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The Cenozoic history of palms: Global diversification, biogeography and the decline of megathermal forests

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Abstract

Aim: Megathermal rain forests and mangroves are much smaller in extent today than in the early Cenozoic, primarily owing to global cooling and drying trends since the Eocene–Oligocene transition (c. 34 Ma). The general reduction of these biomes is hypothesized to shape the diversity and biogeographical history of tropical plant clades. However, this has rarely been examined owing to a paucity of good fossil records of tropical taxa and the difficulty in assigning them to modern clades. Here, we evaluate the role that Cenozoic climate change might have played in shaping the diversity and biogeography of tropical plants through time.

Location: Global.

Time period: Cenozoic, 66 Ma to present.

Major taxa studied: Four palm clades (Calaminae, Eugeissoneae, Mauritiinae and Nypoideae) and their fossil pollen record.

Methods: We compiled fossil pollen occurrence records for each focal palm lineage to reconstruct their diversity and biogeographical distribution throughout the Cenozoic. We use climatic niche models to project the distribution of climatically suitable areas for each lineage in the past, using palaeoclimatic data for the Cenozoic.

Results: For most palm lineages examined, global pollen taxonomic diversity declined throughout the Cenozoic. Geographical ranges for each focal lineage contracted globally and experienced regional-scale extinctions (e.g., Afrotropics), particularly after the Miocene. However, climatic niche models trained on extant species of these focal lineages often predict the presence of climatically suitable habitat in areas where these lineages went extinct.

Main conclusions: Globally, the decline in megathermal rain forest and mangrove extent might have led to declines in diversity and range contractions in some megathermal plant taxa throughout the Cenozoic. Although global climatic trends are an important backdrop for the biogeography and diversity of tropical groups at global scales, their continental- or regional-scale biogeographical trajectories might be more dependent on regional abiotic and biotic contexts.

Jun Ying Lim and Huasheng Huang contributed equally to this work.

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KEYWORDS

Arecaceae, climatic niche modelling, Eocene–Oligocene transition, fossil record, global cooling, palaeoclimate, palynology, tropical forests

1 | INTRODUCTION

Tropical rain forest and mangrove biomes represent some of the most productive and species-rich ecosystems on the planet (Eiserhardt et al., 2017). They are typically characterized by warm temperatures (mean monthly temperature > 18°C) with high mean annual precipitation, the lack of a pronounced dry season and the absence of frosts (Jaramillo & Cárdenas, 2013; Morley, 2000; Willis & McElwain, 2014). Today, such biomes are situated more or less within the confines of the tropics of Capricorn and Cancer (23° N and 23° S of the equator, respectively) but would formerly have extended far beyond the tropics and are therefore referred to as “megathermal” forests to avoid geographical connotations (Morley, 2000, 2011). Megathermal rain forests and mangroves (i.e., with recognizably modern composition and diversity) originated some time between the mid-Cretaceous and the Paleocene (Carvalho et al., 2021; Couvreur & Baker, 2013; Eiserhardt et al., 2017; Ellison et al., 1999; Morley, 2000; Ramírez-Barahona et al., 2020; Ricklefs & Latham, 1993), reaching their maximum extent in the Eocene (Morley, 2000; Willis & McElwain, 2014). However, subsequent global cooling throughout the rest of the Cenozoic (Westerhold et al., 2020) has led to a reduction in their global extent to their current distribution (Pound & Salzmann, 2017; Willis & McElwain, 2014).

The Cenozoic decline in the extent of megathermal rain forests and mangroves is potentially a crucial historical backdrop for understanding the diversity and biogeography of many tropical lineages. In particular, the decline in geographical extent of tropical habitats/biomes is expected to result in reduced diversification rates (decreased speciation rates and/or increased extinction rates) in tropical clades (Condamine et al., 2013; Fine & Ree, 2006; Jetz & Fine, 2012; Lim & Marshall, 2017). Larger areas may support a greater number of individuals and species (Storch et al., 2018), promote speciation by providing opportunities for geographical isolation across landscapes (Kisel et al., 2011) or promote ecological speciation by possessing greater environmental heterogeneity or a greater diversity of habitats (Jaramillo et al., 2006; Kisel et al., 2011; Stein et al., 2014). In addition, as climatic conditions in space change, lineages typically move to track their preferred climates (Mairal et al., 2017; Wiens & Graham, 2005), and where areas with suitable climatic conditions disappear, lineages may be extirpated if they are unable to adapt. Reductions in the extent and connectivity within megathermal biomes may thus have a profound influence on modern biogeographical distributions of tropical taxa (Donoghue & Edwards, 2014; Mairal et al., 2017; Shiono et al., 2018). Thus, understanding how past tropical lineages have responded to past climatic upheaval is crucial for understanding modern-day patterns of tropical diversity.

Despite the potential importance of Cenozoic climate change for global biogeography and diversity, few studies have explored its macroevolutionary and biogeographical implications for tropical plant groups (Kissling et al., 2012; Shiono et al., 2018). Inferences of diversification (Condamine et al., 2013; Couvreur et al., 2011; Rabosky, 2014) and biogeographical histories (Ree & Smith, 2008; Ronquist & Sanmartín, 2011; Matzke, 2014) of extant groups have been made primarily from molecular phylogenies, but there is significant uncertainty over whether, and how well, diversification or biogeographical histories may be recovered reliably from the temporal information inherent in molecular phylogenies alone (Louca & Pennell, 2020; Quental & Marshall, 2011). In particular, molecular phylogenies typically only represent the evolutionary history of lineages that have survived to the (near) present; hence, they may not contain sufficient signal on past diversification trajectories (Quental & Marshall, 2010). In contrast, the fossil record provides direct information on the diversity and biogeography of lineages through time (Crisp et al., 2011; Quental & Marshall, 2010), but the incompleteness of the fossil record in space and time (Jones et al., 2021; Xing et al., 2016) and the difficulty of assigning fossils to modern groups restrict its applicability to plant groups with good fossil records or coarse taxonomic scales (e.g., Meseguer et al., 2015, 2018).

Here, to shed light on the role of Cenozoic environmental change on the diversification and historical biogeography of tropical plants, we focus on fossil pollen records of an iconic group, the palms (Arecaceae). Palms are regarded as a model group for megathermal forest evolution (Couvreur & Baker, 2013) and are well represented in the fossil record (Harley, 2006), where they are one of the earliest recognizable modern angiosperm families (Dransfield et al., 2008). Also, crucially, owing to physiological constraints (the lack of bud dormancy and frost tolerance), they are largely restricted to tropical and subtropical parts of the world and are often used as palaeoclimatic indicators (Morley, 2000), making them an ideal model group for tropical plants. The fossil record of palms might provide crucial insights into how tropical clades have responded to changes in megathermal forest extent and connectivity throughout the Cenozoic.

