



Global biogeography and diversification of palms sheds light on the evolution of tropical lineages. II. Diversification history and origin of regional assemblages

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ABSTRACT

Aim Palms (Arecaceae/Palmae) are a model group for evolutionary studies in the tropics. In two companion papers, we aim to establish a general framework of palm evolution, exploring the geographical distribution of palm lineages and species diversity patterns at global and regional levels. In this, the second paper, we analyse the biogeographical events underlying regional palm assemblages and diversification processes across the family. We investigate the timing and location of diversification rate shifts and test the 'odd man out' pattern of low species diversity observed in the African palm flora.

Location Global.

Methods A complete, dated phylogeny of palm genera and ancestral area reconstructions were used to infer the biogeographical history of regional palm assemblages. Diversification rates for all genera were estimated and significant shifts in diversification rates across the family were identified under a maximum likelihood model.

Results Following their early diversification in Laurasia around 100 Ma, palms dispersed southwards before the end of the Cretaceous. Few dispersal events into Africa, North America and South America were inferred, whereas numerous lineages migrated between Eurasia, the Pacific and the Indian Ocean. Thirteen diversification rate increases were identified. High diversification rates were found only in lineages from Asia, the Americas, the Pacific and the Indian Ocean, but not in any African groups. Diversification decreases were not identified in any lineage.

Main conclusions Dispersal of palms into their present-day distribution started during the Late Cretaceous, consistent with the first fossil records for rain forests in Africa and South America. The few dispersal events into South America and Africa emphasize the isolated position of these continents for most of the Cenozoic. In contrast, high dispersal between Eurasia, the Pacific and the Indian Ocean, notably during the Miocene, can be attributed to geological activity in the region, especially in Malesia. Low species diversity in Africa relative to other regions is explained here by increased *in situ* diversification in Asia, the Americas, the Pacific and the Indian Ocean, rather than by diversification rate decreases in Africa. This may prove to be a general pattern in other organisms showing a similar disparity in richness in Africa.

Keywords

Africa, Ancestral area reconstruction, Arecaceae, boreotropical hypothesis, diversification rates, historical biogeography, Palmae, tropical rain forests.

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INTRODUCTION

Due to their pantropical distribution and inferred mid-Cretaceous origins in tropical rain forest (TRF; Couvreur *et al.*, 2011a), the palms (Arecaceae) may offer general insights into diversification processes across a broad span of evolutionary history in the tropics. In a companion paper (Baker & Couvreur, 2012), we examined the historical biogeography of palm lineages using molecular dating and ancestral area reconstruction methods. In this second paper, we turn to focus on palm diversification history and the biogeography of regional palm assemblages.

In a previous, broad-scale study of palms, the major lineages were found to have accumulated steadily through time under a constant diversification rate, at least until the end of the Oligocene (Couvreur *et al.*, 2011a). However, in order to explain present-day species diversity, it was acknowledged that speciation bursts could have taken place on more recent time frames. A mixed model of diversification was proposed entailing constant accumulation of major lineages punctuated by significant increases in diversification rates concentrated in more recent time frames.

At a regional scale, the African flora is depauperate when compared to other tropical regions, the so-called 'odd man out' pattern (Richards, 1973). This pattern is found in numerous TRF plant families and is especially conspicuous in palms (Moore, 1973; Dransfield, 1988). Africa contains just 65 species of palms, more than tenfold fewer than South America or Southeast Asia (Dransfield *et al.*, 2008). Such a discrepancy has generally been explained by a decrease in diversification rates linked to a deteriorating climate since the Miocene (Morley, 2000; Plana, 2004; Kissling *et al.*, 2012). A detailed analysis of the African palm fossil record documented a reduction in species diversity through time, especially after the Eocene–Oligocene boundary, which was attributed to a decrease in diversification rates linked to an increase in extinction and/or a decrease in speciation (Pan *et al.*, 2006). More recently, Kissling *et al.* (2012) linked random phylogenetic structure inferred for the African palm flora to extinction events and lower net diversification rates. In contrast, South America and numerous islands with diverse palm floras (e.g. Madagascar, Hawaii, New Caledonia) showed strong phylogenetic clustering that was interpreted as being the result of increases in diversification rates. Diversification rate analyses may shed light on differential patterns of diversity between regions, but have not yet been applied directly to these hypotheses.

In this paper, we use the framework established in our companion paper (Baker & Couvreur, 2012) to elucidate the biogeographical processes underpinning the origins of major regional assemblages of palms and to undertake detailed diversification analyses. We use our results to address three key questions about palm dispersal and diversification history. (1) How do spatio-temporal patterns of lineage dispersal explain the composition of regional palm assemblages? (2) Have increases in diversification rates taken place in

palms on recent time scales as hypothesized by Couvreur *et al.* (2011a)? (3) Have African lineages undergone a decrease in diversification over the past 40 Myr as proposed by previous authors (Pan *et al.*, 2006; Kissling *et al.*, 2012)?

MATERIALS AND METHODS

Dated molecular phylogeny and ancestral area reconstruction

The analyses presented here exploit the chronogram of Couvreur *et al.* (2011a), which was derived from the complete genus-level supertree of palms of Baker *et al.* (2009; see Appendix S1 in Supporting Information, Dryad data repository, doi:10.5061/dryad.vb25b35j). Ancestral area reconstructions inferred using a maximum likelihood method under the dispersal–extinction–cladogenesis (DEC) model (Ree *et al.*, 2005; Ree & Smith, 2008) were taken from Baker & Couvreur (2012) and incorporated dispersal probability constraints reflecting geological history (model M₁: Couvreur *et al.*, 2011a; Baker & Couvreur, 2012). Seven geographical areas were defined – A: South America, B: North America (including Central America and the Caribbean), C: Africa (including Arabia), D: Indian Ocean Islands (including Madagascar), E: India (including Sri Lanka), F: Eurasia (to Wallace's Line, including the Andaman and Nicobar islands) and G: the Pacific (including areas east of Wallace's Line and Australia). Genera were assigned to one or more geographical areas based on their natural distributions (Dransfield *et al.*, 2008). Dispersal events between these areas were inferred by comparing ancestral areas reconstructions at adjacent nodes (Ree & Smith, 2008; Buerki *et al.*, 2011) and were collated to explore the biogeographical history of regional palm assemblages. For full details of methods, see the companion paper in this issue (Baker & Couvreur, 2012) and Couvreur *et al.* (2011a).

