remains debated, for example in Rubiaceae (Antonelli et al. 2009; Manns et al. 2012) and Melastomataceae (Morley and Dick 2003; Renner et al. 2001) where alternative ancestral areas (Table 1) have been postulated. At the generic level, Annonaceae provide an interesting case of African origins followed by dispersal and diversification. The species-rich Annonaceae genus *Gutteria* (ca. 300 species) was inferred to have originated in Africa before dispersing and diversifying the Neotropics (Erkens et al. 2009). Other species-rich genera such as *Duguetia* (89 species in the neotropics four in Africa, Maas et al. 2003, Chatrou, pers. comm.) and *Uvaria* (80 species in Africa, 130 SEA and 20 in Madagascar, Zhou et al. 2012) have been reconstructed as being African in origin. This crude approach suggests that the African flora contains higher or similar concentrations of old lineages than other tropical regions. This would rule against the time-to-speciation effect as a reason for higher diversity outside of Africa. However, to properly test the importance of time, one would have to undertake a meta analysis based on the

numerous recently dated species level phylogenies and comparing non-nested clades (Wiens 2011).

Area-for-speciation effect

It has been suggested that area size is correlated with diversity referred to as the “area-for-speciation” effect (Fine and Ree 2006; Losos and Schluter 2000; MacArthur and Wilson 1967). This is derived from the theory of island biogeography where species diversity is related to the size of the islands and immigration rate. For continents or unbounded regions (Cornell 2013), larger areas would contain more species because of more habitat diversity (Connor and McCoy 1979; Kisel et al. 2011; Krefl and Jetz 2007), better opportunities for speciation (Kisel et al. 2011) or higher speciation rates coupled with lower extinction rates due to larger populations (Connor and McCoy 1979; Fine and Ree 2006; Kisel et al. 2011; Losos and Schluter 2000). At a global level area was shown to be a weak predictor of vascular plant species richness (Krefl and Jetz 2007). Total TRF area between regions varies considerably

(Achard et al. 2002; FAO 2001): the Neotropics are estimated to have 652 million hectares (Ha) followed by South-East Asia with 302 million ha and finally Africa (excluding Madagascar) with 195 million ha (Mayaux et al. 2013). However, the Congo Basin contains the second largest extent of continuous TRF (the Congo Basin) after the Amazon (Mayaux et al. 2013). If by larger area it is implied larger *continuous* area then it would be hard to accept the area-to-speciation effect as an explanation for the observed discrepancies.

Past rain forest extent is also suggested as an important factor explaining Africa's lower species diversity. Based on paleo-reconstructions of rain forest extent at four different time frames, African rain forests are inferred to have lost major areas during the Cenozoic significantly more than any other continent (Kissling et al. 2012; Morley 2000). In addition, Africa has known the largest total surface of TRF since the beginning of the Cenozoic (Kissling et al. 2012). Rain forests in South America and South-East Asia have remained relatively constant in size, with a lower rate of forest loss (Kissling et al. 2012). This drastic reduction of area for Africa, especially from the Miocene onwards is thought to have led to the extinction of numerous taxa in Africa (Morley 2000, 2007; Plana 2004; Raven and Axelrod 1974). However, reduction of TRF in Africa was not continuous with alternating periods of expansion followed by reduction since the Oligocene (Morley 2000). These continental scale dynamics have been linked to the origin of numerous endemics plant and animal species, especially in East Africa (Couvreur et al. 2008; Tolley et al. 2013).

Time-integrated species–area effect

Fine and Ree (2006) showed that for major biomes world wide area is not a good predictor for discrepancies in tree diversity between these regions (i.e., tropics versus non tropics). However, when time and area are integrated, high-diversity regions are correctly predicted which they defined as the “time-integrated species–area effect” (Fine and Ree 2006). Regions are more diverse because they are older *and* larger. In a recent study, Kissling et al. (2012) looked at the global phylogenetic structure of palms in space and time and showed that the time-integrated species–area hypothesis was not supported. Indeed, by estimating TRF area change throughout the Cenozoic, there was no correlation between the age and size of the area with local species diversification. However, more integrated metadata analyses should be undertaken to confirm this result which was only based on a single plant family. In addition, as noted by Cornell (2013), environmental variables such as climate are not integrated into the above hypotheses (time, area or a combination of both) suggesting a minor role of climate in explaining species diversity. As indicated above, climate

appears as an important factor for explaining species diversity patterns and should not be excluded from future analyses.

