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Explaining extreme differences in species richness among co-occurring palm clades in Madagascar

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ABSTRACT

Imbalance in species richness among related clades is a pervasive, yet incompletely understood feature of biodiversity. Comparison of species-poor and species-rich clades that have evolved within the same region can shed light on the mechanisms underlying this phenomenon. The long-isolated island of Madagascar is an ideal place for doing this. Madagascar harbours at least ten clades of palms (Arecaceae) that have colonized the island independently and diversified to widely differing degrees, ranging from one to 180 known species. We estimated colonization times and diversification rates for these clades based on an extensive phylogenomic dataset and tested the degree to which clades that arrived in Madagascar earlier have more species (time-for-speciation effect), finding a moderate effect. For context, we tested for time-for-speciation effects in other plant and animal lineages, finding variable but qualitatively similar results. Our findings suggest that variation in diversification rate (i.e. speciation and/or extinction rate) is a major driver of species richness imbalance among Malagasy clades, both in palms and elsewhere. We demonstrate that in palms, differences in diversification rates originated long before colonization of the island, suggesting a minor role of classical 'island radiation' and a stronger role of heritable traits driving diversification rate. Ability to colonize new climates also appears to play a role. Future work should address the interplay between the dynamic environment of Madagascar and the inherited traits of colonizing lineages to fully explain the island's intriguing mix of species-poor and species-rich clades.

Keywords: Arecaceae; climate; diversification rate effect; island radiation; niche evolution; Palmae; palms; phylogeny; phylogenomics; time-for-speciation effect

INTRODUCTION

Imbalance in species richness among related clades is a pervasive feature of biodiversity, but the reasons for this pattern remain debated (Wiens 2011, Harmon and Harrison 2015, Rabosky and Hurlbert 2015, Yu and Wiens 2024). Studies addressing this issue in a defined and controlled geographic setting are needed. Madagascar is a renowned biodiversity hotspot with extreme levels of endemism (Myers *et al.* 2000, Antonelli *et al.* 2022, Tietje *et al.* 2023), making it valuable as a well-delineated 'natural laboratory' for studying *in situ* evolutionary processes (Vences *et al.* 2009). Comprising many lineages of varying size that colonized the island independently, the Malagasy biota lends itself to unpacking the drivers of imbalance in species richness. In Madagascar, this phenomenon occurs across animals and plants, e.g. ants (Camacho *et al.* 2021), chameleons (Giles and Arbuckle 2022), snakes (Burbrink *et al.* 2019), and the plant families Cyatheaceae (Janssen *et al.* 2008), Celastraceae (Bacon *et al.* 2016) and Rubiaceae (Kainulainen *et al.* 2017). For example, the lamprophiid snakes colonized Madagascar twice, resulting in clades of two and > 100 species, respectively (Burbrink *et al.* 2019). But perhaps the most striking example is the palm family (Arecaceae), which colonized Madagascar multiple times, resulting in clades ranging from a single to 180 known endemic species (Dransfield and Beentje 1995, Dransfield *et al.* 2008,

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Eiserhardt *et al.* 2022). This pattern where impressive radiations coexist with species-poor lineages is yet far from fully understood and raises the question: why do some clades diversify extensively while others do not?

Variation in species richness among related clades can arise in two fundamental ways. The simplest explanation is that the largest clades are those that are oldest: the older a clade, the more time it has had to accumulate species ('time-for-speciation effect', Stephens and Wiens 2003). Alternatively, clades may differ in species richness because they produce and/or lose species at different rates. All else being equal, a clade with a high diversification rate (i.e. speciation minus extinction per unit time) should be larger than a clade with a low diversification rate ('diversification rate effect', e.g. Yu and Wiens 2024). These two effects are complementary: any differences in clade species richness that are not due to time for speciation must, by definition, be due to differences in diversification rate. Other hypothesized drivers of species richness, such as 'ecological limits' (Rabosky and Hurlbert 2015) may be important, but affect species richness indirectly *via* the rate of diversification (Wiens 2011). Studies investigating the importance of the time-for-speciation effect vs. differences in diversification rate have yielded contrasting findings (Wiens 2011, Rabosky *et al.* 2012, Scholl and Wiens 2016, Yu and Wiens 2024). In Madagascar, a study on vertebrates suggested that both effects play a role, but that diversification rate variation had a stronger effect than time for speciation (Crottini *et al.* 2012). Similar studies for other taxa are needed to fully evaluate how much variation in species richness can be explained by time for speciation. Only once the extent of the time-for-speciation effect is established can the historical, environmental, or biological processes underpinning diversification rate variation and, ultimately, differences in clade species richness be meaningfully identified.

In an island setting, it is essential to understand if variation in diversification rates among clades, if present, is associated with colonization of the island or not. Classic adaptive radiation theory predicts that colonization of an island should lead to increased diversification if the island harbours unoccupied ecological niche space (Stroud and Losos 2016). It is tempting to think that this might not apply to an old continental fragment like Madagascar, where habitats should be saturated with species. However, Madagascar was severely affected by the Cretaceous-Paleogene mass extinction event (66 Mya) and subsequent climatic changes in the Cenozoic (Wells 2003, Samonds *et al.* 2013), eradicating much of the island's original biota and creating ample new niche space. Most of Madagascar's current biodiversity descends from Cenozoic dispersal events (Crottini *et al.* 2012, Buerki *et al.* 2013, Samonds *et al.* 2013, Antonelli *et al.* 2022) and any colonist lineage may have met considerable ecological opportunities for adaptive radiation. Different lineages would likely have reacted differently to these opportunities, as some lineages are better able to speciate on an island of a given size than others, depending on the spatial scale of gene flow (largely determined by dispersal ability; Kisel and Barraclough 2010). Also, if different habitats are differently saturated with species, e.g. due to different age or isolation (Steinbauer *et al.* 2016), colonist lineages may experience different levels of adaptive radiation depending on the habitat they are pre-adapted to. Finally, the first colonists in any given lineage or functional guild may experience the largest increases in diversification rates (priority effect, Gillespie *et al.* 2020), while the diversification opportunities of later colonists are limited by the descendants of earlier ones. All these dynamics should be expressed as diversification increases at the time of colonization. In contrast, diversification rate shifts before or after colonization may reflect intrinsic evolutionary developments (e.g. key innovations, Burress and Muñoz 2021) or environmental dynamics on the island, such as changes in geomorphology (e.g. Liu *et al.* 2024).

Besides ecological opportunity, intrinsic properties of lineages can be important drivers of diversification rate and hence, species richness (Vamosi and Vamosi 2011). One such intrinsic property is the climatic niche, which strongly determines the geographic distributions of species (Pearson and Dawson 2003) and hence the dynamics of speciation and extinction (Gómez-Rodríguez *et al.* 2015). In Madagascar, steep climatic gradients are considered a primary driver of ecosystem structure and diversity (Rakotoarinivo *et al.* 2013, Antonelli *et al.* 2022), rendering the climatic niche a prime suspect for differences in species richness. This could happen in three main ways. Firstly, diversification may be affected by the breadth of climatic conditions that species can tolerate. The direction of this effect is difficult to predict, as species with narrower climatic niches may be both more prone to allopatric speciation and to extinction, while species with wider niches may be more prone to adaptive speciation (Gómez-Rodríguez *et al.* 2015). Secondly, lineages that evolve their climatic niche easily may show higher diversification rates, as they should be more likely to speciate adaptively and less likely to experience extinction due to changing climate (Gómez-Rodríguez *et al.* 2015, Castro-Insua *et al.* 2018). Finally, climate per se may affect the rates of speciation and extinction, as illustrated by the many studies investigating differences in diversification rates among climatically determined biomes (e.g. Mittelbach *et al.* 2007, Tietje *et al.* 2022). For example, climate is often assumed to affect mutation rates (Metabolic Theory of Ecology, Allen *et al.* 2006, but see Tietje *et al.* 2022). However, a relationship between climate and diversification rate may also arise if assemblages in different climates are differently saturated with species for historical reasons (see above). Further tests of these hypotheses are needed, especially in plants.