Diversification rates

The total number of species for each palm genus was obtained from Dransfield *et al.* (2008) under the assumption that all genera are monophyletic. For each genus, the absolute net diversification rate, resulting from speciation (b) minus extinction (d), was calculated under the assumption of a constant rate, using the estimated stem age following Magallón & Sanderson (2001). Two extreme extinction rates were explored in order to include reasonable bounds (Magallón & Sanderson, 2001): high extinction ($d = 0.95$) and no extinction ($d = 0$). Those taxa lying outside the 95% confidence interval of the generic diversification rate were identified as outliers.

We then identified genera that were significantly more or less diverse in terms of number of species when compared to a constant overall diversification rate. This was performed by generating the 95% (upper and lower) limits of the expected diversity through time (from 0 to 100 Ma) under a constant

birth–death model and under both no extinction ($d = 0$) and high ($d = 0.95$) extinction rates (Magallón & Sanderson, 2001; Couvreur *et al.*, 2011b). Analyses were performed using the R package *LASER* version 2.3 (Rabosky, 2006).

Shifts in diversification rates

In order to test for significant shifts in diversification rates across the whole evolutionary history of palms, we used *turboMEDUSA* (<http://www.webpages.uidaho.edu/~lukeh/software/software.html>), a revamped implementation of the *MEDUSA* function implemented in the R package *GEIGER* version 1.3.1 (Harmon *et al.*, 2008) following Alfaro *et al.* (2009). *TurboMEDUSA* can handle large trees and uses the corrected Akaike information criterion (AIC_c , a basic AIC with a correction for finite sample sizes) for model selection, which is recommended over the AIC (Burnham & Anderson, 2002), especially for parameter-rich models.

TurboMEDUSA is based on the approach of Rabosky *et al.* (2007), which combines an incompletely sampled phylogenetic tree with clade (species) diversity represented at the tips in order to estimate shifts in birth (b) and death (d) rates. The method identifies the most significant number of rates shifts within a given tree and the diversity of species at its tips. This is done by first fitting a general birth–death rate to the whole phylogeny (no rate shifts) corresponding to a two-parameter model (b and d). Then, a rate shift at the optimal location on the tree is identified and a five-parameter model is fitted to the tree [$b1$, $d1$, time of shift (t), $b2$, $d2$]. Both models are then compared and if there is a significant improvement in the AIC_c score the five parameter model is retained. This process continues by adding additional shifts and comparing the resulting models between them using the AIC_c . Once the improvement of the AIC_c is below a certain threshold the analysis is stopped and the optimal number of rate shifts for a given phylogeny has been identified. We ran *turboMEDUSA* under a Linux operating system with the R package *MULTICORE* (version 0.1.7). We set ‘model.limit = 20’, which corresponds to the number of models that are fitted to the phylogeny. We selected the option ‘stop = threshold’ and ‘criterion = aicc’, which indicates that the model fitting will stop once there is no significant increase of the AIC_c value (i.e. ΔAIC_c smaller than the specified threshold).

RESULTS

Dispersal events between major regions

Above the genus level, we inferred a total of 35 dispersal events between regions (Figs 1 & 2) based on the most likely reconstructions at each node. Figure 1 provides an overview of the role of regions as sources and sinks of dispersed lineages. The Indian Ocean and Pacific were found to be the most frequent sinks of palm diversity, receiving eight lineages each. Four dispersal events were inferred into South America

and Africa each, and one dispersal event was inferred into India. Although Laurasia (as Eurasia and North America) was inferred to be the most likely ancestral area for the crown node of palms, subsequent back-dispersal into these regions appears to have been important, with seven dispersals inferred into Eurasia and three into North America. Eurasia was inferred to be the most important source of dispersing lineages (12 lineages), followed by South America (seven lineages), the Pacific (six lineages), the Indian Ocean (five lineages) and North America (four lineages), whereas Africa and India contributed little (one and zero lineages, respectively). To visualize the dispersal history of palms in space and time, dispersal events were depicted on palaeomaps representing four different time frames spanning the Late Cretaceous and Cenozoic (Fig. 2).

Genus diversity

The diversification rates under both zero and high extinction rates for all palm genera with more than one species are shown in Fig. 3 and in Appendix S2. Under no extinction (Fig. 3a), seven genera were found to have significantly higher diversification rates when compared to the rest of the family (*Bactris*, *Balaka*, *Butia*, *Coccothrinax*, *Dypsis*, *Pinanga*, *Syagrus*). When a high extinction rate is factored in (Fig. 3b), six genera (*Bactris*, *Calamus*, *Coccothrinax*, *Dypsis*, *Licuala*, *Pinanga*) were found to have the highest diversification rates. In the latter case, most genera identified as outliers were species rich (more than 50 species). This is visible in Fig. 3b where most of the large circles are concentrated in the upper part of the graph. A total of seven genera were identified as having a significantly lower diversification rate corresponding to old genera with just two species, except for *Eugeissona* which has six species but with a stem age of 80.21 Myr (see Appendix S2).

When compared to the expected species diversity under a general constant birth–death diversification model of palms (Fig. 3c), six genera (*Bactris*, *Calamus*, *Coccothrinax*, *Dypsis*, *Licuala*, *Pinanga*) were found to have significantly more species than expected and one (*Eugeissona*) with fewer than expected.

Shifts in diversification

The background rate of diversification estimated for palms (Table 1) using *turboMEDUSA* under the birth/death model is characterized by an overall net rate of $r = 0.050355$ and an almost null extinction rate ($d = 0.000011$). The threshold for the increase of the AIC_c value was estimated by *turboMEDUSA* to be 6.15 for a tree with 183 tips. This means that all models incurring an increase in the AIC_c value larger than 6.15 only were retained. This criterion was not met when the analysis went from 14 pairwise models to 15 ($\Delta AIC_c = 1.9$) and thus the best fitting model was identified as having 13 rate shifts (Table 1, Fig. 4). All of them corresponded to rate increases from the background rate. No rate