The impact of geology and tectonic movement

Some authors have suggested that plate tectonic differences between regions could have caused differences in species diversity between tropical regions (Hoorn et al. 2010; Lovett et al. 2007; Morley 2000). In South-East Asia, the collision of the two continental plates (Sundaland and Australia) at the beginning of the Miocene (Hall 2009) brought into contact two different floras increasing species richness in the region (see below, Lovett et al. 2007; see Richardson et al. 2012 for review). In addition, intense tectonic activity such as island formations and mountain uplifts were suggested as important factors for increased diversification of certain plant clades (Bacon et al. 2013a; Buerki et al. 2013; Lohman et al. 2011; Nauheimer et al. 2012; Richardson et al. 2014; Su and Saunders 2009; Thomas et al. 2012). In the Neotropics, the Andean uplift provided increased habitat heterogeneity leading to higher diversification rates (Antonelli and Sanmartín 2011; Hoorn et al. 2010). The connection between North and South America via the Isthmus of Panama is also thought to have played a major role in diversification of TRFs with important biotic interchange and immigration followed by speciation (Bacon et al. 2013b; Cody et al. 2010; Erkens et al. 2007; Gentry 1982; Hughes and Eastwood 2006). In contrast, the African continent lay in the center of the African plate (Fig. 3) and was less affected by tectonic movement. This is nicely illustrated by contemporary seismic activity and numerous subduction regions along the Andes and in South-East Asia whereas such activity is quite scarce in Africa. In addition, the mid Cenozoic saw the start of the uplift of the African continent and the initiation of the East African rift valley with an intensification during the mid Miocene leading to its present day elevated configuration (Morley 2000). Uplifted regions tended to be in areas of lower rainfall such as the arid African rift valley. Where mountains formed under wet conditions high species diversity are encountered (Barthlott et al. 2005; Lovett et al. 2007; Mutke and Barthlott 2005) and these topographically complex regions are associated with high speciation rates such as the Eastern Arc Mountains, Mont Cameroon or the Cristal Mountains (Fjeldså and Lovett 1997; Janssens et al. 2009; Roy 1997).

In addition, the African continent was isolated from other landmasses from the late Cretaceous (after the breakup of Gondwana some ~70 Ma) to the Middle Miocene (16–14 Ma, the closure of the Tethys seaway), longer than any other continent (Morley 2000). This isolation has been