Here, we use the palms of Madagascar (Fig. 1) to gain insights into the biotic assembly of one of the world's most remarkable biodiversity hotspots and the drivers of clade species richness in general. Using phylogenomic data, we build the first phylogenetic tree of nearly all Malagasy palm species, and date the tree to infer the history of colonization of the island by palms. Within this framework, we test the relative roles of time for speciation and diversification rate variation in explaining why some Malagasy palm lineages have diversified spectacularly while others have not. We compare palms to other Malagasy plant and animal lineages to assess the relative impact of time for speciation across the island's biota. We identify major shifts in diversification rate that affected the assembly of the Malagasy palm flora, and test for connections between diversification and the climatic niche. We synthesize the results to provide an integrated account of the origin of one of Madagascar's most important and iconic plant groups.

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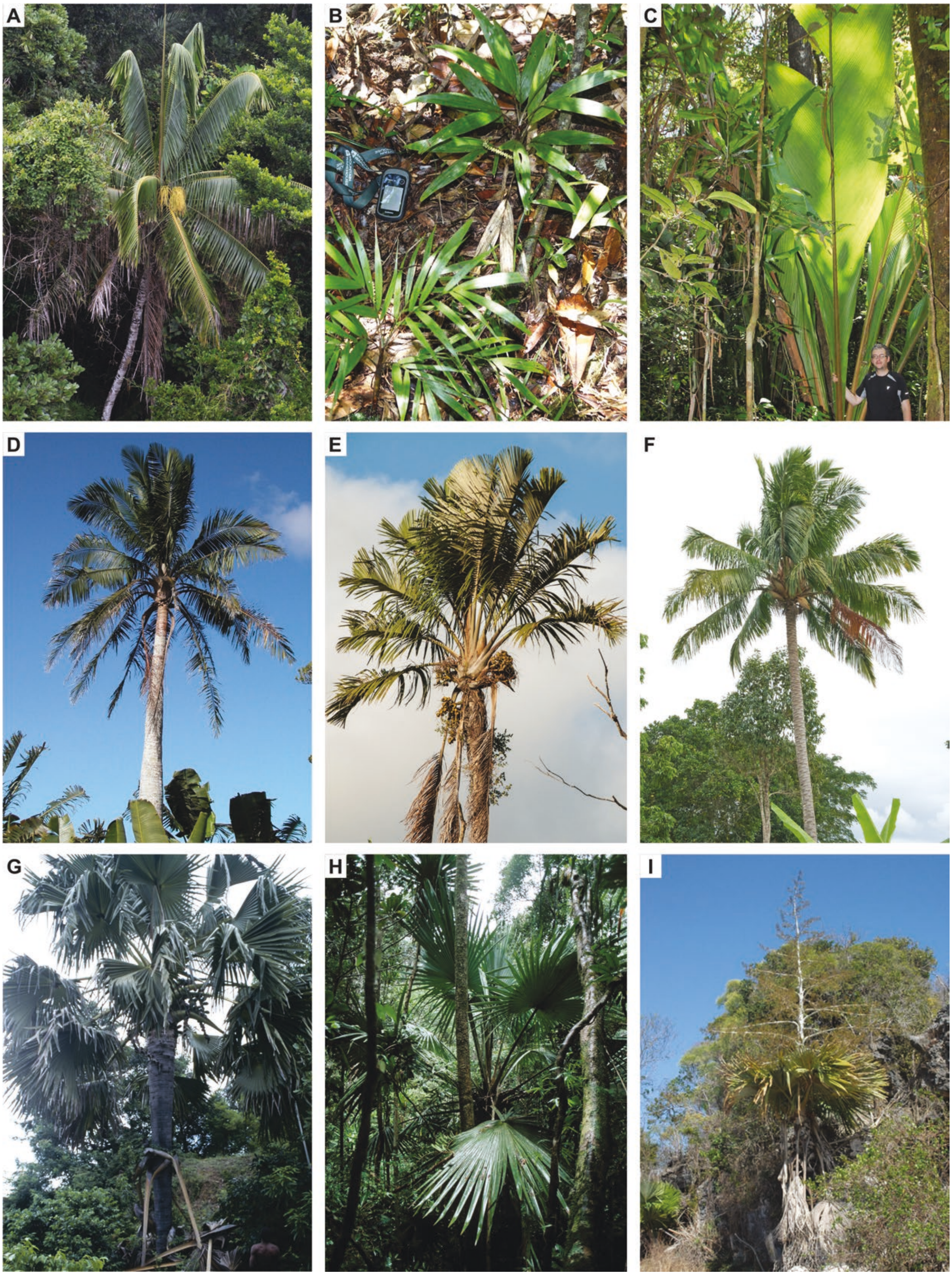

Figure 1. Morphological diversity within and across Malagasy palm clades. A–C subtribe Dypsidinae. A, *Chrysalidocarpus lastellianus* (Baill.) Eiserhardt & W.J.Baker. B, *Dypsis tenuissima* Beentje with handheld GPS unit for scale. C, *Marojejya darianii* J.Dransf. & N.W.Uhl with one of the authors (W.J.B.) for scale. D, *Ravenea* sp. E, *Orania trispatha* (J.Dransf. & N.W.Uhl) Beentje & J.Dransf. F, *Beccariophoenix fenestralis* J.Dransf. & Rakotoarin. G, *Borassus madagascariensis* (Jum. & H.Perrier) Bojer ex Jum. & H.Perrier. H, *Satranala decussilvae* Beentje & J.Dransf. I, *Tahina spectabilis* J.Dransf. & Rakotoarin. Photos W.J.B. (A, E, F), W.L.E. (B, C), M.R. (D), Ross P. Bayton (G), J.D. (H, I).

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MATERIAL AND METHODS

Model group

With 212 endemic species deriving from several independent colonization events, the palms of Madagascar (Fig. 1) are an ideal model for testing the drivers of differences in species richness among clades. Palms are a well-established model group for studies of tropical plant ecology and evolution (Eiserhardt *et al.* 2011, Couvreur and Baker 2013). Compared to other plant groups on the island, the palms are exceptionally well served with data (Dransfield and Beentje 1995, Rakotoarinivo *et al.* 2013, 2014, Antonelli *et al.* 2022). Malagasy palms comprise multiple independent clades scattered across the palm tree of life (Dransfield *et al.* 2008, Baker *et al.* 2009, Baker and Couvreur 2013a, b). These clades vary greatly in size, ranging from one species (e.g. the genera *Voanioala* and *Tahina*) to 180 in subtribe Dypsidinae (Dransfield *et al.* 2008, Eiserhardt *et al.* 2022).

Taxon sampling

We used a published dataset with sequence data for all palm genera (Bellot *et al.* 2024), augmented with sequence data for as many species as possible of the 14 palm genera that have endemic species in Madagascar. This comprised published data for subtribe Dypsidinae (*Dypsis*, *Chrysalidocarpus*, *Marojejya*, *Vonitra*, *Masoala*, and *Lemurophoenix*, Eiserhardt *et al.* 2022) and newly generated data for the genera *Orania*, *Ravenea*, *Beccariophoenix*, and *Borassus* (Supporting information, Table S1). In total, we sampled 183 of the 215 native species of Malagasy palms (*c.* 85%), with all Malagasy palm genera being fully sampled except *Dypsis* (89 of 108 spp., 82%), *Chrysalidocarpus* (44 of 55 spp., 80%), *Ravenea* (17 of 21 species, 81%), and *Masoala* (two of three species, 66%). For statistical analyses involving species richness, we used species numbers that were correct on 10 July 2022, acknowledging that discovery and description of Malagasy palm species new to science is ongoing (e.g. Eiserhardt *et al.* 2018, Dransfield *et al.* 2023, Turk and Rakotoarinivo 2023).

Generation of new DNA sequence data

We generated novel DNA sequence data for 25 species of Malagasy palms, as well as 15 species from other regions that were needed to ascertain the relationships and ages of Malagasy palm clades (Supporting information, Table S1). We targeted 176 nuclear loci developed specifically for palm phylogenomics by Heyduk *et al.* (2016). Laboratory methods followed Eiserhardt *et al.* (2022).

Raw sequence reads were cleaned with Trimmomatic v.0.39 (Bolger *et al.* 2014) using the ILLUMINACLIP and MAXINFO algorithms with a strictness value of 0.5 and a minimum read length of 36 bases. FastQC v.0.11.9 (Andrews 2010) was used to assess sequence quality before and after trimming. We assembled the trimmed reads into contigs with HybPiper v.1.3.1 (Johnson *et al.* 2016) using the SPAdes genome assembler v.3.15.4 (Bankevich *et al.* 2012) and a target reference file for the loci of Heyduk *et al.* (2016). We used standard settings except a lowered coverage cut-off value of 3 to increase exon recovery. We generated 'supercontigs', i.e. recovered homologues to the target sequences (exons) plus flanking non-coding regions. We discarded any contigs that were shorter than 150 bp or 20% of the median contig length for the target gene, as very short contigs are more likely to be assembly artefacts and can be difficult to align.