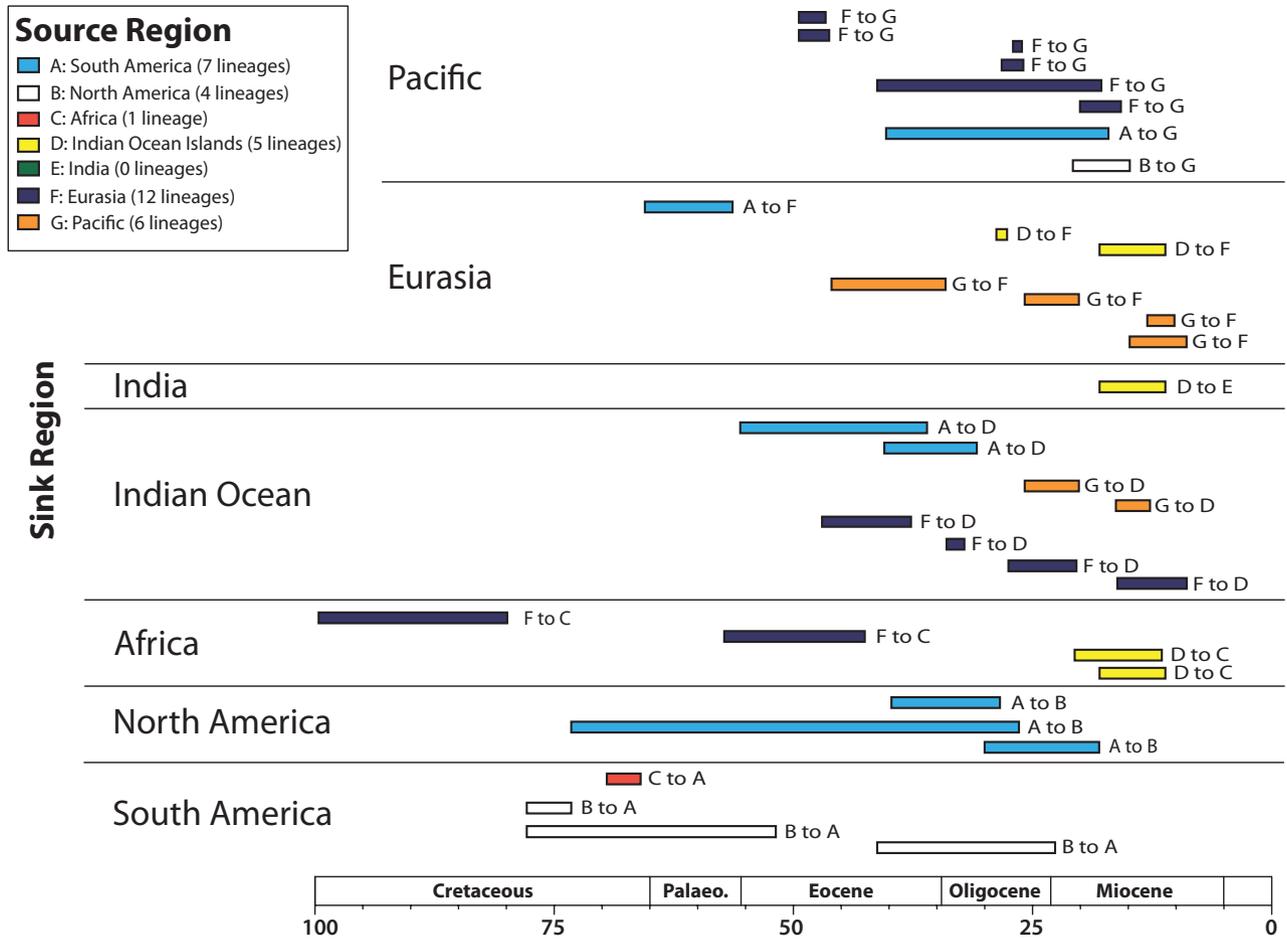


Figure 1 Temporal history of dispersal events in palms. All 35 dispersal events inferred from the most likely ancestral area reconstructions determined by LAGRANGE are illustrated, grouped into sink regions (see Fig. 1 of Baker & Couvreur, 2012 and raw LAGRANGE output at the Dryad data repository: doi:10.5061/dryad.vb25b35j). Each event spans the stem and crown node age of the branch along which it was inferred.

decreases were identified. The most significant rate increase was identified at node 2 which corresponds to the tribe Areceae, but excluding the subtribe Verschaffeltiinae, *Iguanura* and *Masoala*. Rate increases were identified for an extra four other clades and at the stem node of eight genera.

DISCUSSION

Dispersal events and the composition of regional palm assemblages

Our family-wide biogeographical analysis permits an overview of the major dispersal events (above the genus level) during the last 100 Myr that underpin the assembly of regional palm floras (Fig. 1). From its ancestral area in Laurasia (Couvreur *et al.*, 2011a; Baker & Couvreur, 2012; Fig. 2), the family expanded southwards through several dispersals of independent lineages into different regions. However, dispersal was rare during the early evolution of the family with the large majority of discernible dispersal events (i.e. based on analysis of extant lineages) occurring during the Cenozoic

(Figs 1 & 2). The oldest successful dispersals of palms out of the Laurasian ancestral area took place in three early range expansions, one from Eurasia to Africa in the stem lineage of Calamoideae (Late Cretaceous) and two from North America to South America in the stem lineages of Arecoideae and Ceroyloideae (Late Cretaceous–early Cenozoic). These dispersal events correlate well with the first evidence during the latest Cretaceous of the establishment and diversification of TRFs in Africa and South America (Burnham & Johnson, 2004; Morley, 2007; Jaramillo *et al.*, 2010) and the palm pollen fossil record from the Maastrichtian of Africa (Pan *et al.*, 2006).

Despite its high palm diversity (*c.* 730 species; Dransfield *et al.*, 2008), the South American palm flora is almost entirely derived from just four major dispersal events into the continent, three of them from North/Central America and one from Africa (Fig. 1). In a sense, our results support the conclusion of Pennington & Dick (2004) that immigrants of major plant families have played a significant role in the assembly of the Neotropical flora. For palms, the immigrants are entirely pre-Miocene, consistent with a general pattern

