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

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GENERAL DISCUSSION AND SYNTHESIS
7.1 | OVERVIEW

Plant fossil proxies (macro- and micro-) are rarely used in Myanmar except for only two studies using fossil woods from the late middle Eocene Pondaung Formation in the Central Myanmar Basin (CMB) (Licht et al., 2013, 2014a), and a study using tree-rings of teak to reconstruct the climate in the past two centuries of southern Myanmar (Zaw Zaw et al., 2020). Other studies on past climate (e.g., Licht et al., 2014b, 2015) and environment (e.g., Gough et al., 2020; Licht et al., 2019; Westerweel et al., 2020) made use of proxies such as the sedimentary record, gastropods and mammal fossils.

The first theme (chapters 2-4) of my thesis is formed by the palynological study in the late Eocene CMB, which was carried out in the Myanmar Paleoclimate and Geodynamics Research group (MyaPGR). In this part, the general question is: **What can palynological evidence from late Eocene sediments in the CMB tell us about floristic composition and the evolution of the Burma Terrane (BT), plant diversity, vegetation, environment and climate?** (Section 7.2).

In the initial observation of the palynological slides under light microscopy with samples from the late Eocene CMB, I found palms (Arecaeeae) are common and diverse (Chapter 4 and Section 7.3.1). Together with the collection of fossil pollen records, this brought me to explore a further and bigger question: **How did palm composition and diversity and historical biogeography change across time and what was their relationship with climate and geological change?** (Section 7.3). For this part (except Chapter 4) I contributed equally with Dr. Giovanni Bogotá-Ángel (Universidad Distrital Francisco José Caldas, Colombia) to the historical biogeographic story of Mauritiinae palms (Chapter 5 and Section 7.3.2), and Dr. Jun Ying Lim (Nanyang Technological University, Singapore) to the diversification and biogeographic histories of calamoid and nypoid palms combining the fossil record with climatic niche models (Chapter 6 and Section 7.3.3). Authors' contributions were provided in Author Contributions.

In my thesis, I have posed the four research questions (RQs) in Section 1.1. These RQs have been answered and discussed in detail in chapters 2-6 separately. In the following sections, I will now reflect on the answers of the RQs and discuss them systematically, write about related caveats and limitations (sections 7.2 and 7.3), and explore possible further research opportunities (Section 7.4).
WHAT CAN PALYNOLOGICAL EVIDENCE FROM LATE EOCENE SEDIMENTS IN THE CMB TELL US ABOUT FLORISTIC COMPOSITION AND THE EVOLUTION OF THE BT, PLANT DIVERSITY, VEGETATION, ENVIRONMENT AND CLIMATE?

What is the composition of the late Eocene palynoflora in the CMB and what can it tell us about the role of the BT for plant dispersal between India and Asia?

In Chapter 2, I studied the palynoflora from the late Eocene Kalewa section and determined at least 141 sporomorph types. Indicative marker sporomorphs (e.g., *Meyeripollis naharkotensis*, *Cicatricosisporites dorogensis* and *Proxapertites operculatus*) and palynostratigraphy show that the Kalewa section has an age range of c. 38-37 Ma. This range was based on a comparison with a palynological zonation scheme from nearby Indonesia (Witts et al., 2012), which is consistent with the U-Pb zircon age of a tuff layer (Litch et al., 2019) and the age with magnetostratigraphy, U-Pb apatite dating, and apatite fission track dating (Westerweel et al., 2020).

