Plant turnover in response to climate change in the Cenozoic: Palynological insights from Myanmar, Southeast Asia and beyond

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Publication date
2021

Citation for published version (APA):
Diversity declines and range contraction of palms through the Cenozoic

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In preparation

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ABSTRACT

Tropical forests are among the most ancient and diverse biomes on the planet, but their current extent has greatly reduced through the Cenozoic. The decline in tropical forests biomes may cause extinction and range contractions in many tropical plant clades, but has rarely been tested directly at the global scale using the fossil record. To evaluate the role of Cenozoic climate change on the biogeographic and macroevolutionary dynamics, we compiled fossil pollen records for four extant lineages of palm (Arecaceae), each with very different ecologies and modern-day species richness. For each lineage, we estimated their diversity and biogeographic ranges through time, and projected the extent and distribution of climatically suitable habitat through the Cenozoic using climatic niche models. Most lineages showed a general decline in diversity and geographic range in concert with the contraction of tropical rainforests after the Eocene, but the present-day biogeographic distribution of examined lineages was only largely achieved much later after the Miocene. Palms of the subtribe Calaminae, on the other hand, increased in diversity through time while declining in range, their success perhaps driven by evolutionary innovations that allowed them to flourish in the Asian tropics. Climatic niche models underestimate the past fossil ranges of all lineages examined, suggesting that past lineages may have occupied a much broader range of climatic conditions. However, the disappearance of certain clades from certain biogeographic areas sometimes occurs despite the presence of suitable climates. Our findings show that tropical clades may have had very different responses to the environmental changes through the Cenozoic, and that a better understanding of non-climatic and regional factors is crucial to understanding the biogeographic and diversification histories of many tropical clades today.
6.1 | INTRODUCTION

Tropical everwet biomes are among the oldest biomes on earth. Recognizably modern tropical biomes originated sometime between the mid-Cretaceous to Paleocene (Couvreur and Baker, 2013; Eiserhardt et al., 2017; Morley, 2000), reaching their maximum extent in the Eocene (Morley, 2000; Willis and McElwain, 2014). However, subsequent global cooling throughout the rest of the Cenozoic (Zachos et al., 2001) is concurrent with a gradual reduction in tropical forest area to their current distribution today (Willis and McElwain, 2014).

The expansion and subsequent contraction in extent of tropical habitats (e.g., forests, mangroves) through the Cenozoic is potentially an important historical backdrop for tropical lineages, but few studies have explored its macroevolutionary and biogeographic implications on tropical plant groups (Kissling et al., 2012). In particular, we hypothesized that the decline in geographic extent of tropical habitats/biomes will result in reduced diversification rates (decreased speciation rates and/or increased extinction rates) in tropical clades (Condamine et al., 2013; Fine and Ree, 2006; Jetz and Fine, 2012; Lim and Marshall, 2017; Shiono et al., 2018). This is because larger areas may support a greater number of individuals and thus species (Storch et al., 2018), promote speciation by providing opportunities for geographic isolation across the landscape (Kisel et al., 2011), or promote ecological speciation by possessing greater environmental heterogeneity or a greater diversity of habitats (Kisel et al., 2011; Stein et al., 2014). In addition, we hypothesize that changes in the extent and connectivity within tropical biomes will lead to range contractions or disjunctions, and thus have a profound influence on how modern biogeographic patterns were achieved (Donoghue and Edwards, 2014; Mairal et al., 2017).

The fossil record provides direct information on the diversity and biogeography of lineages through time (Crisp and Cook, 2011; Quental and Marshall, 2010) and may thus shed insights on the impact on Cenozoic environmental changes on plant lineages. Nevertheless, the incompleteness of the fossil record in space and time (Xing et al., 2016) may mean that such information is limited to groups with good fossil records (e.g., Meseguer et al., 2015, 2018). This has limited inferences of diversification (Condamine et al., 2013; Couvreur et al., 2011; Rabosky, 2014) and biogeographic histories (Eiserhardt et al., 2017; Matzke, 2014; Ree and Smith, 2008; Ronquist and Sanmartín, 2001) of extant groups from molecular phylogenies, but there is significant uncertainty over whether, and
how well, diversification or biogeographic histories may be reliably recovered from the temporal information inherent in molecular phylogenies alone (Louca and Pennell, 2020; Quental and Marshall, 2011; but see Helms terribly et al., 2020).