We hypothesize that: (1) reductions in megathermal forest extent through the Cenozoic would have led to a global decline in palm fossil pollen taxonomic richness of each lineage through time; and (2) given the strong association of palm lineages with tropical habitats today, reductions in climatically suitable areas would explain contractions in the geographical ranges of these palm lineages through time. We collated data on the exceptional fossil pollen records of four distinct tropical palm lineages [three from the subfamily Calamoideae (Mauritiinae, Calaminae and Eugeissoneae) and one from the subfamily Nypoideae (represented by the monotypic

genus, *Nypa*) (Figure 1)] that have much broader palaeogeographical distributions than in the present day (Figure 2; Bogotá-Ángel et al., 2021; Dransfield et al., 2008). Together, these four lineages make up about one-fifth of the species diversity of the palm family (Table 1). Using newly compiled data on their fossil records, we tracked their diversity and biogeography through time and evaluated the degree to which their biogeographical histories might be explained by changes in the distribution of their suitable climates through the Cenozoic, using climatic niche models based on species occurrence data of their extant relatives.

2 | METHODS

2.1 | Palm lineages and fossil pollen dataset

The focal palm lineages vary in extant species richness and ecology (Figure 1; Table 1). Extant species of Calaminae, Eugeissoneae and Mauritiinae are tropical forest palms, whereas the sole extant species of Nypoideae, *Nypa fruticans*, is a common component of mangrove forests in the Indo-Pacific (Figure 1). Furthermore, they have very different present-day distributions. Calaminae (c. 500 species)

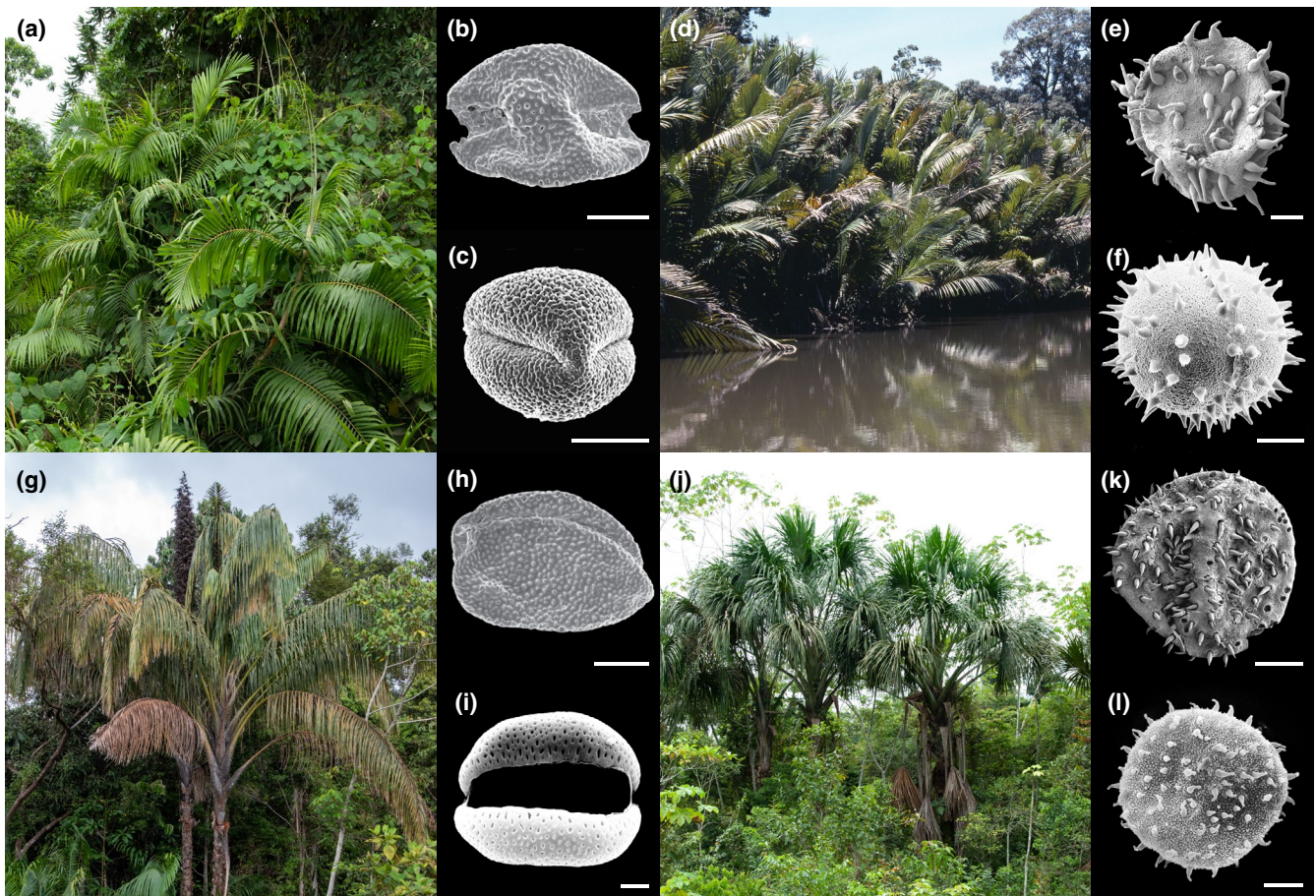


FIGURE 1 Focal palm lineages and pollen grains of extant and extinct representatives under scanning electron microscopy (SEM) (a–c: Calaminae; d–f: Nypoideae; g–i: Eugeissoneae; j–l: Mauritiinae). (a) *Calamus longipinna* K. Schum. & Lauterb., showing flagella, which are sterile, whip-like inflorescences possessing hook-like structures that allow the plants to attach themselves to neighbouring vegetation. (b) Fossil pollen grain of *Dicolpopollis kalewensis* Potonié from the late Eocene (Myanmar). (c) Pollen grain of extant taxon *Calamus viminalis* Willd. (d) *Nypa fruticans* Wurm is a common mangrove species in many parts of the Indo-Pacific and the sole representative of the subfamily Nypoideae. It possesses unique creeping, dichotomizing stems that allow it to grow in soft sediments, often forming large monodominant stands. (e) Fossil pollen grain of *Spinizonocolpites echinatus* from the Paleocene (India). (f) Pollen grain of *Nypa fruticans*. (g) *Eugeissona utilis* Becc., part of a morphologically distinct group of calamoid palms restricted to Borneo and the Malay Peninsula. (h) Fossil pollen grain of *Longapertites retipilatus* Kar. from the late Eocene (Myanmar). (i) Pollen grain of *Eugeissona tristis* Griff. (j) *Mauritia flexuosa* L.f. is part of a small group of tree palms restricted to lowland or riparian ecosystems in South America, which are unique among calamoid palms in bearing fan leaves. *Mauritia flexuosa* exists in vast monodominant stands in tropical South America and is among the most abundant trees in the Amazon. (k) Fossil pollen grain of *Mauritiidites franciscoi* (van der Hammen) van Hoeken-Klinkenberg from the Miocene (Apoporis, Colombia). (l) Pollen grain of *Mauritia* sp. Scale bars: 10 μ m. Credits: Photographs (a), (d), (g) and (j) taken by William J. Baker, Royal Botanic Gardens, Kew; micrographs (b) and (h) produced with permission from Huang et al. (2020); micrograph (e) produced with permission from Shalini Parmar and Vandana Prasad, Birbal Sahni Institute of Palaeosciences; micrograph (k) produced with permission from Bogotá-Ángel et al. (2021); and micrographs (c), (f), (i) and (l) produced with permission from Madeline M. Harley, Royal Botanic Gardens, Kew