Based on the recorded sporomorph types and an evaluation of their botanical affinities, I propose that the vegetation in the late Eocene CMB includes the following types from swamp communities along the coast to dry inland: (1) mangroves/back-mangroves, including mangrove *Nypa* palm *Spinizonocolpites prominatus*, sonneratioid *Florschuetzia cf. trilobata*, *Onkosperma*, which produced the pollen type *Racemonocolpites hians*, and mangrove fern *Acrostichum*; (2) coastal forests, including coastal trees *Barringtonia*, *Casuarina*, and the parent plant of *Proxapertites* spp.; (3) swamp forests along rivers, with herbaceous swamps and marshes, possibly associated with floodplain lakes, including *Meyeripollis naharkotensis*, from a probable Myrtaceous swamp tree, and diverse inland palms from rattan swamps, which produced *Dicolpopollis*; Arecoid palms which produced *Palmaepollenites kutchensis*, and were likely to be swamp trees or shrubs; *Longapertites*, probably derived from perhumid forest trees and ancestral to *Eugeissona* (see Chapter 4); (4) perhumid/wet forests, including peat swamp trees such as the parent plant of *Anacolosidites* and the evergreen tropical forest trees such as *Alangium*, which produced *Lanagiopollis*; (5) evergreen forests, including diverse Sapotaceae mainly from the subfamily Sapotoideae; (6) seasonally dry forests, including Caesalpinioideae, which
produced *Margocolporites*, *Berlinia* type, *Shorea* type and *Pinus* pollen; and (7) montane forests, including conifers producing *Inaperturopollenites hiatus*, and evergreen and temperate deciduous trees. Additionally, pteridophytes and bryophytes (8) are abundant in lowlands. Pteridophytes contain terrestrial wet (e.g., *Schizaeoisporites digitatoides* and *Cyclosorus* type), terrestrial dry (e.g., *Cicatricosisporites doroogensis*, produced by an extinct member of Schizaceae, and *Pterisisporites* spp., produced by *Pteris* spp.), and climbing ferns (*Verrucatosporites usmensis* produced by *Stenochlaena palustris*, and *Crassoretitrites vanraadshooveni* produced by *Lygodium scandens*), while bryophytes are hornworts within the Anthocerataceae including *Phaeoceros* (producing *Anthocerisporis* spp.) and *Saxosporis* growing in permanently wet swampy settings on stones, leaves and woods. These vegetation types grew in three depositional settings: lower deltaic plain (1-2), upper deltaic plain (3-5, 8) and upstream area (3-8). However, the present-day CMB principally hosts moist deciduous forests (Ashton, 2014), which is situated at c. 16-27° N. I suggest the difference of vegetation between in the late Eocene with present-day is due to the northward drift of the BT from the late Eocene near-equatorial position (c. 0-10° N; Westerweel et al., 2020), the two-stages uplift of the IBR (Licht et al., 2019) together with the uplift of the Himalayas that created a rain shadow in the CMB, and later Neogene global cooling and drying.

These sporomorphs comprise abundant Gondwanan and Laurasian elements. All montane forest trees are Laurasian boreal components, while most perhumid/wet and seasonal dry taxa are from Gondwana. The rich Gondwanan and “out-of-India” elements in the late Eocene Kalewa palynoflora together with the early Eocene occurrences of *Palmaepollenites kutchensis* and *Barringtonia* type pollen (Reimann and Aye Thaung, 1981) from the CMB could support growing evidence about the Gondwanan origin of the BT. Scattered, but diverse Laurasian montane pollen, suggest a montane connection between Myanmar and Asia to the north before the uplift of the Himalayan Range along the northern edge of the Indian Plate. After the late Eocene, montane connection between the BT and India was established, indicated by some “out-of-Asia” montane taxa (e.g., *Alnus*, *Tilia* and the Normapolles pollen *Trimagnaporites mixis*).

“Out-of-India” taxa are from the lowlands, including mangroves, perhumid, seasonally dry, or swamp forests, such as *Palmaepollenites kutchensis* (a member of the palm subfamily Areceae), *Lanagiopollis* spp. (*Alangium* sect. *Conostigma*), *Florschuetzia* cf. *trilobata*, (extinct sonneratioid taxon), *Cupanieidites flaccidiformis* (*Mischocarpus* sp.),
Racemonocolpites hians (Oncosperma), Margocolporites spp. (Caesalpinoideae), and Retistephanocolpites williamsi var. (Ctenolophom parvifolius). Considering that these elements are similar to those of the Eocene Indian floras, their presence in the late Eocene CMB provides further evidence for a lowland connection of the BT with the Indian Plate at that time. Nevertheless, they could have occurred in the BT at the same time as or before their appearance in the Indian Plate, dispersing via the Kohistan Ladakh Arc. Further studies from prior to the late Eocene will be in need to answer this question.

“Out-of-Asia” taxa include Pandaniidites spp. (Pandanus), Psilatricolporites operculatus (Alchornea), Discoidites spp. (Brownlowoideae), Corsinipollenites spp. (Jussieu), Ilexpollenites spp. (Ilex) and Retibrevitricolpites triangulatus (parent plant unknown), all of which are from lowland alluvial swamps. This indicates that lowland alluvial swamp habitats were already established on the BT by the late Eocene. However, it was not only until the early Miocene, the formation of the Siwaliks and their precursors (Johnson et al., 1985; White et al., 2002), formed as a result of the uplift of the Himalayan Range (e.g., Ding et al., 2017; Harrison et al., 1992; Valdiya, 2002), that there was a dispersal path for these taxa to India.