Phylogenetic framework

Two phylogenetic analyses were conducted with different taxonomic sampling. The first phylogenetic tree (the 'genus tree') included one species for each genus of palm, using unaligned contigs from Bellot *et al.* (2024), focusing only on the loci of Heyduk *et al.* (2016) for comparability with our other analyses. The second phylogenetic tree (the 'full tree') used the same dataset plus the data of Eiserhardt *et al.* (2022) for Dypsidinae and our newly generated sequences, resulting in a tree that is sampled at the genus level for the whole family, but at the species level within genera that are present in Madagascar. The purpose of building two trees was to test for potential impacts of heterogeneous sampling density across the full tree, which might result in older age estimates in more densely sampled lineages.

Contigs were aligned using the L-INS-i method in MAFFT v.7.490 (Katoh and Standley 2013), and the resulting alignments were then cleaned using trimAL v.1.4. rev22 (Capella-Gutiérrez *et al.* 2009). We used the optrimAl script of Shee *et al.* (2020) to automatically determine the optimal trimming threshold for each gene, testing different trimming thresholds between 5% and 90% missing data for each alignment column. Subsequently, we manually inspected all alignments and removed any obvious alignment errors. Gene trees were computed using Maximum Likelihood implemented in IQ-TREE v.2.1.3 (Minh *et al.* 2020), inferring the best substitution model using ModelFinder (Kalyaanamoorthy *et al.* 2017), and estimating branch support using the UFBoot2 algorithm (Hoang *et al.* 2018). We used ASTRAL-III v.5.7.8 (Zhang *et al.* 2018) to infer a species tree (one species per genus) from the gene trees. Following Baker *et al.* (2022), we collapsed gene tree nodes with a UFBoot2-support value < 30% before running ASTRAL-III.

Divergence time estimation

We estimated divergence times for both the genus tree and the full tree using a relaxed log-normal clock model in BEAST v.1.10.4 (Drummond *et al.* 2012). Following Bellot *et al.* (2024), we calibrated the tree using six high-quality fossils and a secondary calibration point on the root of the tree (Supporting information, Table S2). The root calibration was set as a normal distribution with a 2.5% quantile (lower bound) corresponding to the oldest fossil calibration point, and a 97.5% quantile (upper bound) corresponding to the oldest stem age of palms inferred in previous molecular studies (Bellot *et al.* 2024; Supporting information, Table S2). For computational reasons, and because gene tree conflict can severely bias divergence time estimates (Carruthers *et al.* 2022), we only used the five genes with the highest topological similarity to the species tree (identified using SortaDate, Smith *et al.* 2018; Supporting information, Table S3) to estimate divergence times. However, we fixed the topology to the results of the ASTRAL-III analysis (see above) to still capitalize on the topological information from the full dataset. Substitution models were specified separately for the five genes based on ModelFinder results (see above). We used a birth-death tree prior with incomplete sampling to account for our sparse sampling (one species per genus) across most of the palm

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family, setting a sampling fraction of 7.15% across the whole tree (based on a total of *c.* 2600 species), and using default settings otherwise. The mean clock rate prior was set to a log-normal distribution with a mean of 0.002 and standard deviation of 0.01 (in real space), resulting in a distribution with a 2.5% quantile of 0.000011 and a 97.5% quantile of 0.013 substitutions per site per year, reflecting previous rate estimates in the palm family (Gaut *et al.* 1996). The Markov chain Monte Carlo (MCMC) algorithm was set to 100 million generations with 10 000 trees sampled (one tree per 10 000 generations) and visually assessed using Tracer v.1.7.2 (Rambaut *et al.* 2018) to ensure an effective sample sizes (ESS) above 200 for all priors. The resulting trees were summarized in TreeAnnotator v.1.10.4. (Drummond *et al.* 2012) to generate dated maximum clade credibility trees, discarding the first 10% of the chain as burn-in.

Malagasy palm clades

Based on our phylogenetic results and the biogeographic analysis of Baker and Couvreur (2013a, b), we identified 10 clades that represent independent colonizations of Madagascar. Eight of these colonizations have resulted in at least one endemic species on the island. We refer to these as the Malagasy palm clades (Table 1). Of these, five are strictly endemic. Two (Dypsidinae, *Ravenea*) are mostly endemic but contain a few species on small neighbouring islands (Comoros, Pemba) that clearly originated *via* dispersal from Madagascar. These non-Malagasy species were excluded from species counts in subsequent analyses. The three remaining clades contain species that are not endemic to Madagascar. In the case of *Borassus*, it remains unclear if the two Malagasy species originated from one or two colonization events. We conservatively assume one event in our main analyses to avoid pseudoreplication, but report results for two events as well. Four species that are probably introduced to the island (*Cocos nucifera*, *Elaeis guineensis*, *Phoenix dactylifera*, *Raphia farinifera*) were disregarded.

Time-for-speciation effect: Malagasy palms

We tested for a time-for-speciation effect *sensu* Wiens (2011) by analysing the correlation between the colonization times of Malagasy palm clades and the logarithm of their species richness. The time of colonization of each clade cannot be inferred with certainty, but can be assumed to lie between the clade's stem and crown age. To account for this uncertainty, as well as uncertainty in node age estimates, we calculated the correlation between colonization time and log(species richness) 50 000 times as follows: for each of 5000 trees sampled from the posterior distribution of the BEAST analysis, we performed 10 correlations. For each of those 10 correlations, we randomly sampled a colonization time for each clade from a uniform distribution bounded by the clade's stem and crown age. Correlations were calculated using Spearman's rank correlation coefficient. We used the median of the 50 000 correlation coefficients as an estimate of the overall time-for-speciation effect. Two clades each consisting of a single non-endemic species (*Hyphaene coriacea*, *Phoenix reclinata*) were excluded, as the timing of colonization cannot be inferred from a phylogeny alone in those species.

Time-for-speciation effect: comparison with other plant and animal lineages

We used data from a recent literature review on Malagasy clade ages (Antonelli *et al.* 2022) to test for a time-for-speciation effect across plant and animal lineages and to set the results found for palms into a broader context. This dataset includes information on species richness and crown and stem node ages for 190 Malagasy clades of flowering plants (106 clades), mammals (11 clades), birds (12 clades), and reptiles (17 clades). Similar to our analysis for palms, we calculated the correlation between colonization time and log(species richness) across clades 50 000 times. Here, however, no information on node age uncertainty was available. Therefore, we simply calculated 50 000 correlations sampling colonization time for each clade from a uniform distribution bounded by its stem and crown age. This was done separately for flowering plants, mammals, birds, and reptiles, respectively.

Diversification analysis

We used the Bayesian Analysis of Macroevolutionary Mixtures approach in BAMM 2.5.0 (Rabosky 2014) to test for differences in diversification rates among Malagasy palm clades as well as possible diversification rate increases associated with the colonization of Madagascar. BAMM was applied to the dated full tree (Maximum clade credibility tree), accounting for the proportion of species sampled in each genus. To test if taxon sampling influenced our conclusions on diversification rate differences

Table 1. Malagasy palm clades, ordered by their estimated time of arrival on the island. Estimates of arrival times assume colonization sometime between a clade's stem and crown age, taking the uncertainty of age estimates into account [median (95% confidence interval)]. Diversification rate: median diversification rate (speciation minus extinction) in Madagascar

Clade	Subfamily	Species in Madagascar	Endemicity	Arrival time (Mya)	Diversification rate (Myr^{-1})
Dypsidinae	Arecoideae	180	Subendemic[a]	54.3 (45.7–64.8)	0.0630
Bismarckia, Satranala	Coryphoideae	2	Endemic	48.8 (23.8–65.2)	0.0310
Ravenea	Ceroxyloideae	21	Subendemic[a]	40.0 (26.6–59.6)	0.0388
Malagasy *Orania*	Arecoideae	3	Endemic	39.4 (20.7–63.5)	0.0311
Voanioala gerardii	Arecoideae	1	Endemic	33.2 (1.65–66.4)	0.0314
Tahina spectabilis	Coryphoideae	1	Endemic	25.0 (1.18–56.5)	0.0313
Beccariophoenix	Arecoideae	3	Endemic	18.8 (10.5–37.6)	0.0315
Malagasy *Borassus*	Coryphoideae	2	Not endemic	8.2 (4.9–12.9)	0.0315

[a] Diversified mostly in Madagascar, but contains a few species that have spread to other Indian Ocean islands (Comores, Pemba).