FIGURE 2 Distribution of fossil occurrences through time. Palaeocoordinates for each occurrence and continental configurations were obtained using GeTech palaeo-plate rotational models for the middle of the first stage of each epoch. For simplicity, all occurrences from each epoch, regardless of their exact stratigraphic age, are plotted on a map representing the palaeogeography at the middle of the first stage of each epoch. Holocene (< 11.7 ka) records are plotted on the Gelasian map. Occurrences that traverse more than one epoch stratigraphically are plotted on multiple maps

is most diverse in the (sub-)tropical forests of Asia, tropical Africa and Australia. The six species of *Eugeissona*, which make up the entirety of the tribe Eugeissoneae, are confined to the Malay Peninsula and Borneo. The single species of *Nypa* occurs in mangroves across India, Southeast Asia and the Indo-Pacific. Lastly, the seven species in three genera of Mauritiinae are endemic to tropical South America.

We compiled information on the fossil records of each of these focal palm lineages (Figure 2) by first identifying relevant studies using a taxon search on Palynodata, a comprehensive database of the palynological literature (Palynodata & White, 2008). We

supplemented this with additional references from taxon-focused reviews of the palm fossil record (e.g., Bogotá-Ángel et al., 2021; Dransfield et al., 2008; Harley, 2006). All four focal palm lineages are characterized by rich and abundant fossil pollen records throughout the Cenozoic, which are easily identifiable with great confidence in the fossil record. In general, affinities of fossil pollen form taxa to extant palm lineages is well supported by various shared morphological characters (Table 1).

From these studies, we collated a global dataset of fossil occurrences, in addition to local first and last appearance datums (FAD and LADs, respectively) for each fossil pollen taxon and

TABLE 1 Focal palm pollen taxa and their affinities to extant palm lineages

Palm lineage	Fossil form taxa	Characters supporting affinity	Extant genera (number of species)
Subtribe Calaminae	<i>Dicolpopollis</i>	Disulcate (Harley & Morley, 1995)	<i>Calamus</i> (c. 500)
Subfamily Nypoideae	<i>Spinizonocolpites</i>	Zonasulcate; pollen wall finely reticulate and covered by baculate or echinate spines (Frederiksen, 1980; Morley, 2000; Muller, 1968)	<i>Nypa</i> (1)
Tribe Eugeissoneae	<i>Longapertites</i> and <i>Quilonipollenites</i>	Extended sulcus with thick wall (Morley, 2000; Phadtare & Kulkarni, 1984)	<i>Eugeissona</i> (6)
Subtribe Mauritiinae	<i>Mauritiidites</i> , <i>Grimsdalea</i> and <i>Echidiporites</i>	Exine with indentations; monosulcate (Bogotá-Ángel et al., 2021; Pocknall & Jarzen, 2012; van Hoeken-Klinkenberg, 1964)	<i>Mauritia</i> (2), <i>Mauritiella</i> (4) and <i>Lepidocaryum</i> (1)

Note: Species diversity for each extant genus was obtained from the World Checklist of Selected Plant Families (Govaerts et al., 2020). Genera *Daemonorops*, *Ceratolobus*, *Retispatha* and *Pogonotium* are now considered synonyms of *Calamus* (Baker, 2015; Henderson, 2020).

their putative modern relatives (Table 1) across fossil localities for the Cenozoic. Fossil occurrences are records of a fossil taxon at a particular locality, much like a species occurrence record, whereas local FADs and LADs represent the stratigraphic/temporal range of a fossil taxon at a particular locality. For simplicity, we refer to both types of data as “records”. For each record, we collated information on its stratigraphic age and associated age uncertainty, in addition to the geographical coordinates of the reported fossil locality. Geographical coordinates were georeferenced manually when they were not provided explicitly by the source. This was done by locating them using Google Earth by either cross-referencing maps of the locality (if provided) or searching for the reported name of the locality, and subsequently, extracting the associated coordinates. Fossil occurrences for which stratigraphic uncertainty was too large (i.e., across more than two geological epochs) were not included in our dataset.

To evaluate the robustness of our results to data uncertainty, we additionally scored the quality of data sources into three levels based on the availability of pollen micrographs and whether or not the source was available. We regarded “high-confidence” records as those references that included micrographs of specimens, which allowed us to check the validity of taxonomic identifications, “medium-confidence” records as those from the literature but without micrographs of specimens, and “low-confidence” records as those recorded in the Palynodata database without literature access.

In total, our dataset contained information from 770 references and consisted of 331 records for Calaminae (fossil pollen records of extant genus *Calamus* and the form-taxon *Dicolpopollis*), 366 for Eugeissoneae (*Eugeissona* and the form taxa *Quilonipollenites* and *Longapertites*), 520 records for Nypoideae (*Nypa* and the form-taxon *Spinizonocolpites*) and 529 records for Mauritiinae (fossils of extant genera *Mauritia* and *Mauritiella* and the form taxa *Mauritiidites*, *Echidiporites* and *Grimsdalea*). A list of the literature sources used to assemble the fossil pollen dataset is provided in Appendix 1.

2.2 | Palm diversity through time

We quantified trends in taxonomic richness of pollen form taxa (Table 1) of each palm lineage through the Cenozoic using the compiled fossil data. We treated each fossil species as a separate taxon in our analysis. The three varieties of *Mauritiidites franciscoi* (*Mauritiidites franciscoi* var. *franciscoi*, *Mauritiidites franciscoi* var. *pachyexinatus* and *Mauritiidites franciscoi* var. *minutus*) were treated as separate taxa because they are morphologically distinct (van der Hammen & Garcia de Mutis, 1965). As such, records of *Mauritiidites franciscoi* that were not identified to variety were omitted from the analysis (83 records). We also omitted *Longapertites dupliclavatus* from our analysis (three records) because their proposed taxonomic affinity to Eugeissoneae is doubtful on morphological grounds (for discussion, see Supplementary Discussion in Supporting Information). Overall, our analysis considers 221 records for Calaminae, 428 records for Nypoideae, 269 records for Eugeissoneae and 247 records for Mauritiinae.

Taxonomic richness through time was estimated in two ways: (1) sampled-in-bin diversity; and 2) range-through diversity using the “divDyn” R package (Kocsis et al., 2019). Sampled-in-bin species richness was quantified by counting the number of unique fossil taxa that were recorded within a given time interval (i.e., bin), whereas range-through species richness additionally counted species that were not in the focal bin itself, but had been recorded in bins that were older and younger than the focal time bin. The latter approach assumes that a taxon must always exist at any time between its appearance and its eventual disappearance from the global fossil record, regardless of whether it is detected in time intervals in between. The range-through approach, therefore, accounts for incomplete sampling in the fossil record to some degree. For taxon records that were local stratigraphical ranges (FAD and LAD), we assumed that the given taxon was present in all time bins that were traversed by the stratigraphic range for both methods.