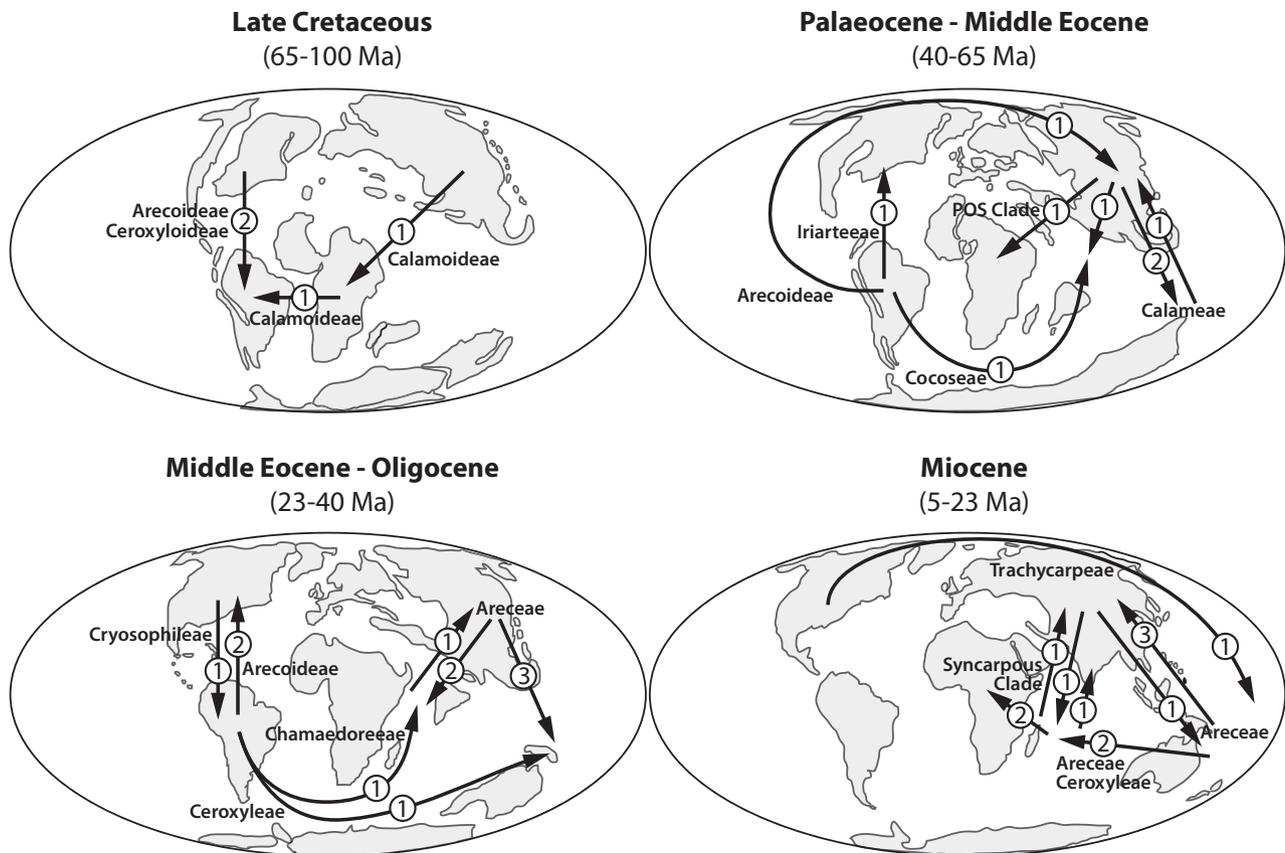


Figure 2 Summary of the dispersal history of palms. Four time frames were chosen to represent the history of the major dispersal events in palms. Arrows represent inferred dispersal events (*not* specific dispersal routes) above the genus level following Fig. 1. Circles on arrows indicate the number of dispersal events that took place in the same direction. Subfamily, tribe or major clade names are indicated on certain arrows (Dransfield *et al.*, 2008). Base maps are derived from Buerki *et al.* (2011).

observed in many plant groups that invaded South America prior to the closure of the Isthmus of Panama (Cody *et al.*, 2010). Nevertheless, the small number of immigrations events contrasts starkly with the high species diversity of South American palms, suggesting that *in situ* diversification, and not immigration, must be the most significant explanation for present-day diversity in the region (Hooen *et al.*, 2010; Kissling *et al.*, 2012). In fact, the large majority of South American palm diversity can be traced back to a single Cretaceous dispersal event in the stem lineage of the Arecoideae (Baker & Couvreur, 2012), the remaining three giving rise to only moderate numbers of species. Numerous early divergences in Arecoideae took place in South America, giving rise to many species rich lineages, such as tribes Cocoseae (*c.* 300 species), Geonomateae (*c.* 80 species), Iriarteae (*c.* 30 species) and Euterpeae (*c.* 30 species). This high speciation activity is also supported by our diversification analyses, which highlight several South American genera with high and significant increases in diversification rates relative to the rest of the family (Figs 3 & 4).

South America has been a source of lineages dispersing into nearby North America, but also to several more distant regions (Eurasia, Indian Ocean, Pacific Ocean; Figs 1 & 2)

that subsequently became important components of those palm floras (e.g. tribe Areceae). Such long-distance dispersals for tropical groups remain hard to explain. Several studies have suggested that a dispersal route for megathermal taxa via Antarctica was possible mainly during the climatic optima of the Palaeocene and Miocene (Morley, 2000; Trénel *et al.*, 2007; Bartish *et al.*, 2011), with lineages diverging once the climate barrier was reinstated. Such a hypothesis was favoured for subfamily Ceroxyloideae (Trénel *et al.*, 2007), in which several species have adapted to cooler, montane conditions. Here, we inferred that palm lineage dispersals from South America to the Indian Ocean and Pacific occurred between 55 and 40 Ma, which might be explained by migration through Antarctica during the Early Eocene thermal maximum (Fig. 1). Some research suggests that this would be unlikely because vegetation in Antarctica during the Eocene has been characterized as closely resembling 'a cool temperate rainforest' (Poole *et al.*, 2001, 2003) unable to support true TRF vegetation in which palms thrive. However, the recent discovery of a near-tropical rain forest fossil pollen flora in the Early Eocene of Antarctica, which included pollen attributed to palms (Pross *et al.*, 2012), indicates that such a dispersal route may indeed have been