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among Malagasy palm clades, we also applied BAMM to the genus tree (one species per palm genus). Initial priors were estimated with BAMMtools (Rabosky *et al.* 2014). Based on this, we first ran a preliminary analysis (as described below) with a prior expectation of a single rate shift. As palms are known for their heterogeneous diversification history (Baker and Couvreur 2013b, Couvreur *et al.* 2015, Cássia-Silva *et al.* 2019), and Bayes factor analysis (Kass and Raftery 1995) of our preliminary results strongly supported three rate shifts, we then ran our final analysis with a prior expectation of three shifts. We initially ran three independent MCMC chains, running for 2 million generations and sampling event data every 1000 steps, to ensure a global optimum was found. We used ESS for evaluating parameter estimate convergence. We hereafter re-ran a final analysis for 5 million generations, sampling every 5000 steps, on which our results are based. For each clade, we estimated the median diversification rate from the crown node to the tips using the *getCladeRates* function in the BAMMtools package (Rabosky *et al.* 2014). To analyse the relationship between the diversification rate and species richness of Malagasy palm clades, we ran a phylogenetic generalized least-squares (PGLS) regression between estimated diversification rates from BAMM and log(species richness) using the R package caper v.1.0.1 (Orme *et al.* 2018).

Climatic niches

In order to calculate climatic niche attributes of clades, we used a dataset of georeferenced occurrence records derived from herbarium specimens of Malagasy palms in botanical institutions with significant Malagasy holdings (AAU, FTG, GE, K, MO, NY, P, TAN, TEF, ZT; herbarium acronyms following Thiers 2024). This dataset is based on records compiled since 1986 (Dransfield and Beentje 1995) and continuously updated by one of the authors (M.R.; see also Rakotoarinivo *et al.* 2014). We thinned the dataset keeping only a single occurrence per species within 0.5’ grid cells, resulting in a final dataset of 2343 records (see Supporting information, Table S4 for number of records per species).

To calculate the climatic niche characteristics of Malagasy palms, we followed the methodology of Castro-Insua *et al.* (2018). Initially, we downloaded climatic data at a resolution of 0.5’ (approximately 0.85 km) from the WorldClim database (Fick and Hijmans 2017). We focused on three temperature variables (BIO1: annual mean temperature, BIO5: maximum temperature of the coldest month, BIO6: minimum temperature of the coldest month) and three precipitation variables (BIO12: annual precipitation, BIO16: precipitation of the wettest quarter, BIO17: precipitation of the driest quarter), as temperature and precipitation are known important drivers of species ranges and richness in palms (Kissling *et al.* 2012, Blach-Overgaard *et al.* 2013). Using these climatic data, we calculated three different features of species niches following Castro-Insua *et al.* (2018). Firstly, the climatic breadth of each species for each variable was determined as the difference between the minimum and maximum values across the geographic records. These niche breadths were then rescaled to a range between 0 and 1 based on the minimum and maximum values across all species. Secondly, we calculated the overall climatic niche breadth for each species by multiplying the breadths for the six climate variables. Thirdly, the species niche position for each climatic variable was determined by calculating the mean climatic conditions of the geographic records of the species, illustrating the climate where the species are predominantly found.

We then calculated similar niche attributes for entire palm clades in Madagascar. Specifically, we calculated (i) clade niche breadth, being the difference between the minimum and maximum value of a climatic variable across all occurrences of all species in the given clade, (ii) mean species niche breadth, representing the mean climatic niche breadth of the species within the clade, (iii) temperature and precipitation niche position of the clades, determined as the average of the niche positions of all species within each clade.

Following Gómez-Rodríguez *et al.* (2015) we used the residuals of a Phylogenetic generalized least squares (PGLS) regression between clade niche breadth and the average niche breadth of the species within a clade as an indicator of niche divergence. Specifically, when niche conservatism is dominant in a clade, the mean of the species niche breadths and the total niche breadth of the clade will be nearly the same. In contrast, large differences in the residuals reflect little or no overlap of species’ climatic niches within a clade, indicating high climatic niche divergence (Gómez-Rodríguez *et al.* 2015).

We used the function *fitContinuous* in geiger v.2.0.10 (Pennell *et al.* 2014) to estimate the ancestral temperature and precipitation niche, respectively, for each Malagasy palm clade, focusing on mean annual temperature (BIO1) and annual precipitation (BIO12). We fitted four different models (Brownian motion, Ornstein–Uhlenbeck, early burst, and white noise) to each clade, and chose the one with the lowest sample-size corrected Akaike information criterion (AIC) to estimate the ancestral state of mean BIO1 and BIO12, respectively for each clade. We used the same analyses to estimate the rate of temperature and precipitation niche evolution for each clade. Since only the Brownian Motion model could be fitted for all clades (including those with fewer than three species), we used these to estimate the rate of niche evolution in BIO1 and BIO12 (σ^2-parameter). Preliminary analysis identified one Malagasy palm clade, *Beccariophoenix* (three spp.), as a major outlier in terms of the rate of niche evolution. This is due to a single species, *Beccariophoenix alfredii*, that recently switched from the humid forest to the dry highlands, causing an exceptionally high rate of niche evolution. Due to this idiosyncrasy, we excluded *Beccariophoenix* from subsequent analyses involving the rate of niche evolution as an outlier.

Effects of climatic niche on diversification rate

Nine linear regression analyses were conducted to evaluate our hypotheses on the association between diversification rate and variables of the climatic niche of clades: (i) niche breadth, (ii) mean species niche breadth, (iii) climatic niche divergence, (iv–v) extant temperature and precipitation niche positions, (vi–vii) temperature and precipitation ancestral niches, and (viii–ix) temperature and precipitation niche evolution rate. To account for the influence of shared phylogenetic history on regression we utilized PGLS regressions using the R package caper v.1.0.1 (Orme *et al.* 2013). All analyses involving R were conducted in R v.4.1.1 (R Core Team 2021).

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RESULTS

Malagasy palm clades and species richness

The phylogenetic data clearly show that palms colonized Madagascar through multiple independent events. The extant Malagasy palm flora comprises five (or six) lineages from subfamily Coryphoideae, four from Arecoideae, and one from Ceroxyloideae. Of these, two are single, non-endemic species (*Hyphaene coriacea* and *Phoenix reclinata*, both in Coryphoideae) that are also widesperad in mainland Africa. For the purpose of our study, we disregard these two colonisation events and focus on those that have resulted in at least one endemic species (Fig. 2; Table 1). All Malagasy palm clades with more than one species have maximum support (Local Posterior Probability = 1) in the tree. Specifically, our results confirm the monophyly of subtribe Dypsidinae, the most species-rich palm lineage on the island (180 species in Madagascar). The only area of uncertainty is in subfamily Coryphoideae, where the dispersal history of genus *Borassus* remains ambiguous, i.e. it is unclear whether the genus has colonized Madagascar once or twice.

Time-for-speciation effect in Malagasy palms

Colonization time varies greatly among Malagasy palm clades (Fig. 3A; Table 1). Subtribe Dypsidinae has the earliest estimated arrival time in Madagascar (median *c.* 54 Mya, Early Eocene), while the species-poor *Borassus* lineage has the latest estimated arrival time (median *c.* 8 Mya, Late Miocene). However, uncertainties around estimated colonization times are large, especially in the monospecific lineages *Voanioala* and *Tahina*. Due to these uncertainties, estimated correlations between arrival time and species richness (time-for-speciation effect) are also fraught with relatively large uncertainty (Fig. 3B; Supporting information, Table S7). When assuming a single colonization of Madagascar by the genus *Borassus*, time for speciation explains just over one quarter of variation in species richness among clades (pseudo-$R^2 = 0.27$; Spearman's $\varrho = 0.52$, 0.12–0.83, 95% confidence interval). The correlation is slightly stronger when two independent colonizations of Madagascar by *Borassus* species were assumed (Supporting information, Table S7).

Time-for-speciation effect: comparison with other plant and animal lineages

The median strength of the time-for-speciation effect (correlation between colonization time and species richness) varies greatly among lineages, from $\varrho = 0.21$ in birds to $\varrho = 0.72$ in mammals (Fig. 3B; Supporting information, Table S7). The overall time-for-speciation effect in flowering plants is slightly lower than in palms (median $\varrho = 0.4$).