For both approaches, we used six equal-interval, 10-Myr time bins that encompassed the past 60 Myr, as opposed to epoch-based time bins, meaning that each bin would represent the same amount

of time and that estimated diversities for each bin were temporally standardized. We did not adopt more sophisticated approaches to control for incomplete sampling of occurrences (see Kocsis et al., 2019) because our data included both local stratigraphic ranges and occurrences, which are not comparable sampling events. Nevertheless, combining both the occurrences and local stratigraphic ranges was appropriate for our diversity metrics, because they make the fewest assumptions, by simply accounting for the global stratigraphic ranges of only recognized taxa (and not undetected taxa) in the fossil record.

To account for stratigraphic uncertainty in the exact ages of fossil occurrences and the bounds of stratigraphic ranges (FADs and LADs), we also adopted a randomization approach. For fossil occurrences, the ages for each fossil were drawn randomly from a uniform distribution within the minimum and maximum age uncertainty of the fossil occurrence. For example, a fossil occurrence in an “Eocene” fossil locality would be assigned an age between the recognized bounds of the geological epoch (56 and 33.9 Ma) and counted in whichever 10-Myr time bin the randomized age fell within. Likewise, age uncertainty for FADs and LADs was accommodated by assuming a randomly sampled age within the recognized bounds of the time interval they were in. For example, if the FAD of a local stratigraphic range was in the Paleocene and the LAD in the Eocene, the randomized age range for that record would be counted in all 10-Myr time bins between (66–56) to (56–33.9) Ma. By adopting this approach, fossil occurrences and stratigraphic ranges with a low age uncertainty (e.g., because of better stratigraphic dating or direct dating of stratum) will be drawn from a smaller range of values, and randomized ages will potentially fall into fewer time bins. We randomized ages for each fossil occurrence, FADs and LADs independently 1,000 times, and calculated the average sampled-in-bin and range-through diversities across randomizations.

In addition, we tested whether the species diversity of each focal lineage was correlated with its geographical range through time. Across all 1,000 age randomizations, we calculated the geographical range for each focal palm lineage in each 10-Myr time bin by intersecting a 500-km-radius circular buffer zone around all fossil localities with palaeocoastlines under a Behrmann cylindrical equal-area projection. Palaeocoordinates for all fossil localities in each time bin and palaeocoastlines were generated using the *reconstruct* function of the “chronosphere” R package (Kocsis & Raja, 2020). Correlation between mean geographical range and mean diversity measures (sampled-in-bin and range-through) across all 1,000 age randomizations was tested using Pearson’s correlation tests.

2.3 | Climatic niche modelling and palaeo-projections of climatically suitable area

To evaluate the climatic suitabilities of focal palm lineages through time, we constructed climatic niche models for each palm lineage. Each model was trained with occurrence data for all extant species in each lineage. This approach treats all occurrences of species in

each lineage as equal, and our climatic niche models therefore represent the climatic preferences of the lineage as a whole and not of individual species. Species occurrence data were obtained from the Global Biodiversity Information Facility (GBIF; downloaded 16 June 2020; GBIF, 2020), and subsequently, cleaned. Occurrence records with potentially erroneous geographical coordinates were identified using the *clean_coordinates* function of the “CoordinateCleaner” R package v.2.0-15 (Zizka et al., 2019) with default parameters and omitted. This included records located in oceans, close to biodiversity institutions, or country and province centroids (imprecise georeferencing), or records where coordinates were zeros or where latitudes and longitudes were identical (data entry errors). Clean GBIF occurrence records were supplemented with georeferenced specimen records from the herbarium of the Royal Botanic Gardens, Kew. Geographical outliers were identified and removed by cross-validating all occurrence points against the World Checklist of Areaceae (Govaerts et al., 2020), a taxonomically complete and expert-curated checklist of palms at the scale of “botanical countries” as defined by the International Working Group on Taxonomic Databases for Plant Sciences (Brummitt et al., 2001). This step ensured that all occurrence points were within the known geographical range of each lineage. Lastly, records with identical coordinates were removed. In total, there were 5,660, 143, 45 and 1,212 georeferenced species occurrences for Calaminae, Nypoideae, Eugeissoneae and Mauritiinae, respectively.

Climatic niche modelling was performed for each lineage using MAXENT (Merow et al., 2013; Phillips et al., 2006) as implemented by the *ENMevaluate* function of the “ENMeval” R package v.0.3.0 (Muscarella et al., 2014). Given that extant species for all focal lineages are largely restricted to (sub-)tropical areas, we chose six bioclimatic variables for the present day (i.e., WorldClim) as predictor variables that would best capture their distributions: Mean annual temperature (bio1), temperature seasonality (bio4), minimum temperature of coldest quarter (bio6), annual precipitation (bio12), precipitation of driest quarter (bio14) and precipitation seasonality (bio15) (Fick & Hijmans, 2017). Rasters for each bioclimatic variable were downloaded using the *get_data* function from the “raster” R package v.3.1-5 at a spatial grain of 5 arcmin (c. 3.4 km at the equator).

We evaluated multiple candidate models with a range of feature class combinations (i.e., “L”, “LQ”, “LQH”, “LQHP” and “LQHPT”) and a range of regularization multipliers (values from 0.5 to 4 in increments of 0.5). Model validation was then performed using *k* random folds (*k* = 10). To reduce the impact of model extrapolation into novel environments, models were “clamped” such that model features were fitted only within the climatic range of the training dataset/observations (Elith et al., 2011; Merow et al., 2013). Background points (*n* = 100,000) were sampled randomly across all terrestrial areas (except Antarctica) globally. Species occurrence points for each lineage were thinned such that only one occurrence point for each raster grid cell was used, in order to reduce the influence of spatial autocorrelation on model parameter estimation (Aiello-Lammens et al., 2015). After thinning, the final number of species occurrences used in our models

was 2,786 for Calaminae, 107 for Nypoideae, 37 for Eugeissoneae and 783 for Mauritiinae. Model selection was performed by identifying models with the lowest Akaike information criterion corrected for small sample size (AICc) and the lowest difference in average area under the receiver-operator characteristic plot between training and testing data ("avgAUCdiff") (Muscarella et al., 2014). Models with low "avgAUCdiff" indicate that training models did not vary greatly when models were fitted and validated on different random subsets of the data. Probabilities of occurrence for the best models under both criteria (AICc and avgAUCdiff) were calculated from MAXENT output using the "cloglog" transformation (Phillips et al., 2017).