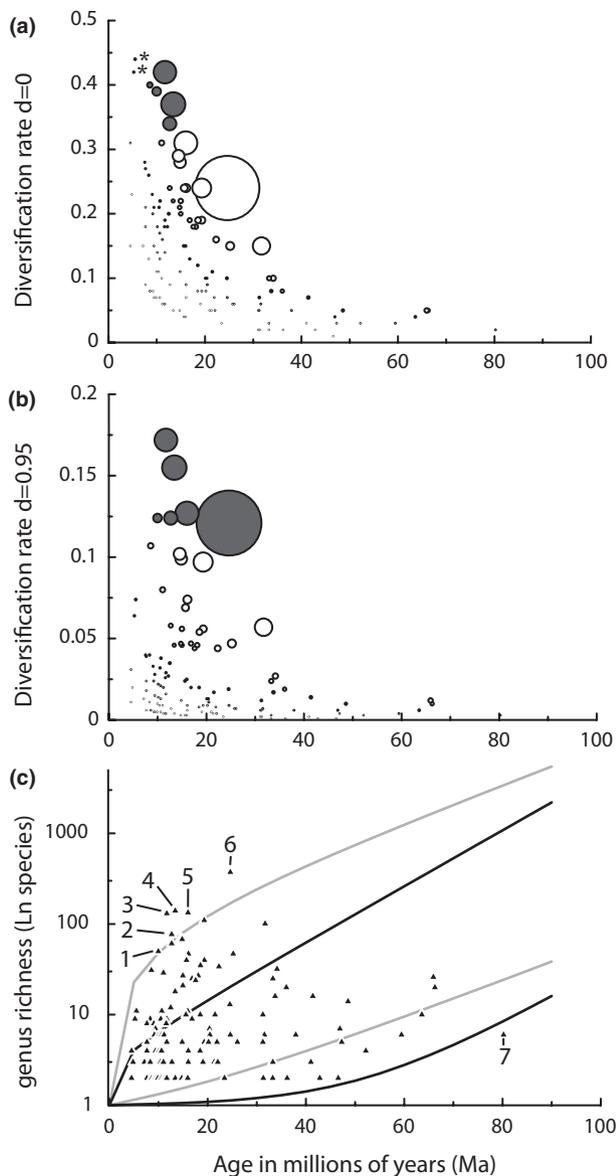


Figure 3 Generic diversification in palms. (a) Diversification rates based on stem node ages of genera under no extinction ($d = 0$). Circle size is proportional to the number of species in each genus. Grey circles (and circles indicated with an asterisk): genera that have a significantly higher diversification rates when compared to the family, which are, from highest to lowest: *Balaka*, *Butia*, *Pinanga*, *Syagrus*, *Coccothrinax*, *Dypsis*, *Bactris*. (b) Diversification rates based on stem node ages of genera under high extinction ($d = 0.95$). Circles proportional to number of species in each genus. Grey circles: genera that have a significantly higher diversification rates when compared to the family which are, from highest to lowest: *Pinanga*, *Dypsis*, *Licuala*, *Coccothrinax*, *Bactris*, *Calamus*. (c) Confidence intervals on expected generic diversity according to stem group age given a constant rate of diversification ($r = 0.039$). Black lines represent 95% confidence intervals under no extinction ($d = 0$), while grey lines are 95% confidence intervals with a high rate of extinction ($d = 0.95$). Outlier genera are numbered: 1, *Coccothrinax*; 2, *Bactris*; 3, *Pinanga*; 4, *Dypsis*; 5, *Licuala*; 6, *Calamus*; 7, *Eugeissona*. See Appendix S3 for a detailed version of this figure with all points labelled.

Table 1 Diversification rate shifts across palms. Diversification rate shifts at nodes indicated on the chronogram in Fig. 4. Estimates for the net diversification (r) and the relative extinction rate (epsilon) for each clade identified using turboMEDUSA are given.

Node number	r	epsilon	ΔAIC_c
1 Background rate	0.050355	1.14×10^{-5}	0
2	0.160617	1.02×10^{-6}	27.759
3 <i>Calamus</i>	0.208314	NA	22.895
4	0.053334	6.66×10^{-1}	16.324
5 <i>Daemonorops</i>	0.121983	NA	17.127
6 <i>Pinanga</i>	0.335405	NA	14.995
7 <i>Dypsis</i>	0.302343	NA	15.354
8	0.289771	1.28×10^{-4}	11.473
9 <i>Licuala</i>	0.256801	NA	13.544
10	0.255672	3.13×10^{-1}	12.413
11 <i>Coccothrinax</i>	0.306059	NA	10.220
12 <i>Chamaedorea</i>	0.200298	NA	10.896
13 <i>Geonoma</i>	0.234600	NA	11.245
14	0.162063	1.74×10^{-6}	10.225

AIC_c , corrected Akaike information criterion.

NA, not applicable; extinction rates cannot be calculated for unresolved clades, in our case stem nodes of genera (L. Harmon, University of Idaho, pers. comm.).

possible. An alternative hypothesis would be dispersal via Africa, possibly South Africa, which has been shown to have supported TRF during the Eocene (Morley, 2000, 2007), followed by extinction.

The palm flora of North America, including Central America (*c.* 250 species) and the Caribbean (*c.* 130 species), can be divided into three main components. First, groups such as the North American Coryphoideae and tribe Cyclospatheae fall within lineages that have persisted and diversified in the Laurasian ancestral area of extant palms. Second, at least three dispersals events have taken place from South America into North America at various times in the Cenozoic from deep within the Arecoideae (Geonomateae, Iriarteae, a subclade of Chamaedoreae). Tribes Reinhardtiae and Roystoneae may also fall into this category. Third, many genera that are predominantly South American (e.g. genera of tribe Cocoseae) appear to have colonized North America, perhaps relatively recently. No other major region appears to have contributed to the North American palm flora.

Dispersal into Africa was inferred only four times at significantly different time periods: twice from Eurasia (once in the Late Cretaceous, once in the Palaeocene) and twice from the Indian Ocean during the Miocene (Fig. 1). Such a pattern could be the result of extinction events masking the true number of dispersals or the result of the isolated position of the African continent from 77 to 55 Ma (Morley, 2000; Plana, 2004; Kissling *et al.*, 2012), which might have provided fewer dispersal opportunities. Because our analysis of dispersals focuses only on events reconstructed on internal branches, it overlooks the presence in Africa of genera such as *Calamus*, *Elaeis*, *Phoenix* and *Jubaeopsis*. These are