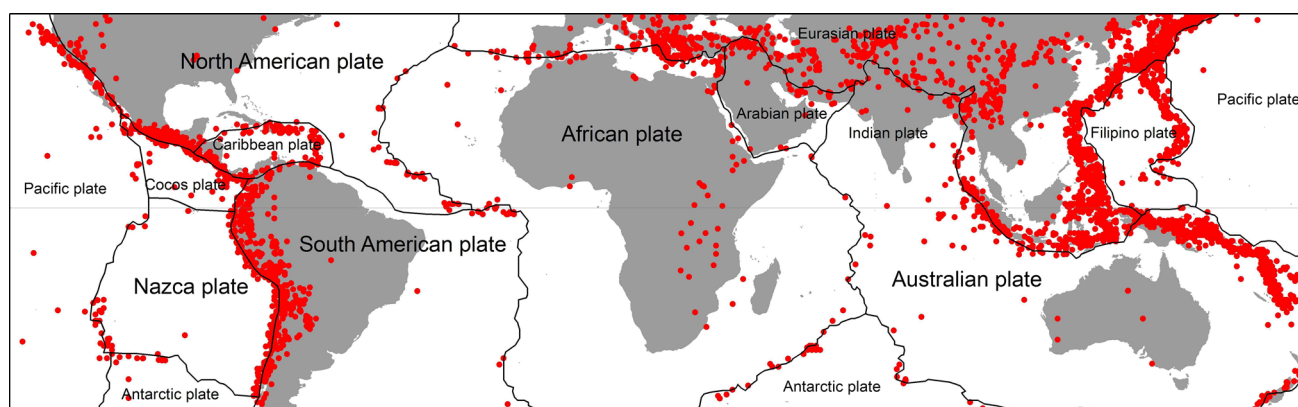


Fig. 3 Distribution of continental and oceanic plates as well as global seismic activity. Africa is subject to less seismic activity than both the Neotropics and South-East Asia

suggested as a possible cause for its lower present-day diversity (Morley 2000) with numerous plant taxa occurring in South-East Asia and the Neotropics, but absent from Africa (amphi-pacific distributions, van Steenis 1962). Morley identified several amphi-pacific megathermal (tropical restricted) plant taxa (mainly genera) having a fossil record distribution suggestive of either survival in Tertiary refuges of North America/South-East Asia or dispersal via Antarctica. In the later case, these taxa did not reach Africa because of its isolated position, whereas South-East Asia and South America were in contact via Antarctica. Dispersal via Antarctica would have been possible up until the early Eocene (55–48 Ma) as global climate was warm and the fossil record indicates the possible presence of TRF like vegetation in Antarctica (Pross et al. 2012). Numerous biogeographic studies (e.g., Buerki et al. 2013; Renner 2005; Renner et al. 2001) underline that even though Africa was cut off from other landmasses, it remained an accessible continent for plant dispersals (either via land bridges or long-distance dispersal) as indicated above (Givnish and Renner 2004; Renner et al. 2001). In addition, isolation in itself might not necessarily lead to less diversification. Indeed, the South American continent has also been isolated for a long period (Morley 2000), yet has undergone high diversification (Antonelli and Sanmartín 2011), especially after successful dispersal events (Erkens et al. 2007; Hughes and Eastwood 2006). Madagascar is another example of a region isolated from other landmasses for over 80 million years, but has known numerous adaptive radiations over time leading to an incredible level of unique biodiversity (Vences et al. 2009).