Table 6.1. Calamoid and nypoid fossil pollen lineages and their modern affinities. Species diversities for each lineage were obtained from World Checklist of Selected Plant Families on 23 June 2020. Calaminae, Eugeissoneae and Mauritiinae belong to subfamily Calamoideae. Genera Daemonorops, Ceratolobus, Retispatha and Pogonotium have been merged in the genus Calamus (Baker, 2015; Henderson, 2020).

<table>
<thead>
<tr>
<th>Lineage</th>
<th>Extant genera (no. of species)</th>
<th>Hypothesized fossil taxa</th>
<th>Characters and references supporting affinity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Subtribe</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Calaminae (tribe</td>
<td><em>Calamus</em> (c. 500)</td>
<td><em>Dicolpopollis</em></td>
<td>Disulcate (Harley and Morley, 1995)</td>
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<tr>
<td>Calameae)</td>
<td></td>
<td></td>
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<tr>
<td>Tribe</td>
<td><em>Eugeissona</em> (6)</td>
<td><em>Longapertites, Quillopollenites</em></td>
<td>Extended monosulcate with thick wall (Morley, 2000; Phadtare and Kulkarni, 1984)</td>
</tr>
<tr>
<td>Eugeissoneae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Subtribe</td>
<td><em>Mauritia</em> (2),</td>
<td><em>Mauritiidites, Grimsdalea, Echidiporites</em></td>
<td>Exine with indentations; monosulcate (Bogotá-Ángel et al., 2021; Muller, 1981; van Hoeken-Klinkenberg, 1964)</td>
</tr>
<tr>
<td>Mauritiinae (tribe</td>
<td><em>Mauritiella</em> (4),</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lepidocaryae)</td>
<td><em>Lepidocaryum</em> (1)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Subfamily</td>
<td><em>Nypa</em> (1)</td>
<td><em>Spinizonocol-pites</em></td>
<td>Zonasulcate, wall finely reticulate covered by scattered baculate or echinate spines (Frederiksen, 1980; Morley, 2000; Muller, 1968)</td>
</tr>
<tr>
<td>Nypoideae</td>
<td></td>
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</tr>
</tbody>
</table>

Here, to shed much-needed light on the role of Cenozoic environmental change on the diversification and historical biogeography of tropical plants, we collated information on the exceptional fossil records of four distinct palms (Arecales) lineages, and track the diversity and biogeography of these lineages through time (Table 6.1, Fig. 6.1). We then evaluate the degree to which their biogeographic histories may be explained by changes in
Fig. 6.1. Focal palm lineages and pollen of extant and extinct representatives. (A-C) Calaminae. (A) *Calamus longipinna* K.Schum. et Lauterb., showing the cirri, extensions of the leaf that possess hook-like structures that allow the plants to attach themselves to neighbouring vegetation. (B) *Dicolpopollis kalewensis* Potonié. (C) *Calamus viminalis* Willd. (D-F) Nypoideae. (D) *Nypa fruticans* Wurmb (Nypoideae) is a common mangrove species in many parts of the Indo-Pacific and sole representative of its subfamily. It possesses unique creeping, dichotomizing stems that allow it to grow in the soft sediments, often forming large monodominant stands (Tomlinson 1986). (E) *Spinizonocolpites echinatus*. (F) *Nypa fruticans*. (G-I) Eugeissoneae. (G) *Eugeissona utilis* Becc. The tribe Eugeissoneae consists of only genus, *Eugeissona* Griff., a group of tree palms restricted to Borneo and the Malay Peninsula. They tend to grow in large colonies. (H) *Longapertites retipilatus* Kar. (I) *Eugeissona tristis* Griff. (J-L) Mauritiinae. (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 commonest trees in the Amazon. (K) *Mauritiidites franciscoi* (van der Hammen) van Hoeken-Klinkenberg. (L) *Mauritia flexuosa*. (B) (H) are from the late Eocene Central Myanmar Basin (Myanmar), produced with permission from Huang et al. (2020).
(E) is from the Paleocene Barmer Basin (India), produced with permission from Shalini Parmar and Vandana Prasad. (K) is from the Miocene Apaporis (Colombia), produced with permission from Bogotá-Ángel et al. (2021). (C) (F) (I) (L) are modern pollen, produced with permission from Dransfield et al. (2008).