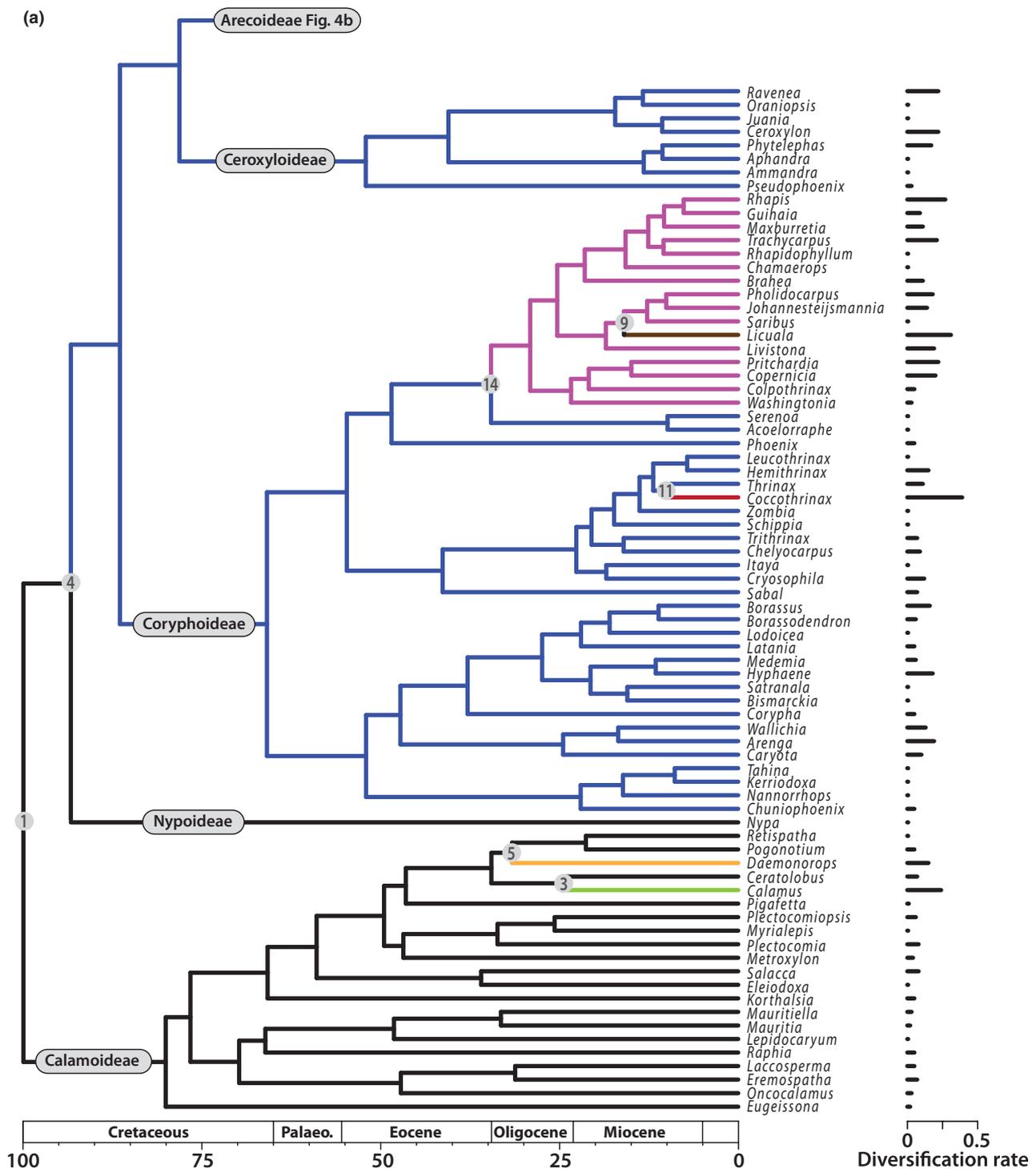


Figure 4 Diversification dynamics across palms. Chronogram of palms representing the 14 different diversification rates inferred across palms using TurboMEDUSA with the location of the 13 rate shifts increase. The figure is divided into two sections: panel (a) covering subfamilies Calamoideae, Ceroxyloideae, Coryphoideae and Nypoideae, and panel (b) covering subfamily Arecoideae only (see summary tree included in panel (b)). No rate decreases were detected. Numbered nodes indicate the location of rate shifts with a colour change indicating the lineages in which the shift has occurred. Bars next to generic names represent diversification rates under no extinction ($d = 0$). Estimates for the net diversification (r) and the relative extinction rate (ϵ) for each clade identified using turboMEDUSA are given in Table 1.

represented in the region by single or very few species, likely dispersals from Eurasia, South America or the Indian Ocean. Nevertheless, our study indicates that Africa and South

America have been colonized by palms on a similar number of occasions, which is remarkable given the more than ten-fold disparity in species richness between the two continents.