Alternative evolutionary histories: extinction versus speciation

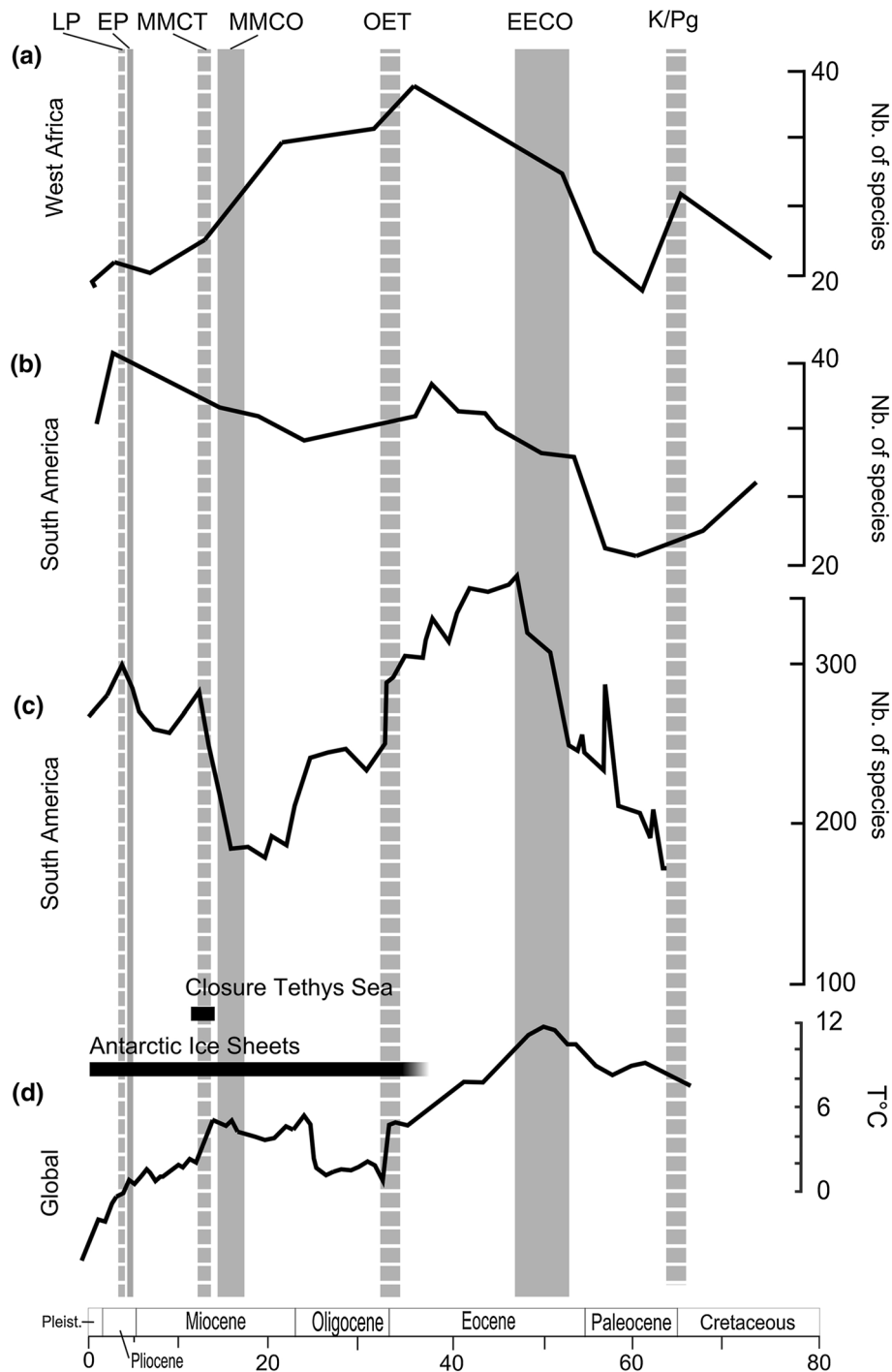
Variation in speciation and extinction rates are the core factors explaining differences in species richness between

regions (Mittelbach et al. 2007; Rolland et al. 2014; Wiens 2011). Higher extinction rates (high extinction hypothesis) in Africa since the Eocene linked to increased aridity over the continent and decreased size of forest area is one of the most important and most widely cited hypothesis to explain the lower African diversity (Morley 2000; Pan et al. 2005; Plana 2004; Raven and Axelrod 1974). In contrast, Gentry (1982, pp. 588) was the first to suggest that “Rather than the flora of tropical Africa being impoverished with respect to the Neotropics, the latter may be considered as uniquely and phenomenally enriched”. Under this hypothesis (high speciation hypothesis), higher species diversity in the Neotropics (and South-East Asia) is the result of higher speciation rates within these regions rather than higher extinction rates in Africa (Baker and Couvreur 2013b; Gentry 1982).

Extinction in Africa, the Neotropics and South-East Asia

Throughout the Cenozoic, TRF floras have been subject to numerous periods of favorable and unfavorable climate influencing diversity levels of TRFs (Jaramillo et al. 2006). I provide a brief comparative synthesis of important periods influencing species diversity throughout the tropics during the Cenozoic (Fig. 4). I focus on the Cenozoic because most plant lineages diversified during that period, although all three regions underwent important geological activity during the Mesozoic. The K/Pg mass extinction event at the end of the Cretaceous (65 Ma) had a negative global impact on vegetation diversity (McElwain and Punyasena 2007) and the TRFs of Africa, Neotropics and South-East Asia were all impacted in similar ways resulting in lower levels of species diversity throughout the Palaeocene (Jaramillo et al. 2006; Morley 2000, 2007). In Africa, the K/Pg event is documented by the extinction of 50 % of gymnosperms taxa (Morley 2000) and around