the distribution of their preferred climates through the Cenozoic. Palms are regarded as a model group for tropical rainforest evolution (Baker and Dransfield, 2016; Couvreur and Baker, 2013), and are well-represented in the fossil record (Harley, 2006), where they are one of the oldest recognizable modern angiosperm families (Dransfield et al., 2008). Due 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 thus often used as paleoclimatic indicators (Reichgelt et al., 2018). The fossil record of palms will thus provide critical insights into how tropical clades have responded to changes in tropical forest extent and connectivity through the Cenozoic.

6.2 | MATERIALS AND METHODS

6.2.1 | Palm lineages

We focused on four palm lineages that are characterized by rich and abundant fossil pollen records that are easily identifiable with great confidence in the fossil record: three from the subfamily Calamoideae (Mauritiinae, Calaminae, Eugeissoneae) and one from the subfamily Nypoideae (represented by the monotypic genus *Nypa*) (Table 6.1, Fig. 6.1). Phylogenetic placement of fossil pollen form taxa for each palm lineage is well-supported by various morphological studies (Table 6.1; Text S6.1 in Supporting Information (SI)). However, we note that the connection between *Longapertites* and *Eugeissona* is not as straightforward as the other focal lineages in this study. A discussion about the uncertainty of the hypothesized affinity of *Longapertites* to *Eugeissona*, and its impact on the results on downstream analyses is discussed in depth in Text S6.1 in SI. Modern day relatives for each of the focal palm lineages also vary in extant richness and ecology (Table 6.1, Fig. 6.1) and paleobiogeographic patterns for these four groups are vastly different from their present-day distributions (Fig. 6.2; Bogotá-Ángel et al., 2021; Dransfield et al., 2008).
Fig. 6.2. Distribution of fossil occurrences through time. Paleocoordinates for each occurrence and continental configurations were obtained using Geotech paleoplate 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 paleogeography at the middle of the first stage of each epoch. Holocene (<11.6 Kya) records are plotted on the Gelasian map. Occurrences that stratigraphically traverse more than one epoch are plotted on multiple maps.

6.2.2 | Fossil dataset

We compiled a global dataset of fossil occurrences as well as local first and last appearance datums (FAD and LADs, respectively) for fossil palm taxa and their putative modern relatives (Table 6.1) across fossil localities for the Cenozoic (Dataset S6.1 in SI). 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. Relevant studies were identified using a taxon search on Palynodata, a comprehensive database of the palynological literature (Palynodata Inc. and White, 2008) which we supplemented with references from taxon-focused reviews of the palm fossil record (e.g., Bogotá-Ángel et al., 2021; Dransfield et al., 2008; Harley, 2006). For each fossil occurrence, FAD, and LAD, we recorded the stratigraphic age/uncertainty, as well as the geographic coordinates of the reported fossil locality. Geographic coordinates were manually georeferenced when they were not provided by the source. 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 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” as those from the peer-reviewed literature but without images of specimens, and “low confidence” as those recorded in the Palynodata database without literature access.

6.2.3  |  **Fossil diversity through time**

We quantified trends in taxonomic richness of each palm lineage (Calaminae, Eugeissoneae, Mauritiinae and Nypoideae) through the Cenozoic using the compiled fossil pollen data. We treated each fossil species as separate taxa in our analysis. The three varieties of *Mauritidiites franciscoi* were treated as separate taxa as they are morphologically distinct (van der Hammen and Garcia de Mutis, 1966). Records of *M. franciscoi* that were not identified to variety were omitted from the analysis. We additionally omitted *Longapertites dupliclavatus* from our analysis (3 occurrences in our dataset) as their proposed affinity to Eugeissoneae is doubtful on morphological grounds (Text S6.1 in SI).

Taxonomic richness through time was estimated in two ways: (1) sampled-in-bin diversity and (2) range-through diversity. Sampled-in-bin species richness was quantified by counting the number of unique fossil taxa that are recorded within a given time interval (i.e., bin), whereas range-through species richness additionally counts species that are not in the focal bin itself, but have been recorded in bins that are older and younger than the focal time bin. The latter approach assumes that a taxon must always exist 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. In so doing, the range-through approach controls for incomplete sampling in the fossil record to some degree. For taxon records that are local stratigraphic ranges (FAD and LAD), we assumed the given taxon was present in all time bins that are traversed by the stratigraphic range for both methods.