In summary, I found that: (1) There was a montane connection between mainland Asia and the BT in the late Eocene; (2) Lowland taxa from mangrove, perhumid and seasonally dry lowland forests may have immigrated into Myanmar from India prior to the late Eocene. This was followed by a lowland connection between the Indian Plate with BT in the late Eocene; (3) Lowland alluvial swamp elements dispersed from Myanmar to India until the early Miocene, possibly following the uplift and erosion of the Himalayan Range, and the formation of extensive floodplains in northern India, which probably bore widespread alluvial swamps; and (4) Palynofloras from the middle to late Eocene Nanggulan Formation (Lelono, 2000), and offshore South Sulawesi (Morley, 2014), display many similarities with the late Eocene Kalewa palynoflora. Considering these plant dispersal routes between the India Plate, BT, mainland and SE Asia, I propose that the BT played a critical role as a corridor and crossroads between Laurasia and Gondwana for plant dispersals, from no later than the late Eocene to early Miocene. Further studies on sediments with earlier ages (e.g., the Paleocene to middle Eocene Paunggyi, Laungshe, Tabin, Tabyin and Pondaung formations) in the CMB will be needed to clarify the earlier phases of plant migration prior to and during the initial collision of the India Plate with the BT, and also of India Plate and the BT with Asia.
7.2.2 How did the vegetation and climate change in the late Eocene CMB, and how does the Burmese paleoflora compare to other contemporary tropical palynofloras in terms of species diversity?

In Chapter 3, I detected six pollen zones (K1-6), based on assemblage evaluation and cluster analysis. From the bottom to the top and throughout the late Eocene Kalewa section these are: (1) K1 (5.8-162.5 m, c. 38.2 Ma, including the two samples below the Kalewa section) is characterized by relatively poor pollen occurrences, while terrestrial fern spores indicative of a dry environment are common. The latter include scattered Cicatricosisporites spores, indicating well drained environment. Seasonally dry forest elements (Pinus and Berlinia type pollen) are present, and mangroves occur in low numbers. The Alchornea swamp is represented by abundant Psilatricolpites cf. operculatus; (2) K2 (162.5-249.4 m, c. 38.2-38.0 Ma) is characterized by common pollen of mangroves (Proxapertites, and Nypa palm that produced Spinizonocolpites) and swamp rattan which produced Dicolpopollis spp. Climbing ferns were relatively abundant; (3) in K3 (249.4-364.6 m, c. 38.0-37.8 Ma), monolete spores are abundant, while hornworts (Anthocerotales) are present in low percentages. Pandaniidites spp. are common; (4) K4 (364.6-436.7 m, c. 37.8-37.7 Ma) is characterized by common Meyeripollis naharkotensis and Sapotaceae pollen. Tree-dominated swamps were widespread; (5) K5 (436.7-519.2 m, c. 37.7-37.5 Ma) is characterized by common Meyeripollis naharkotensis and hornworts (Anthocerotales); and (6) in K6 (519.2-627.5 m, c. 37.5 Ma), pollen are present in the highest percentages of the six zones. Hinterland assemblages are dominated by swamp rattans producing Dicolpopollis spp. Mangrove/back-mangrove pollen and mangrove fern Acrostichum occur in low percentages. Through the whole section, assemblages are dominated by taxa of lowland evergreen forests, due to its near-equatorial position, where it could obtain abundant moisture from the possible monsoonal climate. In summary, the six pollen zones reflect fern and Alchornea swamps, Proxapertites mangroves and rattan swamps, fern swamps, Meyeripollis swamps, Meyeripollis swamps, and rattan swamps from base to top.

Qualitatively, a monsoon-like climate is deduced from the presences of seasonally wet taxa (Meyeripollis naharkotensis, Palmaepollenites kutchensis and diverse Sapotaceae) and seasonally dry taxa (Malvacidites diversus and Pinus pollen). Quantitatively, the bioclimatic analysis results suggest a warm (mean annual temperature: 25.4-25.6 °C) and wet (annual precipitation: 1635-1637 mm) climate in the late Eocene, with a weaker
monsoon. This evidence supports the existence of monsoons in the Eocene Asia (e.g., Herman et al., 2017; Licht et al., 2014b; Su et al., 2020).