To project climatically suitable areas for focal lineages through the Cenozoic, we used palaeoclimate rasters derived from model simulations for the first stage of each epoch of the Cenozoic: Danian (Paleocene, 63.8 Ma), Ypresian (Eocene, 51.9 Ma), Rupelian (Oligocene, 31.0 Ma), Aquitanian (Miocene, 21.7 Ma), Zanclean (Pliocene, 4.5 Ma) and Gelasian (Pleistocene, 2.2 Ma) (Farnsworth et al., 2019). Simulations were based on the UK Met Office coupled ocean-atmosphere general circulation model HadCM3L (version HadCM3BL-M2.1aD with a small modification; model simulations are described in detail by Farnsworth et al., 2019). Model resolution is 3.75° longitude by 2.5° latitude. The atmospheric CO₂ concentrations used for model simulations for each stage are 560, 1,120, 560, 400, 400 and 280 ppm, respectively, and are within the atmospheric CO₂ concentration range estimated from geological proxies (Foster et al., 2017). For each palaeoclimate raster, the same set of six bioclimatic variables used in the MAXENT models were calculated; hence, the models can be projected to palaeoclimatic conditions of each epoch. Our palaeoclimatic data capture global cooling and aridification trends throughout the Cenozoic and therefore capture broad-scale changes in areas with tropical climates through time (Westerhold et al., 2020; Supporting Information Figure S1). In addition, we evaluated the impact of projecting our models to potentially non-analogue palaeoclimates by identifying areas that are outside the climatic range of each focal lineage in the present.

3 | RESULTS

3.1 | Palm diversity through time

The taxonomic diversity of Eugeissoneae-like and Nypoideae-like fossil pollen showed a strong decline through the Cenozoic (Figure 3a), a pattern that was even stronger when restricting our analysis to sources that we classified as "high confidence" (Supporting Information Figure S2). For Mauritiinae, the taxonomic diversity of putative fossil pollen appeared to be fairly stable through the Cenozoic (Figure 3a), but also showed a decline when considering only literature records of "high confidence" (Supporting Information Figure S2). Contrary to the other three lineages, the diversity of Calaminae-type fossil pollen increased gradually through the early Cenozoic (Figure 3a; Supporting Information Figure S2). Sampled-in-bin species richness for all lineages was only slightly lower than range-through species richness, and both metrics exhibited the same broad trends (Figure 3a). The numbers of

fossil "records" (both occurrences and local stratigraphic ranges) for two focal lineages (Eugeissoneae and Nypoideae) showed declines through the Cenozoic, but the numbers of records for Mauritiinae and Calaminae showed a peak in the 20–10 and 30–20 Ma time bins, respectively (Figure 3b). Taxonomic diversity was strongly correlated with geographical range in all focal lineages except for Mauritiinae (Supporting Information Table S1).

3.2 | Palaeobiogeography and climatically suitable areas through time

All focal pollen lineages showed a much broader distribution in the early Cenozoic than their modern-day relatives in the present day. Most clades exhibited gradual range contractions through the early to mid-Cenozoic and underwent continental-scale extirpations after the Miocene (Figure 2). Calaminae-like *Dicolpopollis* pollen was abundant in Eurasia in the early to mid-Cenozoic, but disappeared from the region after the Miocene (Figure 2). It was not until the Pliocene when *Calamus* pollen appeared on the African continent. Only one extant species of *Calamus* occurs in Africa today. Nypoideae-like *Spinizonocolpites* and Eugeissoneae-like *Longapertites* and *Quilonipollenites* pollen were essentially pantropical through the Paleocene to Miocene (Figure 2), but both groups became restricted to Southeast Asia in the late Cenozoic. Mauritiinae-like pollen once extended across India, Africa and South America during the Paleocene, but became absent from India after the Paleocene and absent from Africa after the Miocene, eventually becoming restricted to South America. The observed contractions in geographical range in all focal groups do not appear to be attributable to changes in fossilization potential through time (see Supplementary Discussion in Supporting Information).

MAXENT models of suitable climate based on the present-day occurrences of extant species were broadly congruent with the geographical distribution of fossil occurrences through the Cenozoic (Figure 4; Supporting Information Figure S3). Projected climatic suitabilities using cross-validated MAXENT models with the lowest "avgAUCdiff" between training and testing datasets (Figure 4) were generally similar to models based on the lowest AICc (Supporting Information Figures S3 and S4); hence, we report only the results from models with the lowest "avgAUCdiff". In addition, our model projections do not appear to over-extrapolate into areas with climates outside the climatic range of each lineage in the present (Supporting Information Figures S5–S8).

Climatically suitable areas for Calaminae through the Cenozoic decreased gradually in India and the Nearctic, consistent with the disappearance of *Dicolpopollis* from both areas (Figure 4a). Likewise, climatically suitable areas for Nypoideae were projected as far south as Tasmania in the Eocene, where Nypoideae-like *Spinizonocolpites* has been found, but generally contracted further north in Australasia after the Eocene, consistent with the absence of *Spinizonocolpites* thereafter (Figure 4b). Climatically suitable areas for Eugeissoneae (Figure 4c) and Mauritiinae (Figure 4d) were present in all modern tropical regions, but were generally limited in extent through the Cenozoic. However, there was minor incongruence between the distribution of climatically