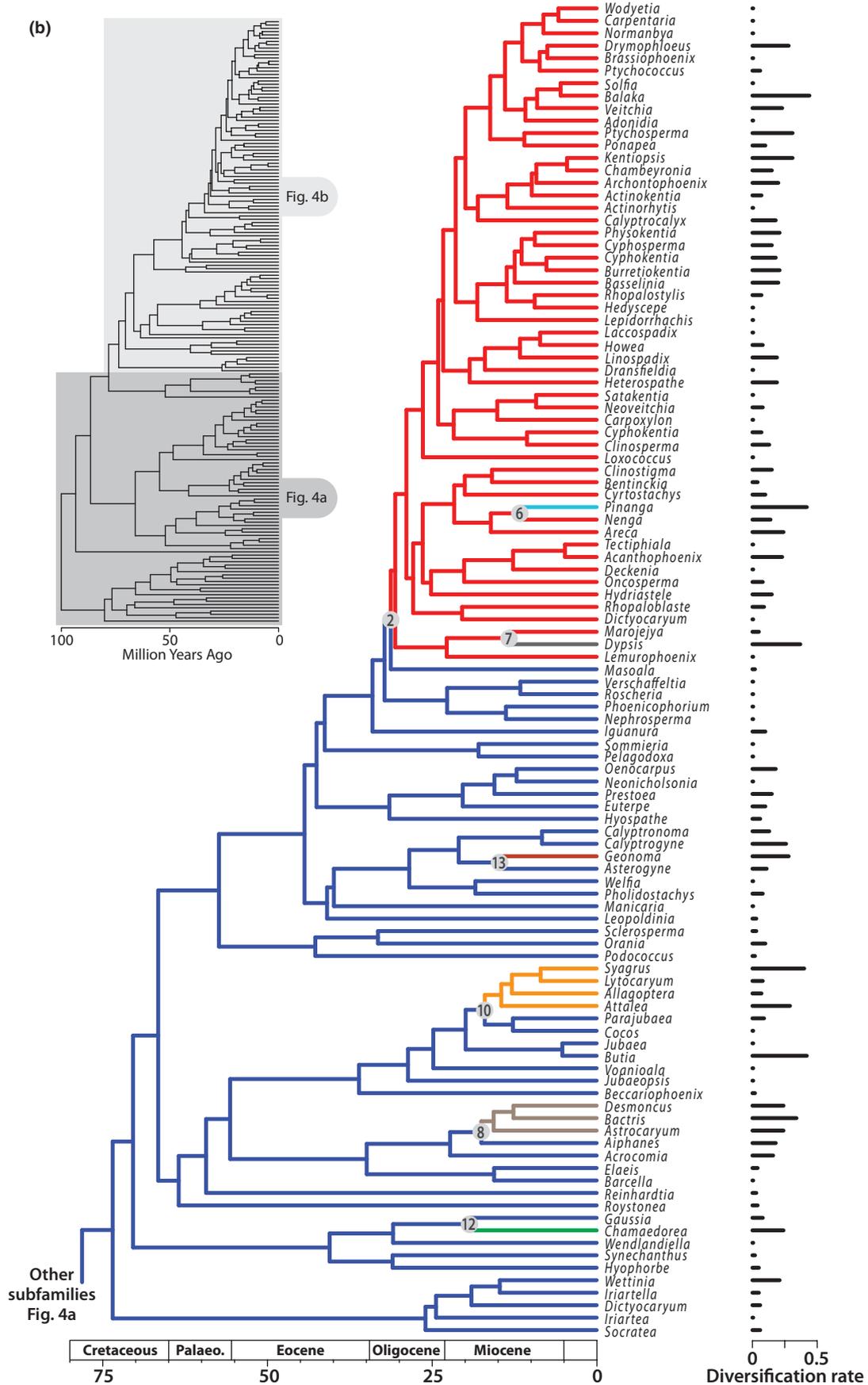


Figure 4 Continued

In addition, Africa was inferred as a source region for only one dispersal event (Calamoideae, dispersing into South America). This contrasts with other pantropical plant families such as Annonaceae, Melastomataceae, Meliaceae or the subfamily Chrysophylloideae (Sapotaceae) for which Africa has been shown to be an important source of dispersal events into other tropical regions (Morley & Dick, 2003; Muellner *et al.*, 2006; Bartish *et al.*, 2011; Couvreur *et al.*, 2011b).

Although not as depauperate as Africa, a relatively small palm flora occurs in India (*c.* 90 species). Only one dispersal event into India was inferred, from the Indian Ocean in the Miocene, suggesting that the modern Indian palm flora is more likely a result of relatively recent colonization than ancient autochthonous lineages. Ancient dispersals onto India probably did take place as indicated by the presence of Cenozoic palm fossils of unclear affinity (Dransfield *et al.*, 2008). However, the rapid latitudinal change in India's position during the Early Cretaceous until collision with Eurasia some 35 Ma (Ali & Aitchison, 2008) is thought to have led to the extinction of numerous lineages (Morley, 2000) including palms. Although the rafting of India has been shown to play an important role in explaining the dispersal pattern of some tropical plant families, such as Melastomataceae (Morley & Dick, 2003) and Crypteroniaceae (Conti *et al.*, 2002), this does not appear to be the case in palms, as found also in Annonaceae (Couvreur *et al.*, 2011b).

In contrast with the regions discussed above, dispersal events into Eurasia, the Pacific and the Indian Ocean are both more numerous (7–8 events per region inferred here) and are concentrated in shorter intervals, notably from the Early Eocene to the Late Miocene (Fig. 2). Eighteen dispersals between them are inferred in our analysis, 16 of which involve Eurasia, highlighting the importance of this region both as a sink and source region for palm lineages. Many of these events occurred within the widespread Indo-Pacific tribe Areceae. These dispersal events correlate with periods of global warming and TRF expansion into the Northern Hemisphere (Morley, 2003). Indeed, during the Eocene, TRF extended into northern Europe and America mainly related to an increase in global temperatures referred to as the Early Eocene Climatic Optimum between 55 and 45 Ma (Morley, 2000; Zachos *et al.*, 2001). A similar situation occurred during the Middle Miocene (Mid-Miocene Climatic Optimum; Zachos *et al.*, 2001) during which TRFs once again extended into northern latitudes (Morley, 2000, 2007). Boreotropical dispersal routes between major tropical regions have been documented in several other pantropical families, including Annonaceae (Erkens *et al.*, 2009; Couvreur *et al.*, 2011b), Malpighiaceae (Davis *et al.*, 2002), Meliaceae (Muellner *et al.*, 2006), Melastomataceae (Renner & Meyer, 2001) and Rubiaceae (Antonelli *et al.*, 2009).

Dispersal between Eurasia, the Pacific and the Indian Ocean was very likely to have been facilitated by the geological events surrounding the Miocene collision of the Australian plate with Southeast Asia (Hall, 2009). The resultant Malesian

Archipelago would have provided new stepping stones, permitting lineages to filter between these regions. We inferred six eastwards dispersals across Wallace's Line and four westwards dispersals, mostly concentrated around the Miocene, supporting recent claims that eastwards migrations across Wallace's Line are more common than westwards transgressions (Richardson *et al.*, 2012). We note also that much of the diversity of important Pacific palm floras, such as that of New Caledonia or Australia (Pintaud & Baker, 2008; Dowe, 2010), is derived from clades that diverged and radiated in the Miocene (Archontophoenicinae, Basseliniinae, Carpoxyliinae, Clinospermatinae, Laccospadicinae, *Livistona*; Crisp *et al.*, 2010; Bacon *et al.*, 2012), which supports hypotheses that endemic biodiversity of these ancient landmasses is at least partly recent (Crisp *et al.*, 2004; Muriene, 2009; Dowe, 2010; but see also Heads, 2010).

Global diversification of palms

Our study indicates that palms have undergone at least 13 diversification rate shifts since the origin of extant lineages. Couvreur *et al.* (2011a) showed that the diversification of major palm lineages conforms to a constant rate and fits most closely to a pure birth model with a constant speciation rate and no (or little) extinction at least for the first three-quarters of the family's evolution (100–24 Ma) up until the Neogene. They also suggested that palm evolution could be the result of a mixed model of diversification with an overall steady accumulation of major lineages punctuated by specific shifts in diversification, especially on shorter time frames. Such a view is supported here, in which the overall background extinction rate is estimated to be close to zero (but see below) coupled with a moderate net rate of diversification (Fig. 4). In addition, all except one of the shifts identified take place within the last 30 Myr (Fig. 4) and 8 within the last 20 Myr. Thus, even though the diversification history of this family appears complex due to several rate shifts, most of these can be attributed to recent events.

The near zero estimated extinction background rate inferred here must be interpreted with caution. It is well documented that phylogeny-based maximum likelihood estimations of extinction rates tend to be close to zero, something that is not generally supported by the fossil record (Purvis, 2008; Rabosky & Lovette, 2008). In a recent study, it was shown that recently radiating clades could hide the extinction signal of older clades (Morlon *et al.*, 2011). In the case of palms, the radiation of tribe Areceae (see below) could have such an effect on the rest of the family and should be further investigated in order to truly test the hypothesis of low extinction rates.