Diversification rate in Malagasy palms

The median diversification rate (speciation minus extinction) of Malagasy palm clades obtained from BAMM varies between 0.031 Myr^{-1} and 0.063 Myr^{-1}. The highest rates occur in the species-rich subtribe Dypsidinae and the lowest rates occur in the species-poor clade comprising the monotypic genera *Bismarckia* and *Satranala* (Table 1). Regression between diversification rate and species richness of clades shows a strong positive relationship ($R^2 = 0.68$; $F_{1,9} = 19.59$, $P = .002$; Supporting information, Fig. S1).

Ancestral high diversification rate and post-colonization rate increases

Our analysis of diversification rate through time (Fig. 4) shows that colonization of Madagascar was not associated with any abrupt changes in diversification rate in seven out of eight Malagasy palm clades. Only in *Ravenea* did we infer a small increase in diversification for the same branch where colonization also likely happened (Fig. 4). Meanwhile, subtribe Dypsidinae, the largest palm lineage in Madagascar, was affected by diversification rate increases both *before* and *after* colonization. Most importantly, we inferred an approximately three-fold increase in diversification rate on the stem branch of tribe Areceae, which includes Dypsidinae among 10 other subtribes. This increase, which happened *c.* 17–40 Myr before Dypsidinae colonized Madagascar, is supported by a very high cumulative posterior probability of 0.92 and is the main reason why the diversification rate is much higher in Dypsidinae than in any other Malagasy palm clade (Fig. 4B). However, Dypsidinae experienced an additional smaller increase in diversification rate after arrival in Madagascar *c.* 50 Mya, i.e. in the branch leading to all genera except *Masoala* (three spp.) and *Lemurophoenix* (two spp.). This increase was followed by a slow and steady decrease in diversification rate towards the tips from *c.* 45 Mya to present (Fig. 4B).

Climatic niche divergence linked to diversification

Out of the climatic niche variables potentially associated with diversification rate, climatic niche breadth (i.e. the range of climatic conditions occupied by the clade) and climatic niche divergence (i.e. the extent to which species in a clade occupy different climates) are significantly positively related to the diversification rate of Malagasy palm clades (Fig. 5; Table 2). None of the other niche variables are significantly related to diversification rate (Table 2). However, it appears that the most species-rich clades, *Ravenea* and Dypsidinae, had the lowest temperature preference when colonizing Madagascar. Also, these clades show the highest rate of change in temperature niche (Fig. 5D). Treating the Malagasy *Borassus* species as two independent clades yields the same conclusions. Models used to infer ancestral climatic niches and rates of niche evolution are reported in the (Supporting information Table S5, S6).

DISCUSSION

Given the extreme long-term isolation of Madagascar, leading to the evolution of a highly endemic biota, it is natural to assume that imbalance in species richness among related clades has arisen *in situ* through explosive radiations in some clades but not others. However, our results suggest that this may in fact not be the case, at least in palms, which are a prime example of species richness imbalance on the island. Instead, we found that the timing of colonization explains just over a quarter of the variation in species richness, suggesting that time-for-speciation effects are also important. The remaining variation largely relates to the high diversification rate in subtribe Dypsidinae. However, the shift to this elevated rate happened prior to the colonization of Madagascar by this group. Counterintuitively, shifts in diversification rate that occurred on the island are, in fact, few and rather small, and therefore play only a minor role in explaining

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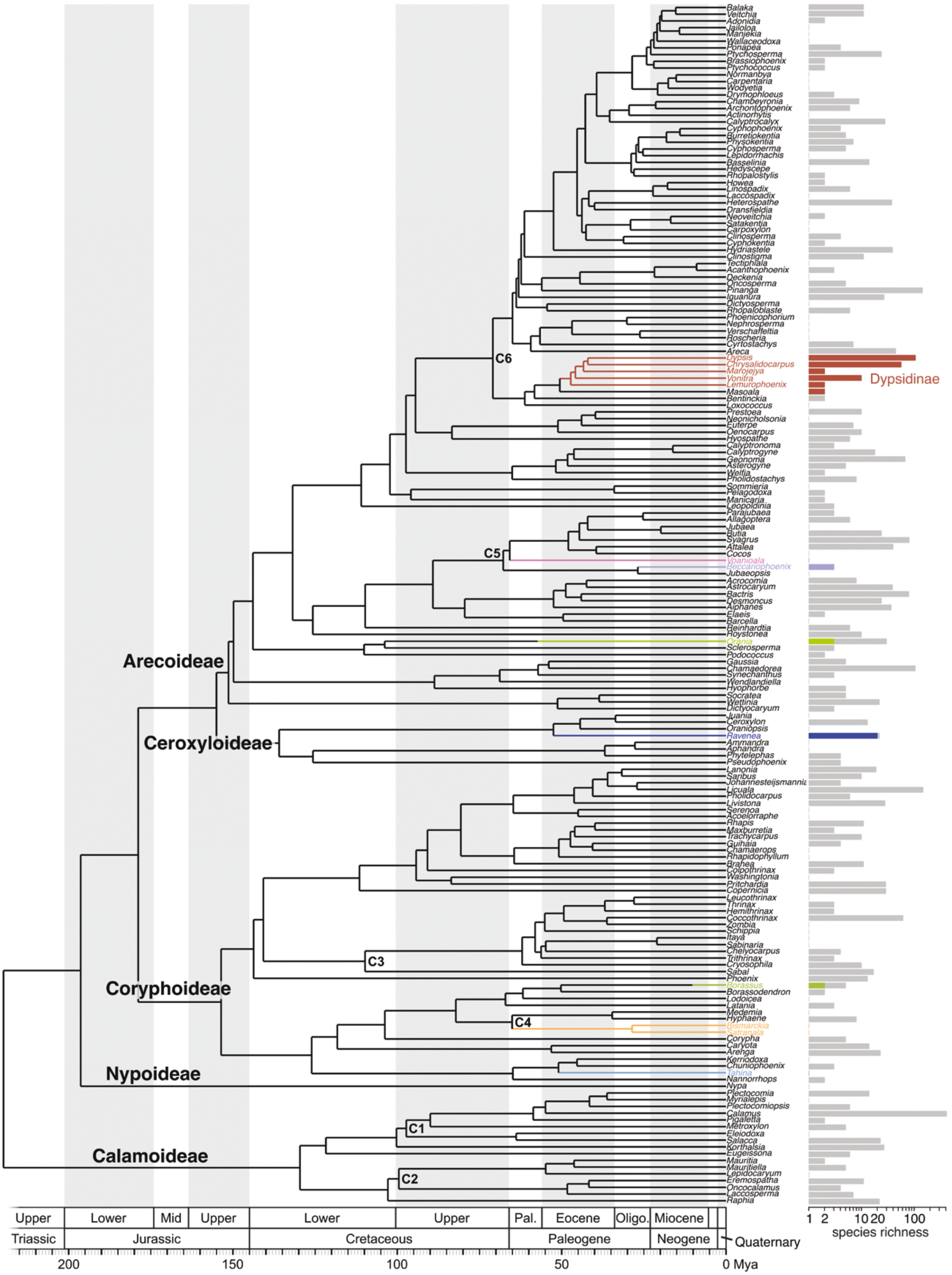

Figure 2. Time-calibrated phylogenetic tree of the palm family (Arecaceae) inferred from 159 nuclear genes and seven temporal calibrations, including six high-quality fossils (C1–C6) and a secondary calibration on the stem node of palms (not shown). Species-level relationships within genera collapsed for visualization purposes. The eight Malagasy palm clades are highlighted in colour. These clades are defined as (a) having endemic Malagasy palm species and (b) being highly likely to have diversified in Madagascar after a single colonization event. Note that