Three dry-wet packages were perceived based on the evaluation of sporomorph distribution patterns (termed “sequence biostratigraphy” in Morley et al., 2021). Based on the very precise magnetostratigraphy for the Kalewa section, the main part of the succession, having a cyclicity of 400 kyr derived from climate signal, coincides very closely with a global sea level oscillation, termed the PrBart-1 sequence. This suggests that global glacio-eustacy drove the sea level changes which determined the pattern of superposition of Yaw Formation sediments. Based on the examination of the high resolution δ¹⁸O and δ¹³C isotope curves (Westerhold et al., 2020), it seems likely that the late Eocene cyclicity seen here may be driven by 1.2 Ma tilt astronomical cycles since several have a duration of 1.1 or 1.2 Ma.

The late Eocene Kalewa palynoflora was compared with four other contemporary palynofloras (Assam, India; central Java, Indonesia; South China; Colombia), all of which were situated in the tropics, and with deposition in fluvial or coastal plain settings. In terms of forest composition and depositional environment, the Kalewa section is more similar to the Assam section than others, as both are deposited in coastal environments and have mangroves (including the nypoid palm Spinizonocolpites) and different dominant pteridophytes. Moreover, they are dominated by seasonal evergreen forests and bear the conifers (e.g., Pinuspollenites).

Rarefaction results suggest that the within-sample richness in the Watupuru section (central Java, Indonesia) is the highest among the five compared late Eocene tropical sites. This corroborates that the “Nanggulan Formation is the only Eocene sedimentary succession which contains a rich and diverse palynomorph assemblages between the Gippsland basin (in eastern Australia) and India” in Lelono (2000). This high diversity attributes to its near-equatorial position and perhumid climate at that time (Morley, 2000). The high species diversity in the late Eocene Myanmar could be due to the India-Asia collision, which had accelerated the plant dispersals between the Indian and Asian plates. The near-equatorial position of the late Eocene BT (Westerweel et al., 2019) in the Paleotropics with a seasonal monsoon-like climate could be another driving factor. Therefore, the BT, acted as a dispersal crossroads, and gained rich species at this time. This corridor may have persisted until the present day, which renders Myanmar as one of the main biodiversity hotspots in the globe (Myers et al., 2000) with c. 12,340 species of
spermatophytes (based on Kress et al., 2003; Yang et al., 2020). The India-Asia collision, along with the Australasian-Sunda collision, resulting in the dramatic increase of plant diversity in SE Asian area, which made this area no longer being the backwater of angiosperm evolution (Morley, 2018a).

7.2.3 Can palynology contribute to our understanding of depositional environments in the late Eocene CMB?

In Chapter 3, the Yaw palynological succession shows assemblage changes that suggest cyclical vegetation change, with periods with increased perhumid taxa during wetter/warmer periods and increased seasonally dry and montane taxa during drier/cooler intervals. There is also a close relationship with the abundance of mangrove/back-mangrove elements and changes in the character of swamp vegetation on the floodplain and periods of warmer/wetter climate.

The succession represented by zone K1, where assemblages indicate a seasonally dry climate, and cooler temperatures, would be consistent with late highstand (HST) or lowstand (LST) deposition by reference to the model of Morley et al. (2021). For Zone K2, assemblages suggest a wetter and warmer climate, and increased mangrove pollen indicates increased marine influence, which would be consistent with deposition in a more aggradational setting within the transgressive systems tract (TST). For the succession spanning zones K3, K4 and K5, most assemblages suggest a slightly drier and cooler climate, and mangrove pollen reaches a minimum, which would be consistent with deposition in a prograding HST setting. The youngest interval, represented by zone K6, yielded assemblages suggesting a warmer and wetter climate, and common Dicolpopholis kalewensis, and shows similarities with zone K2, but without common mangrove pollen. This interval would be consistent with a facies and climatic setting similar to K2, but in a more proximal setting due to the reduced mangrove pollen recovery. This package would thus be in line with proximal deposition within the TST.