Fig. 4 Synthesis of palynoflora diversity evolution between a West African and two South American localities from the Upper Cretaceous till present. **a** Estimated angiosperm pollen types since the Upper Cretaceous of West Africa, reproduced from Morley (2007); **b** estimated angiosperm pollen types since the Upper Cretaceous of South America, reproduced from Morley (2007); **c** pollen and spore diversity dynamics throughout the Cenozoic in South America (Colombia and Venezuela), reproduced from Jaramillo et al. (2006) and Hooen et al. (2010); **d** global temperature variation throughout the Cenozoic reproduced from Zachos et al. (2001). Note the differences in the scale of species number between **a**, **b** and **c**. *Stripped lines* indicate times of major global climate deterioration (transitions); *gray filled lines* represent periods of global climatic optima. *K/Pg* Cretaceous Paleogene mass extinction event, *EECO* Early Eocene Climatic Optimum, *OET* Oligocene Eocene Transition, *MMCO* Middle Miocene Climatic Optimum, *MMCT* Middle Miocene Climatic Transition, *EP* Early Pliocene, *LP* Late Pliocene



47 % of palm fossil taxa in West Africa (Pan et al. 2005). The Early Eocene Climatic maximum (51–53 Ma) marked the height of globally warm temperatures (Zachos et al. 2008) coinciding with widespread TRFs (e.g., occurring in Europe and Antarctica) and the highest levels of TRF diversity ever recorded (Jaramillo et al. 2006; Morley 2007). The rest of the Eocene shows a global cooling that continues throughout the Cenozoic initiated by the formation of the permanent Antarctic ice sheets during the Late

Eocene (Fig. 4). This marks the start of global dropping temperatures (Zachos et al. 2008) resulting in the absolute decline of TRF diversity (Fig. 4) across all regions (Jaramillo et al. 2006; Morley 2007). The late Eocene–Oligocene transition (33.9 Ma) was marked by a sharp drop in global temperatures (Zachos et al. 2008) resulting in numerous extinctions across the tropics (Jaramillo et al. 2006; Morley 2007). Pan et al. (2005) documented a significant decrease in palm morphospecies of Ethiopia

shortly after this time, suggesting that the late Eocene–Oligocene transition rather than Neogene extinctions (Moore 1973) is responsible for the lower species diversity of this family observed in Africa today. Morley (2000) suggested that the South American vegetation was less affected by this event, but in general marked a turnover of species composition towards a modern day composition during the Oligocene. The late Oligocene and early Miocene were characterized by globally warmer climates leading to renewed expansion of TRF which lasted up until the Mid Miocene Climatic Optimum (17–15 Ma). The closure of the Tethys Seaway during the Mid Miocene (16–14 Ma) affected oceanic currents, and this coupled with a decrease of atmospheric CO₂, amplified global cooling and ice sheet growth in Antarctica (Hamon et al. 2013) leading to the Middle Miocene Climatic Transition (MMCT, 14 Ma). However, in South-East Asia, the collision of the Australian plate with Sunda during the Oligocene generated an increase of moisture over the region leading to a significant increase in diversity during the Miocene (Morley 2007, 2012). South America was apparently less impacted by the MMCT with, for example, few extinctions recorded within palms (Morley 2000), although some regions might have been more affected than others. This also coincides with an intense Andean uplift period (between 12 and 4.5 Ma) which is suggested to have played an important role in Neotropical species diversification (Hoorn et al. 2010; Jaramillo et al. 2006). However, some studies suggest that Amazon Miocene diversity might have been higher or equally diverse than modern day assemblages implying some reduction in overall diversity and extinction in the Amazon (Jaramillo et al. 2010; Morley 2007). In Africa, the closure of the Tethys Seaway brought significant drought over the continent resulting in the increase of savannas (Jacobs et al. 1999) and the decrease of TRFs (Morley 2000). By the end of the Miocene African rain forests were restricted to refugia in upland areas and possibly along river systems (Plana 2004). The first half of the Miocene (23–13.8 Ma) is suggested as a determinant period in African vegetation extinction (Morley 2000) gradually affecting modern African rain forest diversity in comparison to other regions (Fig. 4). The Early Pliocene (5.33–3.6 Ma) was a warmer and overall moister interval worldwide (Haywood et al. 2009). In Africa, this led to the increase and diversification of TRFs (Morley 2000; Plana 2004) which is also supported by molecular dating analyses of African plant lineages (Couvreur et al. 2011c; Plana et al. 2004). Finally, during the Late Pliocene (3.6–2.58 Ma) climates changed again becoming dryer and colder leading to another phase of important extinction in Africa that was much faster than the one occurring during Miocene (Morley 2000).