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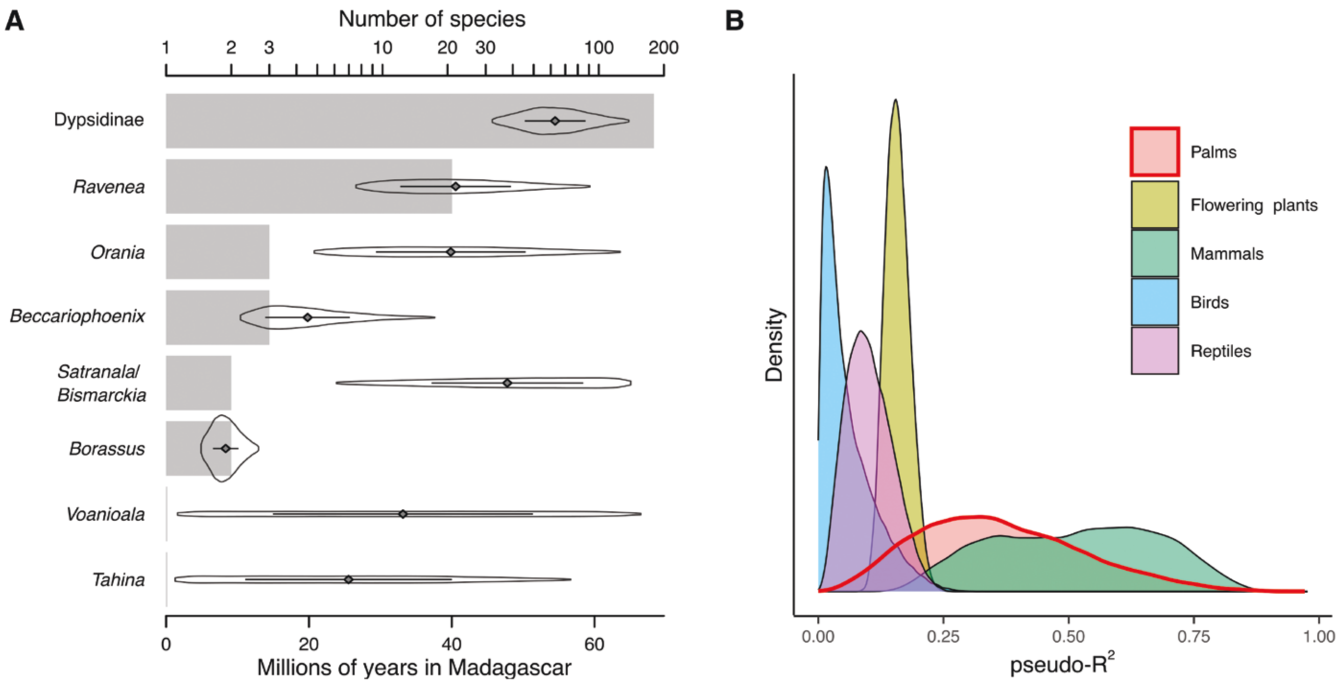

Figure 3. Time-for-speciation effect in Malagasy palms and other lineages. A, species richness (bars) and estimated colonization time (violin plots) across the eight Malagasy palm clades shown in Figure 2. Insets in violin plots show the mean ± one standard deviation. If time for speciation was the sole driver of species richness, mean colonization time and log(species richness) should be perfectly correlated. B, pseudo-R^2 from Spearman correlations between colonization time and log(species richness) in different Malagasy plant and animal clades. The thickened line for palms reflects the data in (A). Data for other plants and vertebrates from Antonelli *et al.* (2022). Other flowering plants $n_{\text{clades}} = 106$, birds $n_{\text{clades}} = 12$, mammals $n_{\text{clades}} = 11$, reptiles $n_{\text{clades}} = 17$.

variation in clade species richness. Moreover, evidence for the impact of climate on diversification rate is weak, despite the known relationship between climate and local species richness in Malagasy palms. Overall, it appears that the stark imbalance in species richness across Malagasy palm clades is mostly due to a combination of time for speciation and inherited variation in diversification rates due to intrinsic, lineage-specific properties.

Time for speciation

Time for speciation is known as a major reason for variation in species richness across the tree of life (Wiens 2011), and it is thus unsurprising that it plays a role in Malagasy palms. Palm lineages that colonized Madagascar earlier have had more time to diversify, and thus comprise more species. Subtribe Dypsidinae, by far the largest endemic Malagasy palm clade, was also first to colonize the island. However, time for speciation is unable to fully explain the spectacular diversity of Dypsidinae, and overall only explains just over a quarter of the variation in species richness among palm clades. Weak to moderate time-for-speciation effects appear to be the rule for Madagascar. Crottini *et al.* (2012) found that time for speciation explained *c.* 10–23% of species richness variation among vertebrate clades, using a similar approach to ours. Comparable studies on other lineages are lacking, but synthesizing age and species richness data for many plant and animal clades (Antonelli *et al.* 2022), we found a similar time-for-speciation effect across flowering plants and vertebrates except mammals (4–31%; Fig. 3B; Supporting information, Table S7). In mammals, time for speciation was much more important (52%; Fig. 3B; Supporting information, Table S7). Taken together, these results suggest that time for speciation, while clearly playing a role, is insufficient to explain the imbalance in clade species richness in Madagascar, and considerable variation in diversification rates must also be involved.

Timing of diversification rate shifts vs. timing of colonization

Perhaps the most surprising result of our analyses is that subtribe Dypsidinae, which is widely celebrated as a 'spectacular radiation' (Dransfield and Beentje 1995) in the context of Madagascar, is in fact not a Malagasy radiation from a macroevolutionary perspective. Rather, it is part of a much broader Indo-Pacific radiation in the palm tribe Areceae, which is underpinned by a three-fold increase in diversification rate (Fig. 4). This increase happened elsewhere, perhaps in Eurasia (Baker and Couvreur 2013a), long before the ancestor of Dypsidinae colonized Madagascar. An increase in diversification rate in the ancestor of Areceae was already predicted by Couvreur *et al.* (2015), and is confirmed here

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Ravenea and subtribe Dypsidinae (in the genus *Chrysalidocarpus*) include some non-Malagasy species, but these have undoubtedly originated from Malagasy ancestors. In *Orania* and *Borassus*, respectively, only a subclade of the genus is present in Madagascar; here, the coloured part of the branch reflects the stem age of the Malagasy clade. Note also that in the genus *Borassus*, it remains unclear if the two species are derived from one or two colonization events, but we (conservatively) assume a single event in our analyses. Bars indicate the species richness of each genus according to POWO (2024).

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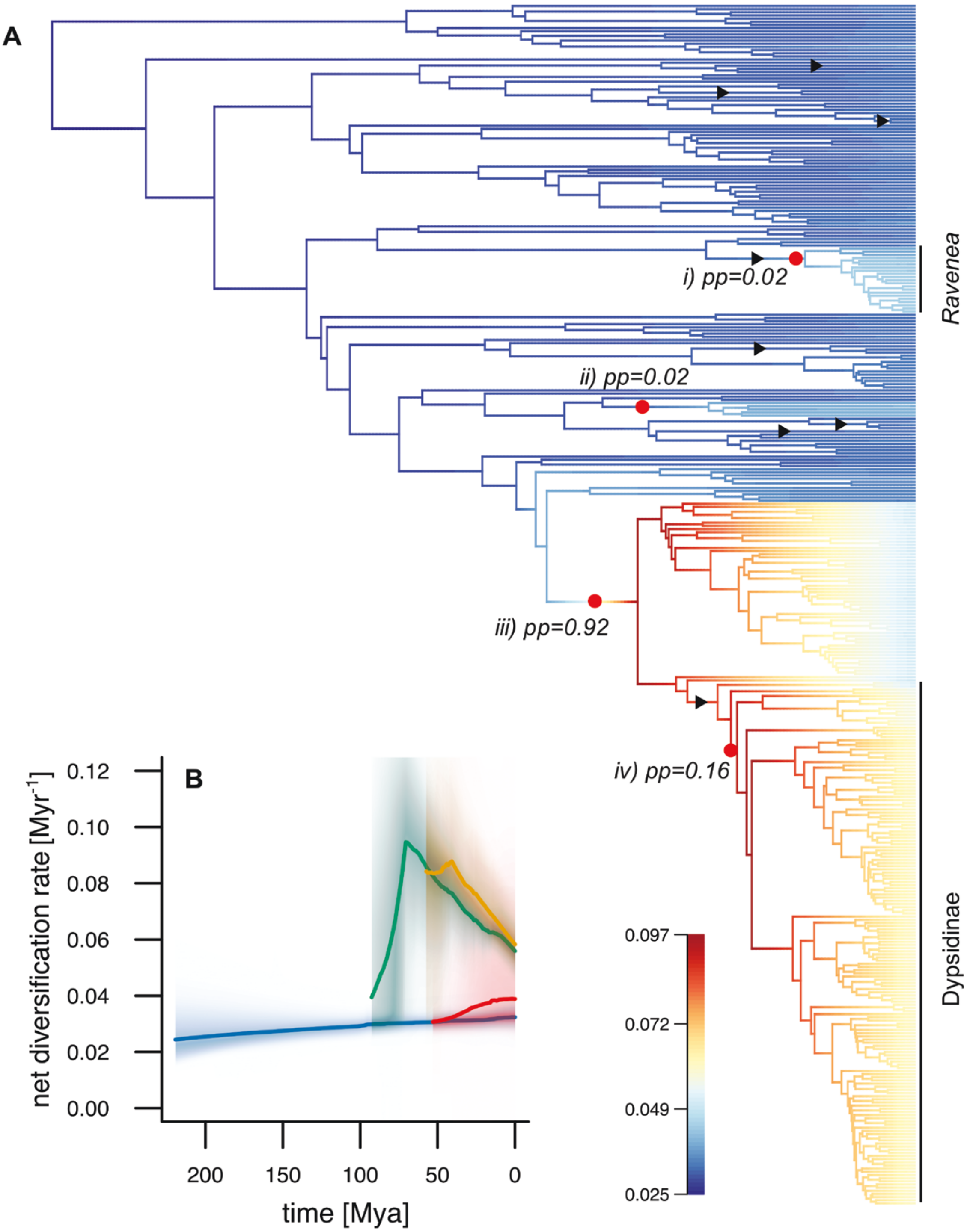