This model implies that there was limited deposition on the delta plain at times of sea level lowstand. It is possible that channel sands at 80 m and 140 m may be lowstand feeder channels, but these were not sampled. Other than for this interval times of lowstands would have been represented by unconformities on the delta plain coinciding with the positions of sequence boundaries.
Chapter 4 is based on a quantitative analysis of the pollen data and focuses on changes in composition of palm and mangrove elements throughout the late Eocene Kalewa section. I identified three environmental zones: (1) a fluvial environment within the uppermost reaches of tidal influence in the lower part of the Kalewa section, indicated by abundant Acrostichum spores but low proportion of mangrove elements; (2) a closer proximity to a paleoshoreline in the middle part of the section, suggested by increasing percentages of mangrove elements; and (3) a fluvial setting without tidal influence towards the top, indicated by the increasing proportion of Dicolpopollis coupled with the reduction of Acrostichum spores. Therefore, I propose a general environmental change from a tidally influenced setting to a fluvial setting without tidal influence. This scenario is consistent with the results of previous sedimentological studies on the depositional environment of the late Eocene Kalewa section (Licht et al., 2019). The CMB was placed on the southern margin of Eurasia and at c. 40 Ma it was open towards the Bay of Bengal (Licht et al., 2019; Westerweel et al., 2019, 2020). These findings provide further context to Licht et al. (2019), who concluded that there was a shift from the barrier-bound estuary to fluvial setting. Such shift in setting was the result from basin overfilling due to the incipient uplift of the Indo-Burman Ranges, blocking the direct connection between central Myanmar and the Indian Ocean (Licht et al., 2019; Westerweel et al., 2019).

In combination with the results of Chapter 3, the palynological data from the late Eocene Kalewa sedimentary record suggest that the shift from upper tidal to fluvial environment with two cycles of transgressive to highstand systems tracts.

7.3  |  HOW DID ARECACEAE (PALMS) COMPOSITION AND DIVERSITY AND HISTORICAL BIOGEOGRAPHY CHANGE ACROSS TIME, AND WHAT WAS THEIR RELATIONSHIP WITH CLIMATE AND GEOLOGICAL CHANGES? – A TRILOGY ON PALMS

7.3.1  |  Diversification history of palm and palm-like taxa in the Paleogene of the CMB, India and SE Asia

In Chapter 4, I found that palm and palm-like (PPL) taxa are common and diverse in the late Eocene CMB. Similarly, palms are very abundant in SE Asia nowadays, particularly Calamoideae and Nypoideae. To disentangle their diversification history in this region, I
collected their Paleogene global pollen fossil records, assessed their distribution across time, and observed a compelling reduction in the distribution ranges after the Eocene. This shrinking could be due to global climate and geographic changes at the EOT, but further test will be needed. However, for the diversification history of palm fossil form-genera Longapertites, Spinizonocolpites and Dicolpopollis, and palm-like genera Proxapertites in the Paleogene India and SE Asia, it is more intricate.

Longapertites, Spinizonocolpites and Proxapertites were particularly diverse in the early and middle Eocene India. This could be critically controlled by tectonic activities, especially with the middle Eocene India-Asia collision situated in a tropical position creating a northern Indian “hotspot”. During the late Paleocene and early Eocene, the collision of the Indian Plate with the Kohistan-Ladakh Arc (Chatterjee and Scotese, 1999), and their subsequent collision with Asia, would have resulted in an archipelagic area analogous with the Western Tethys during the Eocene, the Arabian Sea during the early Miocene, and the present-day Indonesian Archipelago. An ideal setting for species differentiation in the sense of “hopping hotspots” of Renema et al. (2008), would have been provided by such a high-relief archipelago in a wet tropical region. Diversification of coastal taxa Spinizonocolpites in such a setting would be expected, and could explain the greatly increased numbers of taxa in Longapertites and Proxapertites compared to other tropical regions during the Paleocene and Eocene. Such a “hotspot” would have been in place with respect to coastal taxa until the late Eocene establishment of a land connection between the Indian Plate and Asia (Klaus et al., 2016). A diversity hotspot, in an archipelagic area with a perhumid climate could have facilitated the early diversification of rainforest taxa, such as Dipterocarpaceae that are preserved as wood fossils in the underlying late middle Eocene Pondaung Formation (Licht et al., 2014a). The rainforest taxa may subsequently have dispersed to the Sunda region following India-Asia collision (Morley, 2018a).

Dicolpopollis was very diverse in the middle and late Eocene of the SE Asia (e.g., Lelono, 2000; Morley, 2018a). This was possibly, but not exclusively due to the warm and perhumid climate. However, its diversity largely declined in the Oligocene, which is likely due to the change to a more monsoonal climate following the EOT (Morley, 2018a). Similarly, diversity of Longapertites, Spinizonocolpites and Proxapertites across India and SE Asia declined, which is probably also influenced by the global cooling at the EOT.