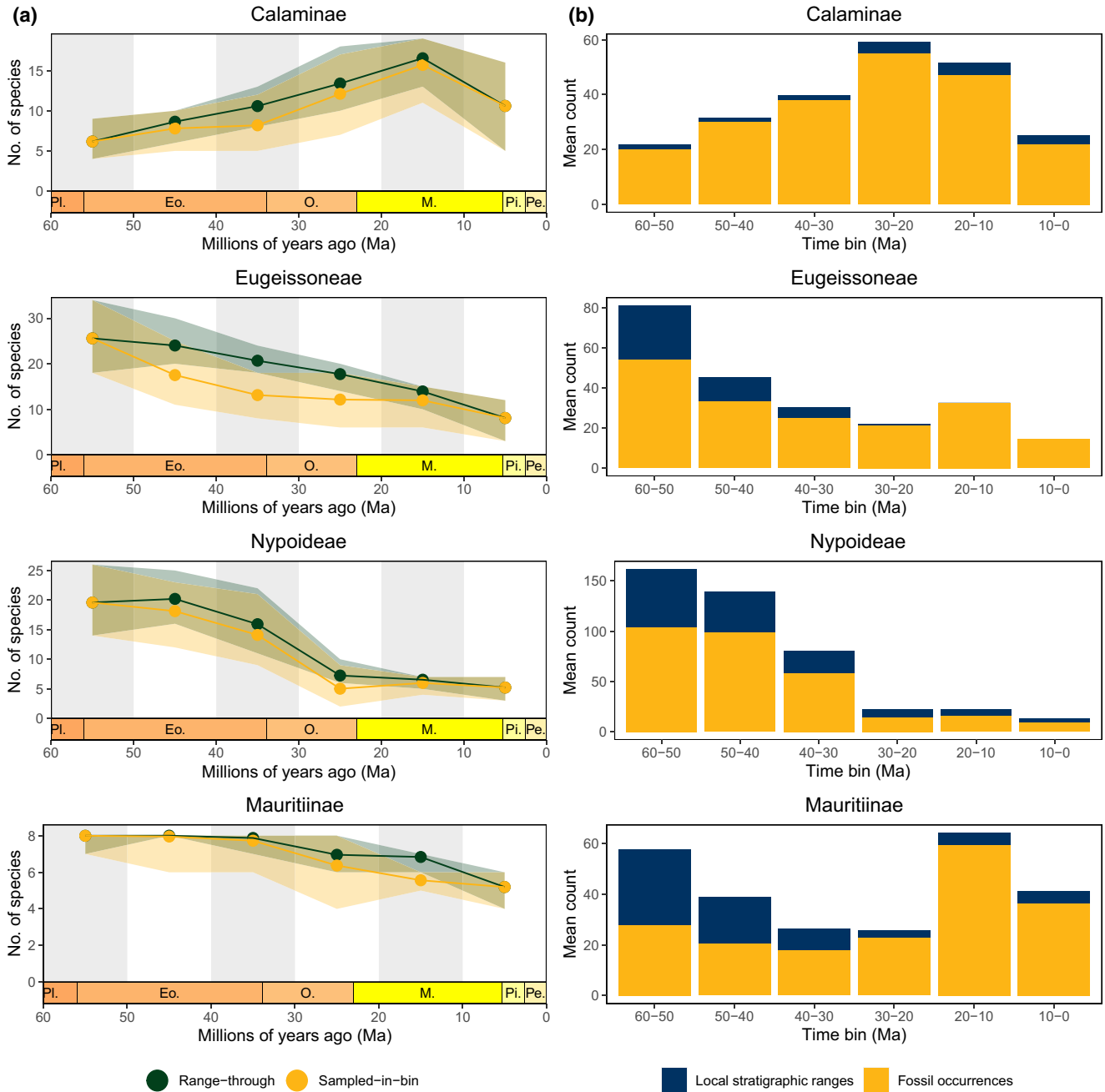


FIGURE 3 (a) Diversity and (b) number of records of fossil pollen of focal palm lineages through the Cenozoic. (a) Diversity was calculated using six equal-interval 10-Myr bins (alternating grey and white bands in background). Stratigraphic uncertainty of fossil occurrences and the boundaries of stratigraphic ranges [first and last appearance datums (FAD and LADs, respectively)] of fossil taxa were accounted for by randomly assigning ages within the age uncertainty reported in the associated study. Points represent mean sampled-in-bin (yellow) and range-through (dark green) species richness for each time bin across randomizations, and coloured shaded areas represent the minimum and maximum sampled-in-bin (yellow) and range-through (dark green) species richness. Pl. = Paleocene, Eo. = Eocene, O. = Oligocene, M. = Miocene, Pi. = Pliocene, Pe. = Pleistocene. (b) Stacked barplots representing the number of fossil occurrences (yellow) and local stratigraphic ranges (dark blue) that fell in or overlapped with each 10-Myr time bin, averaged across age randomizations

suitable areas and the fossil record. For example, climatic niche models for Calaminae and Nypoideae suggest low climatic suitability in Western Europe from the early to mid-Cenozoic, in stark contrast to the abundant *Dicolpopollis* and *Spinizonocolpites* records of the region at that time (Figure 4a,b).

Overall, there were no consistent global trends in climatically suitable areas through the Cenozoic among lineages, and our model projections were unable to explain regional-level extinctions observed in fossil distributions (Figure 4). For example, climatically suitable coastal areas for Nypoideae generally remained extensive through the

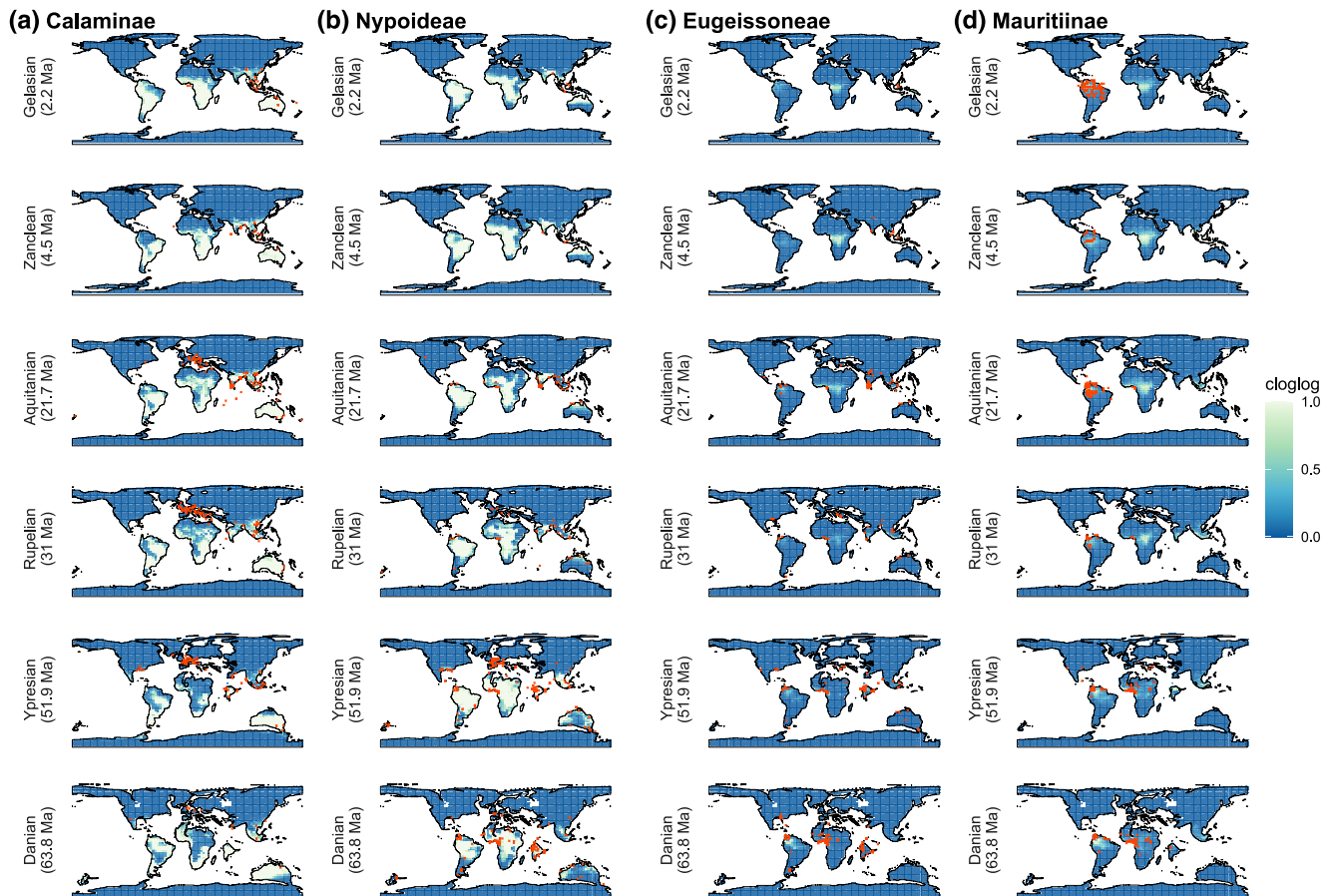


FIGURE 4 Climatic suitabilities of focal palm lineages through the Cenozoic: (a) Calaminae; (b) Nypoideae; (c) Eugeissoneae; and (d) Mauritiinae. Lighter colours represent areas with high cloglog values (high climatic suitability/probability of occurrence), whereas darker colours represent areas of low cloglog values (low climatic suitability/probability of occurrence), based on MAXENT climatic niche models with the smallest difference in area under the curve between training and test datasets. Red points represent fossil pollen occurrences for each lineage for each time epoch. Holocene and Pleistocene occurrences were plotted on the Gelasian maps

Cenozoic, although the fossil record revealed a drastic decline in the observed geographical range of the Nypoideae-like *Spinizonocolpites* (Figure 4b). *Eugeissona*-like pollen was found globally for most of the Cenozoic, but became restricted to East Asia after the Miocene despite the continued presence of suitable habitat in the Neotropics and Afrotropics (Figure 4c). Climatically suitable habitat for Mauritiinae persisted in West Africa long after Mauritiinae-like pollen taxa (*Grimsdalea* and *Mauritiidites*) disappeared from the fossil record in Africa.