For both approaches, we used six equal-interval, 10 million-year time bins that encompass the past 60 million years, as opposed to epoch-based time bins so estimated diversities for different time bins may be directly compared. We did not perform more sophisticated approaches to control for incomplete sampling of occurrences (e.g., Kocsis et al., 2019) as our data comprised both stratigraphic ranges and occurrences, which possess different statistical properties. Stratigraphic ranges are not occurrences per se and cannot be used to estimate detection probabilities. Combining both occurrences and stratigraphic ranges is appropriate for our diversity metrics as they are both not model based and makes 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 as well as the bounds of stratigraphic ranges (FADs and LADs), we additionally used a randomization approach. For fossil occurrences, the ages for each fossil were randomly drawn from a uniform distribution within the minimum and maximum age uncertainty of the fossil occurrence. For example, a fossil occurrence in a “Eocene” fossil locality would be assigned an age between the recognized bounds of the geological epoch: 56 and 33.9 Mya and counted in whichever 10-million year time bin the randomized age fell within. Similarly, age uncertainty for FADs and LADs was accommodated by assuming a randomly sampled age within the recognized bounds of the time interval they are in. For example, if the first appearance of a fossil taxon is in the Paleocene and last appearance of a fossil taxon is in the Eocene at a particular locality, then that taxon will be assumed to occur in all 10-million year time bins between (66-56) and (56-33.9) Mya for that record. Under 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. 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.
6.2.4 | Species occurrence data

Species occurrence records for extant members of each palm lineage (Table 6.1) were obtained from the Global Biodiversity Information Facility (GBIF, https://www.gbif.org) (https://doi.org/10.15468/dl.prgnvt) on 16 June 2020. Occurrence records with potentially erroneous geographic coordinates were first identified using the “clean_coordinates” function of the “CoordinateCleaner” R package v2.0-15 (Zizka et al., 2019) under default parameters and omitted. This included records that were 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. Geographic outliers were further identified and removed by cross-validating all occurrence points against the World Checklist of Palms (Govaerts et al., 2015), 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 geographic range of each lineage.

6.2.5 | Environmental niche modeling

Six bioclimatic variables for the present day (i.e., WorldClim) were used as predictor variables: mean annual temperature, minimum temperature of coldest quarter, temperature seasonality, annual precipitation, precipitation of driest quarter and precipitation seasonality (Fick and 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 arc minutes.

Environmental niche modeling was performed for each lineage using Maxent (Elith et al., 2011) as implemented by the “ENMevaluate” function of the “ENMeval” R package v.0.3.0 (Muscarella et al., 2014). We evaluated multiple candidate models with a range of feature class combinations (i.e., “L”, “LQ”, “LQH”, “LQHP”, “LQHPT”) and 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). Background points (n = 100,000) were
randomly sampled across all terrestrial areas (except Antarctica) globally. Species occurrence points for each lineage were thinned so only one occurrence point for each raster grid cell was used, to reduce the influence of spatial autocorrelation on model parameter estimation (Aiello-Lammens et al., 2015). Model selection was performed by identifying models with the lowest AICc scores and lowest average AUC difference ("avgAUCdiff") between training and testing data (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). As projected climatic suitabilities using cross-validated models with the lowest "avgAUCdiff" between training and testing datasets were generally similar to models based on the lowest AICc, we present only the results from models with the lowest "avgAUCdiff".