This brief synthesis (Fig. 4) underlines the fact that all main TRFs blocks underwent some degree of extinction throughout the Cenozoic apparently correlated with global climatic changes. Even though our knowledge on the Cenozoic dynamics of palynofloras has increased (Jaramillo et al. 2006), it remains hard to quantify the differences and the intensity of these extinction phases between continents.

Have African plant lineages undergone more extinction?

In parallel to the fossil record, diversification analyses of important TRF-restricted plant lineages have provided valuable insights into the evolution and diversification of TRFs (Couvreur et al. 2011a; Davis et al. 2005). If extinction was the main cause of lower species diversity in Africa then we would expect to detect significant diversification decreases along African lineages (increase of extinction over speciation rates). As indicated above, palms exhibit one of the most extreme cases of discrepancies between Africa and the other tropical regions and are often cited as a key example to illustrate this pattern (e.g., Lovett et al. 2007). Based on a complete generic dated phylogeny of palms in combination with accurate knowledge of generic diversity, and using a clade specific diversification model (Alfaro et al. 2009; Morlon 2014), Baker and Couvreur (2013b) inferred that none of the African palm lineages underwent a significant decrease in diversification rates. In contrast, rate increases were detected along several Neotropical and South-East Asian lineages as well as for a Malagasy genus. These results suggest that decreases in diversification rates are not necessary to explain the present-day diversity of palms in Africa. Such a hypothesis was also supported by a global phylogenetic community analysis of palms that clearly identified the Neotropics, SEA and certain island regions (e.g., Madagascar) as undergoing high in situ diversification, whereas Africa had mostly non-significant results (Kissling et al. 2012). A similar result was obtained for Annonaceae where no significant rate decreases were identified for African lineages based on a family-wide analysis (Erkens et al. 2012). In fact, the largest rate increase of the family was found at the stem of two African genera (*Monodora* and *Isolona*). Based on a larger generic sampling and a better resolved phylogeny of Magnoliids (Annonaceae being one of the most diverse families), a single significant rate shift increase was identified in Annonaceae (Massoni 2014; Massoni, Couvreur and Sauquet, unpublished) corresponding mainly to South-East Asia and Neotropical clades. Finally, the family Chrysobalanaceae has over 80 % of its diversity concentrated in the Neotropics. Bardon et al. (2013) found that

these differences are linked to higher speciation rates in the Neotropics, when compared to the Paleotropics.

Overall, these results support Gentry's "high speciation hypothesis" that maybe extinction in Africa does not need to be invoked to explain its lower species diversity. Estimating extinction rates from molecular phylogenies is hard (Rabosky 2010), but the approaches used in the above studies were based on new and better adapted models (Morlon 2014) that have been shown to detect rate declines based on empirical data (Morlon et al. 2011). Thus, although these approaches should be viewed with caution, they provide valuable insights into diversification dynamics where the fossil record does not.

Role of human impact of tree species diversity

Finally, another hypothesis that was suggested by Richards (1973) is that human impacts and disturbances on TRF diversity are stronger in Africa because of the longer human occupation than in the Neotropics or South-East Asia. This would have led to less (or even no) true primary forests across Africa resulting in a diminished diversity. We are still far from fully understanding human occupation, land use and their impacts of species diversity in TRFs. Studies have shown important influences of humans on species diversity in Central African rain forests and not just for the last few decades, but for longer periods (millennia) too (van Gemerden et al. 2003). However, the overall idea that the Amazon was generally "pristine" with low population density and limited impact on its environment has been challenged recently and remains highly debated (Heckenberger et al. 2003; McMichael et al. 2012; ter Steege et al. 2013). It will be challenging to assess how the occupation of TRFs by humans has impacted diversity (van Gemerden et al. 2003) and if differences in species numbers can really be explained by different degrees of human impact.