Figure 4. Diversification history of Malagasy palms within the context of the whole palm family, as estimated using BAMM. A, phylorate plot of our full tree, which includes all palm genera and most species of Malagasy palms. Branch colour indicates the net diversification rate [Myr^{-1}]. Dots mark four inferred diversification rate shifts (pp: posterior probability). The most pronounced rate shift (iii) is an increase in diversification rate in tribe Areceae, which includes the largest Malagasy palm clade, subtribe Dypsidinae. Additional rate increases are inferred early in the diversification history of Dypsidinae (iv) and the Malagasy genus Ravenea (i), respectively. The fourth inferred rate shift (iii) is unrelated to Madagascar. Arrowheads (▶) show inferred dispersals to Madagascar (cf. Table 1). B, average net diversification rate over time for all palms (blue), *Ravenea* (red), Areceae including Dypsidinae (green), and Dypsidinae (orange). Shading around lines shows confidence intervals.

with species-level sampling. The reason for this increase in diversification rate—perhaps involving some intrinsic key innovation—remains unknown and is the subject of ongoing research (S. Bellot *et al.*, unpublished data). Palms of subtribe Areceae are diverse across the Indo-Pacific and perhaps their diversification in Madagascar is merely part of their overall 'success story' across this island-dominated region.

Notwithstanding their inherited elevated diversification rate, Dypsidinae show evidence of a further, albeit relatively weak, rate increase after their colonization of Madagascar (Fig. 4). This

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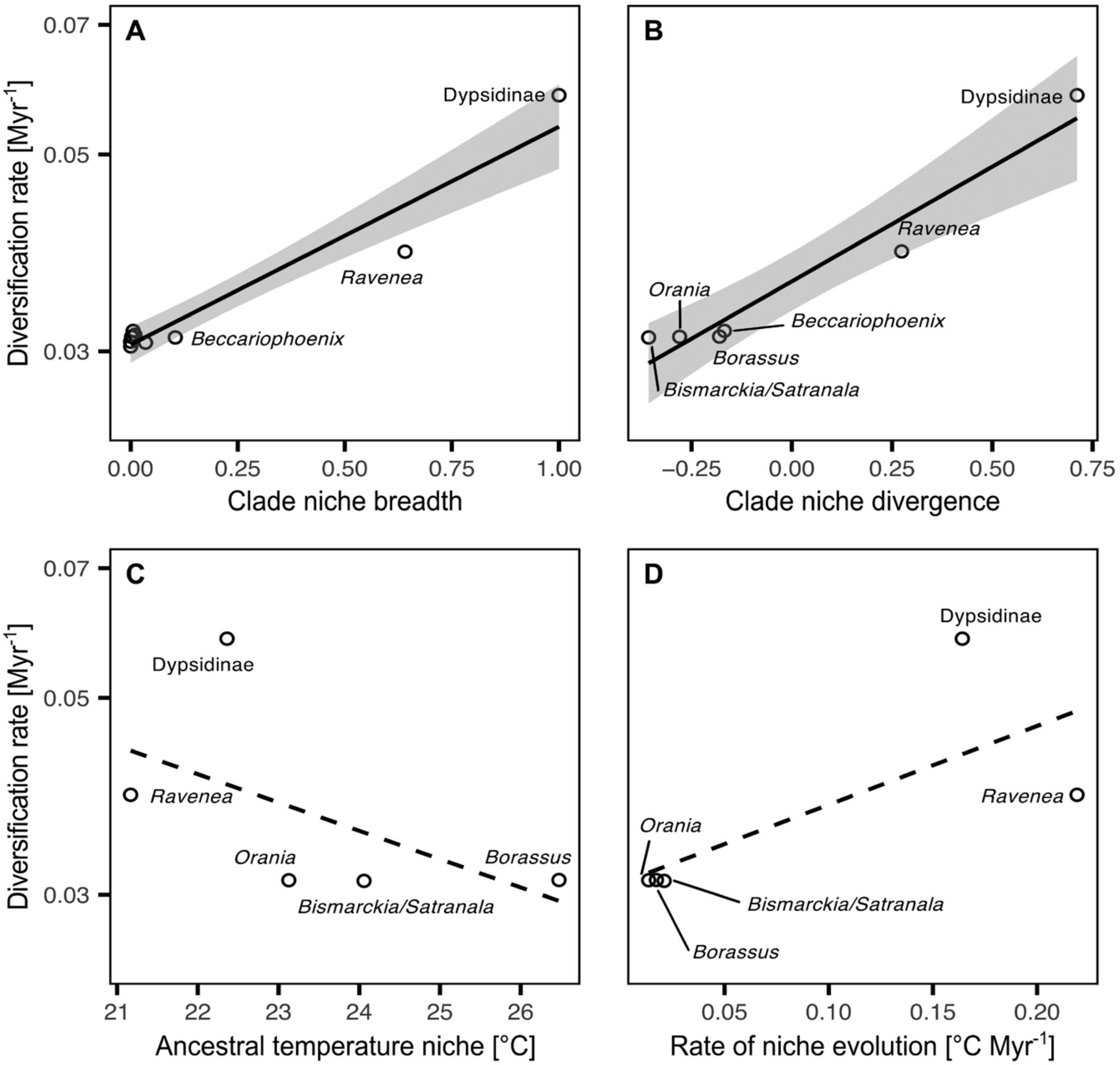

Figure 5. Relationships between diversification rate and climatic niche variables across Malagasy palm clades. A, climatic niche breadth of clades, based on three temperature and three precipitation variables, rescaled to a range of 0–1. B, climatic niche divergence, measured as the residuals of a regression between overall clade niche breadth and the average niche breadth of the species within the clade. C, temperature niche of the clade's most recent common ancestor, i.e. the mean annual temperature across the range of the ancestral species, estimated from temperature data for extant species using macroevolutionary models of continuous trait evolution. D, rate of temperature niche evolution derived from Brownian Motion models of trait evolution. Regression lines from phylogenetic generalised least-squares regression (solid: significant, dashed: non-significant, $\alpha = 0.05$). 95% confidence intervals shown with grey shading for significant relationships.

might reflect the 'early burst' of an adaptive radiation (Gillespie *et al.* 2020), especially considering that Dypsidinae were likely the first of the extant palm lineages to colonize Madagascar (Fig. 3A), and thus likely met relatively empty ecological niche space. This is circumstantially supported by the observation that the diversification rate subsequently decreased again and is now comparable to the rest of Areceae (Fig. 4). Interestingly, our results suggest that the rate increase did not happen immediately after colonization, but rather *c.* 4–12 Myr later in the ancestor of all Dypsidinae except *Masoala* (three spp.) and *Lemurophoenix* (two spp.). This might indicate that a certain amount of evolutionary change was necessary to enable the initial colonists to diversify. Alternatively, radiation may have been delayed by a lack of suitable habitat, and only happened once the climate had become sufficiently wet-tropical for palm diversity to unfold (Wells 2003). Of note, a moderate diversification rate increase was also inferred at a similar time in the ancestor of *Ravenea* (Fig. 3), suggesting that this group, too, underwent some degree of adaptive diversification after colonizing Madagascar. However, these inferences may also be artefacts of sampling, given that only Malagasy palms are represented at the species level in our analysis, and remain to be confirmed with a full species-level