6.2.6 Paleoprojections of climatically suitable area

To project climatically suitable areas for the various clades through the Cenozoic, we used the same set of bioclimatic variables as for the modern projections, but with paleoclimate fields in place of modern climate observations from Worldclim. The paleoclimate data fields are derived from model simulations using the UK Met Office coupled ocean-atmosphere general circulation model HadCM3L (version HadCM3BL-M2.1aD; Valdes et al., 2017) applied to the first stage of each epoch: Danian (Paleocene, 63.8 Mya), Ypresian (Eocene, 51.9 Mya), Rupelian (Oligocene 31.0 Mya), Aquitanian (Miocene 21.7 Mya), Zanclean (early Pliocene, 4.5 Mya) and Gelasian (early Pleistocene, 2.2 Mya). The model simulations are identical to those described in Farnsworth et al. (2019). The model resolution is 3.75 degrees longitude by 2.5 degrees latitude. Atmospheric CO₂ concentration used for model simulations for each stage are 560 ppm, 1120 ppm, 560 ppm, 400 ppm, 400 ppm and 280 ppm, respectively, and are within the atmospheric CO₂ concentration range estimated from geological proxies (Foster et al., 2017). In addition, we included a global pre-Industrial scenario (280 ppm) under modern paleogeographies, for comparison with the Worldclim climatologies. "cloglog" values for each raster cell under each paleoclimatic scenario were calculated.
6.3 | RESULTS

6.3.1 | Fossil pollen record of focal palm lineages

We focused on four focal palm lineages: Calaminae, Nypoideae, Eugeissoneae and Mauritiinae (Fig. 6.1). Extant species of Calaminae, Eugeissoneae and Mauritiinae are generally tropical forest palms, whereas the sole extant species of Nypoideae, *Nypa fruticans*, is a common component of mangrove forests in tropical Asia (Fig. 6.1). We collated all pollen fossil occurrences and stratigraphic records (hereafter “records”) for all fossil taxa thought to represent past lineages for these four afore-mentioned focal palm clades (Table 6.1; Dataset S6.1 in SI). This was done with a semi-systematic search of the literature, including a recent review of the Mauritiinae fossil record (Bogotá-Ángel et al., 2021). Fossil affinities for each taxa were reviewed, and some potentially fossil taxa of dubious affinity to our focal lineages were omitted (see Text S6.1 in SI). In general, affinities for each fossil taxon to modern-day groups are well-supported by the presence of shared characteristic pollen morphological features (Table 6.1), but the connection between *Longapertites* and extant *Eugeissoneae* is not as straightforward as the other fossil taxa to their corresponding modern clades. The implications of an alternative interpretation of the fossil record of *Longapertites* and its connection to modern palm lineages on downstream analyses is discussed in detail in Text S6.1 in SI. Nevertheless, we acknowledge that even when supported by morphological evidence, all fossil taxon assignments should be considered hypotheses.

Our dataset consisted of 331 records for Calaminae (fossil records of extant genus *Calamus* and the extinct taxon *Dicolpopollis*), 366 for Eugeissoneae (*Eugeissona* and extinct taxa *Quilonipollenites* and *Longapertites*), 520 records for Nypoideae (*Nypa* and the extinct taxon *Spinizonocolpites*) and 529 records for Mauritiinae (fossils of extant genera *Mauritia* and *Mauritiella*, and extinct taxa *Mauritiidites*, *Echidiporites* and *Grimsdalea*) (Dataset S6.1).

6.3.2 | Diversity through time

We quantified taxonomic diversity of pollen taxa for each lineage in six ten-million year time intervals (between 60 Mya to the present) with two metrics: (1) “sampled-in-bin”
diversity, a count of unique fossil taxa in each time bin, and (2) “range-through” diversity, which additional accounts for temporal gaps in the appearance of fossil taxa. Taxonomic diversity of Eugeissoneae-like and Nypoideae-like fossil pollen showed strong declines through the Cenozoic (Fig. 6.3B-C), a pattern that was stronger when restricting our analysis to sources that we classified as “high confidence” (Fig. S6.1 in SI). For Mauritiinae, taxonomic diversity of putative fossil pollen appears to be fairly stable through the Cenozoic (Fig. 6.3D), but similarly showed a decline when only considering literature records of “high confidence” (Fig. S6.1 in SI). In contrast to the three other lineages, diversity of Calaminae-type fossil pollen increased gradually through the early Cenozoic (Fig. 6.3A, Fig. S6.1 in SI). 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 (Fig. 6.3).