Migration routes of the parent plant of Dicolpopollis in India and SE Asia is of great
interest to biogeographers, but has not yet been clear. The oldest record of *Dicolpopollis* in SE Asia is in the Paleocene (e.g., in Sarawak; Muller, 1968), with a consistent occurrence in India are from the Eocene onwards. Although there are some presumed Paleocene *Dicolpopollis* records from India (e.g., Mathur and Jain, 1980), the ages of these deposits is still under debate. This indicates a dispersal from SE Asia to India, which is in line with Morley (2018a), and corroborated by molecular data that Indian Calamoidae are deeply nested within Sundanian clades (Baker et al., 2009; Barrett et al., 2016). Caution should also be taken with respect to the increasing diversity in *Dicolpopollis* during EOT in India, as this could be due to the issue of synonymy in the Paleocene or insufficient localities in the Eocene. These problems could also exist in other taxa, but have been well resolved in Sunda.

The general lower diversity of these form-genera in Myanmar could be due to its higher latitude, as the latitudinal gradient affects the distribution of modern palms including Calamoideae (Eiserhardt et al., 2011), showing that species diversity increased closer to the equator. Since only few Paleogene sites have been palynologically evaluated in Myanmar and even continental SE Asia, it is not reliable to take them as conclusive evidence for the paleogeographic distribution and diversity of palms in this region. Thus, further work in Myanmar and continental SE Asia will be needed to fully explain the perceived changes noted in the species richness of these form-genera.

### 7.3.2 Historical biogeography of Mauritiinae – a palm subtribe endemic to the present-day Neotropics

Chapter 5 presents the global Mauritiinae pollen fossil record dataset from the Late Cretaceous onwards. The fossil record suggests a Gondwanan (African) origin at c. 94-83 Ma (Atta-Peters and Salami, 2006; Boltenhagen, 1967; Fo and Fa, 2018), which is situated in the “Palmae Province” (Herngreen et al., 1996). This is much older than phylogenetic stem mean age for Mauritiinae (c. 66 Ma in South America; Baker and Couvreur, 2013a, b; Couvreur et al., 2011), and the fossil calibration point for this stem node (72-66 Ma; Schrank, 1994). The biogeographic history of Mauritiinae palms is dynamic, and thought to be driven by climate and geological change.

During the early Paleogene, it became widely distributed across Africa, South America, Middle Asia and India. At that time, tropical terrestrial land coverage was much larger than
at present (Morley, 2007). This expansion was caused by reduced latitudinal temperature under “greenhouse conditions” in the Late Cretaceous to the Eocene, particularly global climatic optima (e.g., the Paleocene–Eocene Thermal Maximum at c. 56 Ma and the Early Eocene Climatic Optimum during c. 53-49 Ma). The opening of the Atlantic Ocean in the Cretaceous, and transatlantic dispersals could have favored such expansion. The extinction of Mauritiinae in India during the Eocene may relate to the change to a perhumid climate from a seasonal tropical humid climate in the Paleocene. The change in India to a perhumid climate would also account for the absence of Mauritiinae from SE Asia, especially because during the middle Eocene India was the dispersal path for perhumid taxa to SE Asia (Morley, 2018).

During the EOT (c. 33.9 Ma), the geographic range of Mauritiinae contracted severely, coinciding with a reduction of global temperature and sea level, which impacted the distribution of coastal plants. Some researchers also linked this contraction to regional environmental change (e.g., aridification of Africa: Couvreur et al., 2011; Kissling et al., 2012; Pan et al., 2006). The taxon went extinct in Africa, and from the Oligocene onwards it is largely restricted to the Neotropics. The restriction and persistence is further substantiated by data from the Eastern Cordillera and the Middle Magdalena Basin (Colombia) where Mauritiidites is common in pollen zones during early Eocene and Oligocene (Pardo-Trujillo and Jaramillo, 2014; Rodríguez-Forero et al., 2012).