The most significant rate shift identified took place early within the evolutionary history of the Areceae [Fig. 4, node 2: 30.6 Ma; 95% highest probability density (HPD) 23.6–38.1], the largest tribe in the palm family which contains 59 genera and 660 species distributed throughout the Indo-Pacific region (Norup *et al.*, 2006; Baker *et al.*, 2011). This is

consistent with the hypothesis that the tribe underwent a rapid radiation (Hahn, 2002), which could be linked to its immensely wide distribution from Pemba Island (East Africa) eastward to Samoa. The capacity of the tribe to disperse appears to be almost unrivalled in palms, perhaps due to the relatively small and attractive nature of its fruit. This may have allowed it to exploit changing opportunities for island colonization in the Indian and Pacific Oceans (Hall, 2009), resulting in a combination of allopatric speciation and *in situ* diversifications (Kissling *et al.*, 2012). An important role for Malesia is also suggested by the high number of genera identified to have undergone a rate increase and showing high rates of diversification (four out of 13 shifts are in Malesian genera), especially under a high extinction model (Fig. 3).

The reason behind other rate increases is hard to advance without additional detailed studies of morphology or ecology (Moore & Donoghue, 2007; Roncal *et al.*, 2011). For example, the evolution of epidermal spines in the South-Central American subtribe Bactridinae (a unique character within the tribe Cocoseae) could be viewed as a key innovation that provided increased protection against herbivores. Interestingly, we do recover an increase in diversification, but only for part of the subtribe (node 8, *Desmoncus*, *Bactris* and *Astrocaryum*). Such a pattern could be consistent with the idea of a 'phylogenetic fuse', a delayed increase in speciation in relation to the evolution of a key innovation (Cooper & Fortey, 1998; Smith *et al.*, 2011), or an artefact related to the conflicting phylogenetic hypotheses within the subtribe (Eiserhardt *et al.*, 2011).

Even though turboMEDUSA provides an important step forward in pin-pointing shifts in diversification rates, there are two important drawbacks to note (Alfaro *et al.*, 2009). First, the results only allow the identification of rate shifts within the resolved parts of the tree, and thus, in our case, not *within* genera. A lack of significant rate changes leading up to a genus does not mean that subclades *within* the genus, which are not resolved in our tree, have not undergone rate shifts (Alfaro *et al.*, 2009). For example, the Pacific genus *Pritchardia* (27 species) is generally interpreted as having undergone an island radiation in the Hawaiian subclade within the genus (Hodel, 2007; Baldwin & Wagner, 2010; Bacon *et al.*, 2012). However, our analysis does not identify an increase in diversification at the stem node of the genus. Based on a dated molecular phylogeny that included most *Pritchardia* species, Bacon *et al.* (2012) estimated the origin of the Hawaiian endemics to be 3.5 Ma, whereas the crown node of the genus was estimated to be 10.57 Ma. Thus, although the genus as a whole might not have significantly different net diversification rate compared to its relatives, it is highly likely that the Hawaiian subclade has undergone a diversification increase and deserves further investigation.

Second, the identification of a rate change along the stem of a genus could be due to faster diversification of subclades rather than the genus as a whole (Alfaro *et al.*, 2009). This is an important caveat for the rate increases identified for genera.

Finally, our study does not identify a decrease of rates anywhere across the tree. This is noteworthy, especially in relation to the African palm flora, for which low species richness has been attributed to a decrease in speciation rates and/or an increase in extinction rates linked to aridification in Africa since the Miocene (Moore, 1973; Morley, 2000; Pan *et al.*, 2006; Kissling *et al.*, 2012). In contrast, our results suggest that African genera or clades have either been diversifying at the general background rate (e.g. Ancistrophyllinae, Raphiinae), or at the same rate as the more inclusive clade to which they belong (e.g. Podococceae, Sclerospermeae, Hyphaeninae). In other words, our data suggest that a rate decrease is not necessary to explain present-day diversity of palm diversity in Africa, given an effectively zero background extinction rate for palms. These results support an alternative hypothesis that the large number of palm species in other regions when compared to Africa is the result of *increased* diversification rates *within those regions* rather than the result of a decrease of rates in African lineages. Lower species richness in Africa could be the result of fewer diversification opportunities due to the less complex landscape or fewer vegetation types (Plana, 2004). We caution that these results were based on a genus-level sampling of all palms, although our diversification analyses do account for the species diversity of the genera. Nevertheless, species level phylogenies of African clades, such as subtribe Ancistrophyllinae, will provide important tests for hypotheses regarding the origin and diversification of African palm diversity. In addition, the hypothesis advanced here should be investigated in other tropical plant lineages showing a similar distribution pattern.

CONCLUSIONS

Through rigorous molecular dating, ancestral area reconstructions and diversification analyses, our studies (see also Baker & Couvreur, 2012) provide a new baseline for palm biogeography and new insights that are relevant to other tropical lineages. Following their Cretaceous origins in Laurasia (Couvreur *et al.*, 2011a; Baker & Couvreur, 2012), the Cenozoic history of palms was dominated by significant interchange between North and South America, and among Eurasia, the Pacific and the Indian Ocean. In comparison, India and Africa have played a minor role, although events within these regions may have been obscured by extinction. Although the role of major geological processes, such as the Miocene evolution of the Malesian Archipelago, is clear, the importance of dispersal events in the biogeographical history of palms is unequivocal.

Numerous increases in diversification rates from a general background rate were identified, most of them occurring recently. This lends support to the hypothesis of Couvreur *et al.* (2011a) that the diversification history of palms could be linked to a mixed model of steady background diversification punctuated by generally recent increases in diversification rates. Species diversity in palms is apparently not linked to any identifiable decrease in diversification rates. Given an

effectively zero background extinction rate, increases in diversification rates, and not decreases as generally suggested, appear to contribute to the significant disparities observed between the species-rich palm floras of South America and Southeast Asia and the less diverse African flora. This hypothesis remains to be tested in other pantropical plant families that show similar patterns of low species richness in Africa (Richards, 1973).

The future development of concepts of palm biogeographical history now rely on improving our understanding of higher level relationships, which remains limited in certain groups (e.g. tribe Areceae) and increasing taxon sampling at the species level (e.g. Bacon *et al.*, 2012), which will reveal missing detail, especially within more recent time frames, and more accurate inferences of diversification history. As demonstrated by this study, the palm family is a promising study group that will continue to shed light on the evolutionary history and diversification processes of tropical lineages and the biomes in which they exist.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Complete genus-level chronogram for the palm family.

Appendix S2 Stem node ages and diversification rates estimated for palm genera.

Appendix S3 Expected generic diversity.

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