6.3.3 | Paleobiogeography and climatically suitable areas through time

As expected from our hypothesis, we found that all focal pollen lineages examined showed a much broader distribution in the early Cenozoic than their modern-day relatives in the present-day. Most clades exhibited range contractions through the early to mid-Cenozoic, and underwent continental-scale extirpations after the Miocene (Fig. 6.2). Calaminae-like *Dicolpopollis* pollen was once abundant in Eurasia in the early to mid-Cenozoic, but disappeared from the region after the Miocene (Fig. 6.2). It is not until the Pliocene when *Calamus* pollen appears on the African continent, where one extant species of Calamus exists today. Nypoideae-like *Spinizocolpites* and Eugeissoneae-like *Longapertites* and *Quilonipollenites* pollen were essentially pantropical through the Paleogene to Miocene (Fig. 6.2), but both groups become restricted to Southeast (SE) 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. Observed contractions in geographic range in all focal groups do not appear to be due to changes in fossilization potential through time (Text S6.2 in SI).
Fig. 6.3. **Diversity of fossil pollen of focal palm lineages through the Cenozoic.** Diversity was calculated using six equal-interval 10-million year bins (alternating grey and white bands in background). Stratigraphic uncertainty of fossil occurrences and the boundaries of stratigraphic ranges (FADs and LADs) of fossil taxa was 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, whereas colored
shaded areas represent the minimum and maximum sampled-in-bin (yellow) and range-through (dark-green) species richness.

To test if the observed changes in the geographic ranges of the fossil record may be explained by changes in the extent of climatic suitable areas for each focal lineage, we fitted Maxent species distribution models to species occurrences of extant taxa from each focal lineage separately. We then used these models to predict the distribution and extent of climatically suitable areas through the Cenozoic using paleoclimatic maps for each epoch of the Cenozoic: Paleocene (63.8 Mya), Eocene (51.9 Mya), Oligocene (31 Mya), Miocene (21.7 Mya), Pliocene (4.5 Mya) and Pleistocene (2.2 Mya). Our projections of suitable climate based on the present-day occurrences of extant species were broadly congruent with the geographic distribution of fossil occurrences through the Cenozoic (Fig. 6.4). Climatically suitable areas for Calaminae through the Cenozoic decreased gradually in India and the Nearctic, consistent with the disappearance of Dicolpopollis from the Nearctic and India (Fig. 6.4A). Similarly, climatically suitable areas for Nypoideae were projected as far south as the south of Australia in the Eocene where Nypoideae-like Spinizocolpites has been found, but generally contracted further north in Australasia after the Eocene, consistent with the absence of Spinizocolpites thereafter (Fig. 6.4B). Climatically suitable areas for Eugeissoneae (Fig. 6.4C) and Mauritiinae (Fig. 6.4D) were present in all modern tropical regions, but were generally limited and constant in extent through the Cenozoic. However, there were minor disagreements between the distribution of climatically suitable areas and the fossil record. Specifically, climatic niche models for Calaminae and Nypoideae suggest low climatic suitability in Western Europe from the early to mid Cenozoic, in stark contrast with the abundant Dicolpopollis and Spinizocolpites records of the region at that time (Fig. 6.4A-B).

Overall, there were no clear and consistent global trends in climatically suitable areas through the Cenozoic among lineages, and our model projections were unable to explain regionally-level extinctions observed in fossil distributions (Fig. 6.4). For example, climatically suitable coastal areas for Nypoideae generally remain extensive through the Cenozoic, even as the fossil record reveals a drastic decline in the observed geographic range of the Nypoideae-like Spinizocolpites (Fig. 6.4B). 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 (Fig.
6.4C). Climatically suitable habitat for Mauritiinae persists in West Africa long after Mauritiinae-like pollen taxa (*Grimsdalea* and *Mauritiidites*) disappear from the fossil record in Africa.
Fig. 6.4. Climatic suitabilities of focal palm lineages through the Cenozoic. (A) Calaminae. (B) Nypoideae. (C) Eugeissoneae. (D) Mauritiinae. Lighter colors represent areas with high cloglog values (high climatic suitability/probability of occurrence) whereas darker colors represent areas of low cloglog values (low climatic suitability/probability of occurrence), based on Maxent climatic niche models with the smallest difference in AUC 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 both Pre-industrial and Gelasian maps.