4 | DISCUSSION

4.1 | Palm diversity through time

For three of the four focal palm lineages examined (Eugeissoneae, Nypoideae and Mauritiinae) (Figure 3), global pollen taxonomic diversity declined gradually throughout the Cenozoic, providing support for our hypothesis that the loss of megathermal forests might have driven declines in diversity in tropical plant groups. Global climate cooling and drying (Westerhold et al., 2020), particularly after the Eocene–Oligocene greenhouse-to-icehouse transition (c. 34 Ma), would have

led to substantial global reductions in megathermal rain forest and mangrove forest area. Tropical rain forests now cover only a small fraction of their estimated extent in the Paleocene–Eocene (Fine & Ree, 2006; Jetz & Fine, 2012; Kissling et al., 2012; Morley, 2000). Likewise, tropical mangrove forests reached their maximum extent in the Paleocene–Eocene (Morley, 2000), especially with the formation of the Saharan sea in northern Africa, which would have been connected to the Tethys Ocean from the south (Couvreur et al., 2021). However, as the tropics contracted into lower latitudes and the Tethys Ocean closed following the northward movement of the African plate and India, mangrove habitats became less extensive over time (Gee, 2001). For tropical rain forest taxa (Eugeissoneae and Mauritiinae) and tropical mangrove taxa (e.g., Nypoideae), the decline in megathermal rain forest and mangrove forest extent, respectively, might in turn have driven a decline in the species richness through elevated extinction rates (for example, owing to increased competition and the smaller area) and/or reduced origination rates (owing to a reduction in opportunities for speciation) (Jaramillo et al., 2006; Kisel et al., 2011; Lim & Marshall, 2017). The “area effect” on diversification is also consistent with the fact that geographical ranges of most focal lineages were positively correlated with their pollen taxonomic diversity (Supporting Information Table S1).

Our findings are also consistent with other lines of evidence. The Eocene–Oligocene boundary has been associated with a reduction in diversity at the local or regional scale in the tropics (e.g., fossil pollen assemblages in the Neotropics: Jaramillo et al., 2006; and palm fossil assemblages in the Afrotropics: Pan et al., 2006). Molecular phylogenies of African calamoids, which are less well represented in the fossil record, also seem to harbour a signal of an ancient extinction event at the Eocene–Oligocene boundary (Faye et al., 2016), suggesting that general Cenozoic cooling and drying trends in Africa might have been particularly harsh on many tropical lineages. The observed Cenozoic decline in tropical groups is also in stark contrast to plants adapted to arid environments, which become more successful as arid habitats became more extensive at the expense of tropical ones during the latter half of the Cenozoic (Barbolini et al., 2020; Willis & McElwain, 2014). For example, many arid-adapted plant lineages, including palms of seasonally dry habitats (Cássia-Silva et al., 2019) and various succulent groups (Arakaki et al., 2011), appear to have diversified mostly between the late Oligocene and the late Miocene.

Nevertheless, although we found that the reduction in megathermal forest habitats might have led to a decline in many tropical plant groups through the Cenozoic, regional and/or biotic factors might also play a huge role in shaping the diversity trajectories of tropical clades. For example, we found that although Calaminae became limited geographically to the Southeast Asian and African tropics, pollen taxonomic diversity of the group has increased gradually through time (Figure 3). As the most diverse palm group in Southeast Asia containing the world's largest palm genus (*Calamus*), their evolutionary success might have been promoted by the following factors: (1) the geographical complexity of Southeast Asia, with its many islands and archipelagos, which might have afforded many opportunities for allopatric speciation (Baker & Couvreur, 2012, 2013; Onstein et al., 2017); and (2) key innovations such as the evolution of modified stems and leaves that allow them to latch onto and climb adjacent plants (Figure 1; Isnard & Rowe, 2008) might have provided them with an evolutionary advantage in Southeast Asian forests (Couvreur et al., 2015), where the forest canopies are also among the highest in the world (Banin et al., 2012). Calamoid genera in Southeast Asia that are climbers are also diverse (e.g., *Plectocomia* and *Korthalsia*). Diversification rate analysis on molecular phylogenies is consistent with our analysis of the diversity of *Dicolpopollis* through time: *Daemonorops* (now regarded as a synonym of *Calamus*; Baker, 2015; Henderson, 2020) and *Calamus* have been identified as genera with higher than average diversification rates (Baker & Couvreur, 2013). African forests also harbour a large proportion of climbing species (Couvreur et al., 2015; Kissling et al., 2019), but there is only one species of Calaminae in Africa. This suggests that their current diversity patterns and biogeography might be explained by rapid diversification of the lineage in Southeast Asia, where ecological opportunities might be abundant, as opposed to Africa, where they might be contemporaneous with many other climbing taxa and experience greater interclade competition.

One potential caveat of our diversity estimates is that our diversity trends might be driven by changes in fossil sampling. Unfortunately, because our data were composed of both local stratigraphic ranges and fossil occurrences, accounting for detection probabilities by looking at the temporal distribution of fossil occurrences (e.g., Xing et al., 2014) would be inappropriate. This is because local stratigraphic ranges may be derived from multiple temporal samples at a particular site, whereas a given fossil occurrence represents only a single temporal sample at a particular locality; hence, they do not represent comparable sampling events. Sampled-in-bin and range-through diversity measures do not appear to differ greatly, suggesting that temporal sampling appears to be fairly complete for most taxa. Nonetheless, diversity in most of our palm lineages, particularly Calaminae, Eugeissoneae and Mauritiinae, strongly mirrors overall changes in the number of records through time (Figure 3b). There is a minor exception, with Mauritiinae pollen diversity decreasing through time although the number of records was high in the most recent time bins (Figure 3b). Although we caution that our recovered diversity trajectories are confounded by changes in sampling effort, the present-day species richness of some groups (Eugeissoneae and Nypoideae) is far lower than their fossil pollen diversity at any point of their evolutionary history (Table 1). This suggests that there must have been some decline in diversity even if it is unclear from our results exactly when these declines might have begun or how quickly these declines might have precipitated.