Conclusions and perspectives

This review highlights several conclusions about explaining differences in plant species richness between tropical rain forests in continental Africa, the Neotropics and South-East Asia. First and foremost, differences in plant species diversity between those regions have yet to be formally conducted by controlling for area size. Also most diversity metrics are based on tree species with DBH higher than 10 cm, which, in the case of TRFs can significantly underestimate the true species diversity. However, with the increase of TRF plot data (De Cáceres et al. 2012; Gonmadje et al. 2012; ter Steege et al. 2013), comparative analyses of TRF *tree* species can and should

be undertaken (Parmentier et al. 2007). Ideally, more detailed plot data including epiphytes, lianas and small trees should be taken into account, although this can prove a difficult task. Only then can we really assert that the African rain forest is truly less species-rich than those from other regions. Second, based on the present review the lower plant species diversity encountered in Africa cannot and should not be related to a single cause (e.g., increased aridification). It is probably the result of numerous intricate causes impacting speciation, extinction and/or migrations such as present and past adverse climate, geology, time and area and even human impacts. Recent diversification analyses of pan tropical plant families support the "high speciation hypothesis" over the "high extinction hypothesis". As analytical methods evolve to integrate more realistic models of evolutionary dynamics coupled with better sampled phylogenies (Rabosky et al. 2013; Stadler 2013) more robust tests of these hypotheses will emerge. Third, models exploring species diversity patterns of TRFs between continents integrating several variables should be privileged in future comparative analyses (Kreft and Jetz 2007). For example, Jetz and Fine (2012) showed that integrating area, productivity over time and temperature best explained current species diversity of vertebrates across 32 bioregions compared to single predictors. Thanks to increased data collection from TRFs worldwide such analyses are now becoming possible and more effort should be undertaken to use them in a comparative manner. Finally, most studies have linked climatic, geological or historical processes for explaining species diversity patterns. However, it will be relevant to explore the effects of alternative variables such as plant functional diversity (species traits) or demographics which have been suggested to effect ecosystem dynamics and long-term stability (Díaz and Cabido 2001). Even though such databases are still patchy at best for TRFs they are starting to become better inventoried (Swenson 2013). Baker et al. (2014) found that shorter turnover time per species (mortality) is strongly linked to higher species diversity and higher diversification rates in Amazonian trees. Undertaking similar, but comparative analyses between TRFs of all three major regions would no doubt provide additional insights into regional differences of species richness. Finally, if they are present-day differences between regions in terms of species diversity, it will be important to know how diversity in these regions will cope with future climate change. For that, intercontinental comparative phylogeographic studies can test how climate change drives community assembly and evolution within the same biota (Hickerson et al. 2010), but in different regions. Here "comparative" would not relate to species distributed in the same region (co-distributed) as generally implied, but to multiple different species in different TRF regions/continents. Studies could

also focus on intercontinental meta populations of the same species (e.g., *Symphonia globulifera*; Dick et al. 2003).

“Why are there fewer plant species in African rain forests?” remains an understudied question with numerous preconceived and largely untested ideas for which we are still far from having a synthetic explanation. Surprisingly, formal comparative studies between Africa, the Neotropics and South-East Asia are scarce impeding the understating of the observed differences. As ecological, taxonomical, and paleobotanical data continue to emerge independently from all three main TRF blocks, it will be important to apply an interdisciplinary approach that includes taxonomists, evolutionary biologists, ecologists, paleobotanists, climatologists, geologists and archeologists to synthesize these data at an intercontinental level. Only then shall more detailed answers to this question start to emerge leading to a better understanding of TRF biodiversity evolution in general.

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