6.4 | DISCUSSION

Tropical rainforests in the present-day cover only 38% of their estimated extent in the Eocene (Kissling et al., 2012). Global climate since the Eocene–Oligocene greenhouse to icehouse transition (c. 33.9 Ma) is marked by cooling and drying, which drove the disappearance of tropical rainforest climates and the shrinking of rainforest areas while leading to the expansion of arid habitats such as grasslands (Willis and McElwain, 2014). Our findings support the hypothesis that the loss of tropical areas may have had a profound impact on the macroevolutionary dynamics and biogeographic history of tropical plant groups. Using the fossil record of four focal palm clades, we show that the that the decline in extent of tropical areas through the Cenozoic, including habitats such as rainforests and mangroves, is not only associated with the dramatic declines in geographic range in all our focal groups (Fig. 6.2), but also diversity declines in Eugeissoneae, Nypoideae and Mauritiinae (Fig. 6.3).

The Eocene–Oligocene boundary has been associated with the decline in diversity in tropical pollen assemblages (e.g., in the Neotropics; Jaramillo et al., 2006; palms in the Afrotropics; Pan et al., 2006). However, our results suggest that while the Eocene–Oligocene transition is undoubtedly an important inflection point in the history of tropical biomes, the continued global cooling and aridification that followed through to the Miocene (Zachos et al., 2001) had a cumulative effect on the biogeography and diversity of lineages. For example, the modern biogeographic distribution of the palm lineages examined was only achieved after the Miocene following continental-scale extirpations (e.g., Calaminae from Western Europe, Nypoideae and Eugeissoneae from Africa and Americas, Mauritiinae from Africa) (Figs. 6.2, 6.4). The disappearance of predominantly rainforest groups such as Mauritiinae and Eugeissoneae from Africa may be linked to continental
aridification between the Oligocene to the Miocene (Couvreur et al., 2021) which may have promoted regional extinction or reduced opportunities for speciation as tropical forests contracted in Africa.

Consistent with our findings, molecular phylogenies of other African calamoids, which are less well-represented in the fossil record, seem to harbor a signal of an ancient extinction event at the Eocene–Oligocene boundary (Faye et al., 2016) suggesting that general Cenozoic cooling and drying trends on Africa may have been particularly harsh on many tropical lineages. Palms of drier habitats appear to show a consistent, reversed pattern of diversification. While palm lineages of seasonally dry habitats may have colonized these habitats since the Paleocene, most extant clades did not diversify until after the late Oligocene (Cássia-Silva et al., 2019). For mangroves-specialists Nypoideae, the decline in diversity and geographic range were in line with major changes in paleoextent in mangrove habitats through the Cenozoic (Fig. 6.3; Gee, 2001). Major floristic elements of mangrove habitats first originated in the Late Cretaceous in the Tethys ocean and connected water bodies (Descombes et al., 2018; Ellison et al., 1999; Tomlinson, 1986). Mangrove habitats probably reached their maximum extent in the Paleocene and 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, mangrove habitats became less extensive over time.

Nevertheless, while the decline in tropical forest areas was probably an important global driver, our climatic niche models suggest that climate only played a partial role in the historical biogeography and diversity of our palm clades. While Calaminae became geographically limited to the SE Asian and African tropics, their diversity has gradually increased through time (Fig. 6.3), and they are now the most diverse palm group in SE Asia (c. 500 species). Their evolutionary success may have been promoted by (1) the geographic complexity of SE Asia, with its many islands and archipelagos, may have afforded many opportunities for allopatric speciation (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 (Fig. 6.1; Couvreur et al., 2015; Isnard and Rowe, 2008) may have provided them an evolutionary advantage in SE Asian forests (Couvreur et al., 2015), where the forest canopies are also among the highest in the world (Banin et al., 2012). Most other calamoid genera in SE Asia are climbers and are also diverse (e.g., Plectocomia, Salacca...
and Korthalsia). Diversification rate analysis on molecular phylogenies is consistent with our analysis of the diversity of Dicolytopollis fossils 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 and Couvreur, 2013b). African forests also harbor a large proportion of climbing species (Couvreur and Baker, 2013; Kissling et al., 2019), but there is only one species of Calaminae in Africa. This suggests that their current diversity patterns and biogeography may be explained by rapid diversification of the lineage in SE Asia where ecological opportunities may be abundant, as opposed to Africa where they may be contemporaneous with many other climbing taxa and thus experience greater interclade competition. This may also explain why Calaminae is not more diverse in the Afrotropics, even though there is climatically suitable habitat throughout most of the Cenozoic (Fig. 6.4A).