4.2 | Palaeobiogeography and climatically suitable areas through time

All focal palm lineages showed a gradual contraction in their geographical ranges from higher latitudes throughout the Cenozoic, coincident with global cooling and drying trends (Figure 2). Calaminae and Nypoideae disappeared from higher latitudes (e.g., Western Europe) during or after the Miocene, whereas aridification of the African continent between the Oligocene and the Miocene (Bogotá-Ángel et al., 2021; Couvreur et al., 2021) might explain the disappearance of predominantly rain forest groups, such as Mauritiinae and Eugeissoneae, from Africa (Figure 2). Nevertheless, although these broad biogeographical trends are well supported by our dataset, we caution on the use of some of these fossil occurrences because associated studies might not be easily verifiable (e.g., if a study does not provide a micrograph of specimens). For example, the Eocene occurrences of Mauritiinae-like pollen in North America and Europe (Figure 2) are doubtful, because Mauritiinae primarily has a Gondwanan distribution (Bogotá-Ángel et al., 2021). The Miocene record of *Nypa* in western North America (Figure 2) should not be taken at face value, because it is the only record at such a high latitude and no Nypoideae-like *Spinizonocolpites* have ever been recorded from the region. Future studies reconstructing the detailed biogeography of these lineages should take into account the uncertainties associated with outlier fossil occurrences.

In contrast to our hypothesis, the climatic niche models suggested that global climatic trends might provide only a partial explanation for observed biogeographical trajectories in the fossil record. Although all the focal palm lineages that we examined suffered continental-scale extirpations, particularly after the Miocene (e.g., Calaminae from Western Europe, Nypoideae and Eugeissoneae from Africa and Americas, and Mauritiinae from Africa; Figures 2 and 4), our climatic niche models generally project the presence of climatically suitable areas in those continents for those lineages to the present day (Figure 4, Supporting Information Figure S3).

Given that our climatic niche models are trained on the present-day species occurrence and climatic conditions, our Cenozoic model projections come with several caveats: (1) early lineages might have had a different climatic niche from extant lineages today; (2) the realized climatic range of lineages in the present day is not fully representative of the fundamental climatic range of the lineage; (3) issues with projecting niche models to non-analogue climates (Elith et al., 2010; Yates et al., 2018); and (4) inherent uncertainties in the palaeoclimatic models used. The greenhouse gas forcing component in our palaeoclimatic models are based on atmospheric CO₂ concentrations that are within the range reconstructed from geological proxies (Foster et al., 2017), but there remains significant uncertainty in CO₂ concentration reconstructions, where estimates may vary as much as 500–1,000 ppm in some time periods (Foster et al., 2017). In addition, palaeogeographical uncertainty can contribute to palaeoclimatic uncertainties through the effect of continental configuration on climate (e.g., surface albedo and ocean circulation patterns; Lunt et al., 2016). We were unable to evaluate the roles of various sources of palaeoclimatic model uncertainty owing to the high computational costs of running such palaeoclimatic models. In addition, given the restricted distribution of some of our focal lineages today (e.g., Eugeissoneae in only some parts of Southeast Asia), it is possible that the distribution of extant members of these lineages might reflect only a subset of the potential climatic range that they could occupy. Our models do not extrapolate beyond the climatic range of each lineage (Supporting Information Figures S5–S8); hence, the presence of fossil occurrences for some of focal lineages (Calaminae and Nypoideae) outside projected climatically suitable areas raises the possibility that at least some of our focal palm lineages were able to survive in a broader range of climatic conditions than those available to them in the present.

Nonetheless, our results suggest that short-term climatic perturbations or indirect biotic and abiotic factors might have a greater influence on extinctions at the regional scale. For example, the extirpation of Mauritiinae might be driven by the loss of wetland habitats in western Africa following Miocene aridification, a factor that palaeoclimate models might not be able to capture fully. In contrast, the continued presence of Mauritiinae taxa, such as *Mauritia*, in the Neotropics might have been facilitated by suitable regional climatic conditions that emerged during the Neogene that were related to the interception of wet air masses from the Intertropical Convergence Zone (ITCZ) by the Andes orographic barrier and

by the extensive wetlands associated with the Andean orogeny (Bogotá-Ángel et al., 2021; Hoorn et al., 2010; Rull, 1998).

The extirpation of Eugeissoneae from the Afrotropics and Neotropics might reflect an inability of the group to compete and diversify in those rain forests through time (Baker & Couvreur, 2013). Even in Southeast Asia, where they still persist, Eugeissoneae are not diverse or regionally abundant, and unlike some calamoid groups in Southeast Asia, species of Eugeissoneae do not possess adaptations for climbing. In contrast, the disappearance of Nypoideae from Neotropical and African mangroves from the Miocene onwards does not appear to be attributable to competition. Mangrove habitats in the Neotropics and western Africa do not appear to be saturated ecologically (Ricklefs & Latham, 1993), suggesting that the absence of *Nypa* is not likely to be attributable to competitive exclusion from ecologically similar species. It has been suggested that Neogene drying trends might have led to the extinction of *Nypa* in the Neotropics (Ricklefs & Latham, 1993), but *Nypa* has been introduced to western Africa and some parts of Central America, where it appears to naturalize readily (Duke, 1991). This confirms the presence of suitable environmental conditions outside of tropical Asia in the present day (Supporting Information Figure S4). Taken together, possible factors shaping their current distribution might include: (1) severe and short-lived climatic perturbations; (2) changes in sea level (such as the terminal Eocene sea-level fall, which would have pushed the coastline below the shelf break, resulting in the loss of mangrove habitat; Morley, 2000); and/or (3) the isolation of mangrove biogeographical regions from each other following the closure of the Tethys (Descombes et al., 2018; Ricklefs & Latham, 1993).

4.3 | Conclusions

Our study shows that the loss of megathermal rain forests and mangroves during the later half of the Cenozoic has led to global declines in diversity and range contractions in at least some tropical groups. We also find that fossil occurrences of our focal palm lineages often extend beyond model projections based on the present-day climatic niche of extant taxa, suggesting that our focal palm lineages might have had broader climatic ranges in the past. Thus, the non-analogue “hothouse” world of the Paleocene–Eocene might have promoted a much broader distribution and diversification of tropical lineages. Nevertheless, observed regional extinctions of our palm lineages even from regions with suitable climates suggests that the role of global climatic trends in shaping the regional trajectories of tropical lineages is likely to be context dependent and will be mediated by local or regional abiotic and biotic factors. Short-term regional-scale environmental perturbations might be important for understanding extinction dynamics, because such perturbations might trigger extinctions or changes in vegetation composition that might be hard to reverse (e.g., tipping points) even if prior climatic conditions are restored. Moving forward, we suggest that further research into why different tropical lineages respond so differently to global change will

provide greater insights into the drivers shaping modern-day patterns of diversity (e.g., taxonomic composition and species richness) among the different tropical realms of the world.

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DATA AVAILABILITY STATEMENT

Data (including the fossil pollen dataset) and code are publicly available in a Dryad digital repository (<https://doi.org/10.5061/dryad.9cnp5hqhx>).

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BIOSKETCH

Jun Ying Lim's laboratory integrates various fields, such as biogeography, macroevolution, geological history and macroecology, to gain a better understanding of the diversity of plants in space and time.

Huasheng Huang is interested in the past vegetation, climate and environment in Southeast Asia, China and the Mediterranean and in the evolutionary history and global biogeography of plants.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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