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Table 2. Univariate phylogenetic generalized least-squares regression models testing the relationship between diversification rate and climatic niche characteristics of Malagasy palm clades. Significant relationships at $\alpha = 0.05$ are highlighted in bold. Adjusted R^2, F-values on 1 and 9 degrees of freedom, and model slope with 95% confidence intervals (CI) are listed

Predictor variable	Adj. R^2	F	*P*	Slope (95% CI)
(i) Species niche breadth				
Mean species niche breadth	0	0.0052	0.94	-0.001 (± 0.05)
(ii) Evolutionary flexibility of the niche				
Clade niche breadth	**0.68**	**20.18**	**0.002**	**0.024 (± 0.12)**
Niche divergence	**0.71**	**13.1**	**0.022**	**0.601 (± 0.46)**
Rate of temperature niche evolution	0.40	0.088	0.16	0.30027 (± 0.48)
Rate of precipitation niche evolution	0	0.1908	0.68	0.03 (± 0.025)
(iii) Different rates in different climates				
Temperature niche position	0.056	1.532	0.25	-1.021 (± 1.90)
Precipitation niche position	0	0.1933	0.672	0.1410 (± 0.45)
Ancestral temperature niche	0.28	0.6226	0.19	-2.56 (± 0.1652)
Ancestral precipitation niche	0.01725	0.070	0.8041	0.46254 (± 4.84)

phylogeny of all palms. Why other palm clades did not experience diversification rate increases when colonizing Madagascar remains unclear.

Diversification rate and climate

Our results tentatively support the idea that lineages with more flexible climatic niches (i.e. less phylogenetic niche conservatism) show higher diversification rates. In keeping with this idea, we found that clades with higher diversification rates both occupy a broader range of climates, and comprise species with more divergent niches *sensu* Castro-Insua *et al.* (2018) (Table 2; Fig. 5A, B). Rates of niche evolution as estimated from a Brownian Motion model were also positively related to diversification rate (Fig. 5D; Supporting information, Fig. S2E), albeit not significantly (Table 2). While these relationships suggest that diversification in Malagasy palms *involves* adaptation to new climates, they cannot prove that this adaptation in fact *drives* diversification. However, this is still a significant insight, as it demonstrates that the clades that diversified most vigorously clearly did so by radiating broadly into the island's different climates (Fig. 5A), rather than just utilizing the same climate space more efficiently, for example, by evolving a variety of different growth forms that co-occur locally. Meanwhile, we found no evidence of faster-diversifying clades partitioning niche space more finely, i.e. the average niche breadth of species was totally unrelated to diversification rate (Table 2). Similar results have been obtained globally in amphibians (Gómez-Rodríguez *et al.* 2015), birds (Cooney *et al.* 2016), and mammals (Castro-Insua *et al.* 2018).

Intriguingly, we found little evidence of clades diversifying more vigorously in certain climates than in others (Table 2, extant and ancestral temperature and precipitation niche). The absence of a precipitation effect seems particularly counterintuitive considering that previous studies have emphasized the humid forests of Madagascar as centres of recent diversification (Vences *et al.* 2009, Antonelli *et al.* 2022), and precipitation is a major known driver of local palm species richness in Madagascar (Rakotoarinivo *et al.* 2013). In particular, two most species-rich Malagasy palm clades, Dypsidinae and *Ravenea*, both have their centre of diversity in the humid east. However, other clades that have scarcely diversified (*Voanioala*, Malagasy *Orania*) are even more narrowly adapted to humid conditions, preventing a significant relationship (Supporting information, Fig. S2). This result in Malagasy palms is consistent with global findings showing that diversification rates do not differ among palms occurring in dry vs. humid forests (Cássia-Silva *et al.* 2019). However, there seems to be a (non-significant) negative relationship between temperature and diversification (Fig. 5C; Supporting information, Fig. S2B), probably reflecting the ability of Dypsidinae and *Ravenea* to speciate along altitudinal temperature gradients.

The unknowable role of extinction

Although we have interpreted our results mostly in relation to speciation, extinction may also play an important role in explaining diversity imbalance. However, this role is likely to remain unknown for the foreseeable future. Inferring extinction from phylogenetic data with confidence is difficult, if not impossible (Rabosky 2010, Louca and Pennell 2020). The fossil record can provide important insights (Morlon *et al.* 2011) but is scarce for plants in Madagascar (Antonelli *et al.* 2022), with no known palm fossils. We see two main ways in which extinction may influence our results. Firstly, observed variation in diversification rate may in fact be driven by variation in extinction. For example, it is possible that some of the relatively old, species poor palm clades (e.g. *Voanioala*, *Tahina*, *Satranala*/*Bismarckia*) with low net diversification rates are in fact remnants of formerly more diverse Malagasy radiations. Cyclic diversification of lineages with initial radiation followed by low or negative diversification, ultimately ending in extinction, is a well-known phenomenon (Donoghue and Sanderson 2015) that may weaken the time-for-speciation effect. In fact, it is entirely possible that our analysis omits additional colonizations of Madagascar by palms that have not left any extant descendants. Secondly, extinction of non-Malagasy relatives may have biased our estimates of colonization times, making species-poor lineages appear older. Although the palm fossil record is relatively good overall (Dransfield *et al.* 2008, Bellot *et al.* 2024), there are undoubtedly many unknown extinct lineages. This source of error is particularly likely to affect Malagasy clades whose closest relatives are geographically highly

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disjunct, with no obvious direct colonization routes (e.g. *Tahina*, *Voanioala*). Overall, substantial new palaeobotanical discoveries are probably our only hope of understanding the role of extinction in shaping species richness imbalance among Malagasy palm clades.

CONCLUSION

We chose Madagascar as the setting to study the drivers of imbalance of species richness among clades because it is a well-established and relatively closed 'natural laboratory' for investigating *in situ* evolutionary processes (Vences *et al.* 2009). We fully expected to find the reasons for species richness imbalance *in* Madagascar, and hoped to gain insights into the drivers of speciation on the island. To our surprise, however, we found that it is necessary to look elsewhere to understand the tremendous imbalance in species richness among Malagasy palm clades. To explain the spectacular diversification of subtribe Dypsidinae on the island, we now need to address the question: what kind of evolutionary change allowed the palm tribe Areceae to sustain highly elevated diversification rates in geographic settings as different as the Malay Archipelago, the Pacific islands, and Madagascar? At the same time, macroevolutionary analyses like the ones presented here are too coarse to reveal what drives speciation in Madagascar. Undoubtedly, evolutionary responses to environmental gradients and changes (such as climate and geomorphological dynamics, Wells 2003, Roberts *et al.* 2012, Liu *et al.* 2024) will have affected speciation in some clades more than others, contributing to species richness imbalance on Madagascar. We believe that a better understanding of these effects is needed before scaling up to clade-level comparisons, and landscape-scale analyses of speciation are required to achieve this. In the face of continuing rampant overexploitation and habitat loss in Madagascar (Ralimanana *et al.* 2022), such studies are not only important, but also urgent if we wish to understand the drivers underpinning Malagasy biodiversity before it is extinguished.

SUPPORTING INFORMATION

Supplementary data is available at *Evolutionary Journal of the Linnean Society* online.

Table S1. Sequence data newly generated for this study.

Table S2. Fossil information and fossil prior settings in the BEAST analysis.

Table S3. Results from SortaDate showing the five genes with the highest topological similarity to the species tree (Bipartition).

Table S4. Number of unique occurrence records per palm species at 0.5' (approximately 0.85 × 0.85 km).

Table S5. Model evaluation and rates of temperature niche evolution.

Table S6. Model evaluation and rates of precipitation niche evolution.

Table S7. Spearman's rank correlation *rho* between estimated clade arrival time and clade species richness for different organismal groups in Madagascar.

Figure S1. The relationship between diversification rate and log(species richness) in Malagasy palm clades.

Figure S2. Relationships between diversification rate climatic niche variables in Malagasy palm clades.

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COMPETING INTERESTS

The authors declare no competing interests.

DATA AVAILABILITY

Data associated with this study are available here: https://doi.org/10.5061/dryad.7d7wm383r

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