The importance of non-climatic factors is also demonstrated by the relatively species-poor Eugeissona (sole genus in Eugeissoneae), now limited to the SE Asian tropics. Diversification rate analyses based on molecular phylogenies suggest that Eugeissona has a low diversification rate relative to the background rate of the palm family (Baker and Couvreur, 2013b). Their current distribution is probably a product of regional extinction outside of the Asian tropics, but climatically suitable habitat based on their present-day occurrences in SE Asia was available in Africa and South America throughout the Cenozoic (Fig. 6.4). While it is possible that Eugeissoneae lineages in the past may have had much broader climatic preferences than those of extant species, the low diversity of Eugeissoneae probably reflects an inability to compete and diversify in SE Asian forests. Eugeissona do not possess adaptations for climbing like many other calamoid groups. Climbing palms are much more abundant in Indotropical forests compared to the Neotropics (Kissling et al., 2019; Muscarella et al., 2020). Furthermore, most Eugeissona species appear to grow in marginal habitats such as steep cliffs (Dransfield et al., 2008), which may partly explain their restricted distribution today (Morley, 2018a).

While Nypoideae are now confirmed to the Indotropics, climatic niche models confirm the presence of suitable environmental conditions outside of the region through the Cenozoic (Fig. 6.4). However, they become noticeably absent from the Neotropical and African mangroves from the Miocene onwards. Mangrove habitats in the Neotropics and W. Africa do not appear to be ecologically saturated (Latham and Ricklefs, 1993), suggesting that the absence of Nypa is not likely due to competitive exclusion from
ecological similar species. Furthermore, *Nypa* has been introduced to West Africa and some parts of Central America, where they appear to naturalize readily (Dransfield et al., 2008; Duke, 1991). This confirms the presence of suitable environmental conditions outside of the Indotropics in the present day (Fig. S6.2 in SI), consistent with the predictions of our climatic model (Fig. 6.4). Range contraction and regional extinction in *Nypa* has been argued to be due to the more pronounced Miocene drying trends in Africa and the Caribbean (Latham and Ricklefs, 1993), but projections of our climatic model suggest the presence of climatically suitable areas on the western coast of Africa and in the Neotropics throughout the Cenozoic. One possibility is that particularly severe and short-lived climatic perturbations (e.g., Middle Miocene climatic optimum) or indirect factors (e.g., Eocene sea-level fall and reduction in shelf area; Morley, 2000), coupled with the isolation of mangrove biogeographic regions following the closure of the Tethys (refugium hypothesis; Latham and Ricklefs, 1993) may have resulted in and maintained their current distribution.

Lastly, Mauritiinae disappear from the African fossil record after the Miocene, even though our climatic niche models predict the continued presence of suitable climates (Fig. 6.4). We hypothesize their extirpation form the continent may be driven by the loss of wetland habitats in West Africa following Miocene aridification, a factor which paleoclimate models are not able to capture. The persistence of Mauritiinae taxa like *Mauritia* in the Neotropics may have been facilitated by the formation of extensive wetlands associated with the Andean orogeny during the Neogene (Bogotá-Ángel et al., 2021; Hoorn et al., 2010; Rull, 1998).

Overall, our study shows that while the “collapse” of the tropics through the Cenozoic have led to the decline of some tropical groups, the regional trajectories of tropical lineages will depend on the regional abiotic and biotic context or “evolutionary arenas” (Nürk et al., 2020). A better understanding of why different tropical lineages respond differently to the global climatic trends of the Cenozoic may help explain differences in the diversity and composition between the different tropical realms of the world.

### 6.5 ACKNOWLEDGEMENTS

J.Y.L is supported by the Nanyang Technological University Presidential Postdoctoral Fellowship. H.H. acknowledges the China Scholarship Council grant (CSC 201604910677) and the University of Amsterdam. W.D.K. acknowledges funding from the Netherlands
organization for Scientific Research (824.15.007) and the University of Amsterdam (via a starting grant and through the Faculty Research Cluster “Global Ecology”). We thank Daniel Latorre for reviewing an early draft of the manuscript; Shalini Parmar and Vandana Prasad for kindly providing Fig. 6.1E.

6.6 | SUPPORTING INFORMATION

Supporting Information can be found online in figshare doi: 10.21942/uva.14308142.