In the Neogene, the geographic range of Grimsdalea magnaclavata expanded, facilitated by Andes uplift and prolonged wetland conditions in western Amazonia (e.g., Hoorn, 1994a). In the Pleistocene (at c. 1.3 Ma), Grimsdalea went extinct, which is thought to be related to a major cooling event and habitat disappearance (Pocknall et al., 2001). Sea level fall may also have played a role, causing a loss of habitat for taxa with coastal distributions such as is known for Nypa palms (Morley, 2000). The distribution and abundance of Mauritia, estimated by pollen records (mostly referred as Mauritia-Mauritiella), indicates they were mainly controlled by climate change, particularly during the Last Glacial Maximum (e.g., Rull, 1998; Salgado-Labouriau, 1997; van der Hammen and Absy, 1994). Their abundance, particularly in swampy areas of western Amazonia and the Cerrado, where wet regional climate together with poorly drained soils likely prompted their evolutionary success (Lima et al., 2014; Melo et al., 2018).

Most pollen records of Mauritia-Mauritiella are restricted to the Holocene. The transition from Mauritiidites to Mauritia-Mauritiella is less clear, due to the absence of
continuous continental sedimentary records from the Pliocene and Pleistocene in the Neotropics, and thus will need further study. Similarly, the remarkable absence of *Lepidocaryum* pollen records could be an artefact of taxonomic under-reporting. Future studies on sedimentary records should pay careful attention on pollen morphological details such as the monosulcate versus monoulcerate condition in *Mauritiidites*, when compared with monoulcerate *Mauritia-Mauritiella* and monosulcate *Lepidocaryum*. Only in this way we may completely understand the ecological position of Mauritiinae in transition to the Quaternary.

**7.3.3 Diversification and biogeographic histories of subfamilies Calamoideae and Nypoideae: combining the fossil record with climatic niche models**

Chapter 6 investigates the role of Cenozoic climate change on diversification and biogeographic trajectories of subfamilies Calamoideae and Nypoideae by combining the fossil record with climatic niche models. The fossil record suggests that relatively species-poor extant lineages (e.g., Nypoideae with one species, Eugeissoneae with six species and Mauritiinae with seven species) were much more diverse, and all focal palm groups were much more geographically widespread in the past. This is also generally supported by climatic niche models. Generally cooler and dryer climate throughout the Cenozoic (Westwerhold et al., 2020; Zachos et al., 2008) should have played an important role in this process. For instance, the African palm fossil record shows a decline of diversity during the EOT, when a global cooling event occurred (Pan et al., 2006). Although the EOT is undoubtedly an important inflection point in the history of tropical biomes, the modern biogeographic pattern for all studied palm lineages was only achieved after the Miocene and resulted from continental extirpations (e.g., Calaminae from Western Europe, Nypoideae and Eugeissoneae from Africa and Americas, Mauritiinae from Africa). Climatic niche models do not support an extensive decline in climatically suitable habitat after the Eocene. This indicates that the modern biogeographic distribution for all studied palm lineages is shaped by the rapid global cooling after the Middle Miocene Climate Optimum (MMCO; c. 17-14.5 Ma). The fossil records display the highest diversity for Eugeissoneae, Mauritiinae and Nypoideae during the late Paleocene and early Eocene, which could be due to the high global temperature and sea levels at the time, when the maximum sea level was c. 150 m than at present (Kominz et al., 2008; Miller et al., 2005;
Van Sicke et al., 2004). As all palm lineages here show different evolutionary histories, each focal lineage will be briefly discussed separately now below.

**Calaminae.** The Calaminae are common in Eurasia but absent in Africa during the Paleogene and Miocene. This taxon disappears from Europe in the Miocene but appears in Africa in the Pliocene and Quaternary. Analyses of diversification rates with molecular phylogenies (Baker and Couvreur, 2013b) and the fossil record show similar results: *Calamus* has higher than average diversification rates, while fossil *Dicolpopollis* is diverse through the Cenozoic. At present, the Calaminae are extremely diverse (c. 500 species) in SE Asia, and this could be due to the geographic complexity of this region, with many islands and archipelagos providing abundant ecological opportunities, which may have helped promote its specification (Onstein et al., 2017). Another important reason is its strong adaptation to the SE Asian tall forests with its modified stems and leaves to latch onto and climb adjacent plants (Couvreur et al., 2015; Isnard and Rowe, 2008).

**Eugeissoneae.** Eugeissoneae are pantropical in the Paleogene and Miocene, but became restricted to South-SE Asia in the Pliocene and Quaternary. The fossil record of *Eugeissona*-like *Longapertites* pollen suggests that this lineage may not only have been much more diverse in the past, but also had more widespread distribution. However, molecular phylogenies display a low diversification. Besides, climatic niche models show suitable habitat in Africa and South America throughout the Cenozoic based on their present-day occurrences in SE Asia. It is possible that Eugeissoneae lineages in the past may have had climatic preferences which the models inadequately capture from extant lineages. The fossil record also shows that *Eugeissona* has a downward diversity trajectory, indicating a higher extinction rate than speciation rate. The current SE Asia-restricted distribution of *Eugeissona* is likely due to regional extinction outside the Asian tropics, while its present-day low diversity may be attributed to its inability to compete without adaptations for climbing like Calaminae.

**Mauritiinae.** The biogeographic history of the Mauritiinae was discussed in Section 7.3.2. Climatic niche models project the presence of climatically suitable habitat for Mauritiinae in Africa and India throughout the early Cenozoic, in congruence with fossil occurrences in western Africa and India. They also suggest that climatic suitability generally declines from the Miocene to the present, consistent with the disappearance of Mauritiinae type pollen from those two biogeographic regions after the Miocene (i.e., result in Section 7.3.2). The extinction of Mauritiinae in Africa may be explained by the early
Oligocene–Miocene aridification and general Cenozoic cooling and drying in this region. In contrast, its successful persistence in South America may have been facilitated by the formation of extensive wetlands associated with the Andean orogeny during the Neogene (Hoorn, 1994a; Hoorn et al., 2010).

**Nypoideae.** Nypoideae was pantropical in the Paleogene. The diversity and geographic range of Nypoideae is highest in the late Paleocene–early Eocene and subsequently declined, which is consistent with major changes in paleoextent in mangrove habitats through the Cenozoic (Gee, 2001), such as the habitat loss at the EOT after rapid sea level fall. The absence of *Nypa* in Neotropics and western Africa is not possibly due to the competition failure with ecologically similar species, as (1) mangroves habitats in these regions do not seem to be ecologically saturated (Latham and Ricklefs, 1993); (2) *Nypa* has been readily introduced to western Africa and Central America (Dransfield et al., 2008; Duke, 1991); and (3) climatic niche models project suitable ecological conditions outside of the Indotropics. Its absence outside of the Indotropics is likely shaped by regional extinction, due to severe and short-lived climatic perturbations (e.g., the MMCO) or non-climatic factors (e.g., changes in oceanic salinity from the closure of the Panama Isthmus), but rather than broad climatic trends of the late Cenozoic.

### 7.4 | OUTLOOK

Exploratory studies were carried out in the CMB (e.g., Licht et al., 2013, 2014a, b, 2015), prior to the foundation of the Myanmar Paleoclimate and Geodynamics Research group (MyaPGR) and the initiation of my PhD project in 2016. All these studies provide an excellent basis for the present and future palynological studies in the CMB. Particularly, accurate age constraints (U-Pb zircon dating, Licht et al., 2019; magnetostratigraphy, U-Pb apatite dating, and apatite fission track dating, Westerweel et al., 2020) and previous environmental interpretations (Licht et al., 2019; Westerweel et al., 2020) on the late Eocene Kalewa section provide a good foundation for the palynological study on this section.

Macrofossils (e.g., leaves, fruits and seeds) have not yet been studied in the CMB, and could form good proxies to quantitatively construct past vegetation, climate and environment (e.g., Kershaw, 1983; Mosbrugger and Utescher, 1997; Xia et al., 2009). Broadly in SE Asian region, there has been barely any paleobotanical studies so far. In the
preliminary investigations, I have collected several fossil leaves from the CMB but not studied them yet. Thus, further palynological and paleobotanical studies in the Cenozoic (e.g., the Paleocene–Miocene Paunggyi, Laungshe, Tilin, Tabyin, Pondaung, Shwezetaw, Tonhe, Letkat and Natma formations in the CMB) of Myanmar and even SE Asia will be needed to deepen our understanding of the vegetation, climate and environment histories in these regions, and the evolution of the BT through the Cenozoic.

More works will be also needed to further complement the reconstruction of diversification and biogeographic histories of palms. The abundant macrofossil records of palms (e.g., Dransfield et al., 2008; Gee, 2001; Harley, 2006) could form important complementary data to the fossil palm pollen record. However, the nearest living relative (NLRs) of palm macrofossils are sometimes difficult to determine. As yet, the macrofossil record has not been sufficiently explored, and holds great promise. Further work on the phylogenies of palms (e.g., Kuhnhäuser et al., 2021) will also improve the story of biodiversification and historical biogeography of this family and shed more light on the understanding of the impact of global climate and geological change on tropical rainforests.