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Mangrove distribution and diversity during three Cenozoic thermal maxima in the Northern Hemisphere (pollen records from the Arctic – North Atlantic – Mediterranean regions)

Short running title: Cenozoic North Hemisphere mangrove diversity

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ABSTRACT

Aim: Past pollen records reveal the changes in latitudinal distribution of plants in relation to climate, particularly their expansion in response to global warming. The maximum northward expansion of the mangrove genus *Avicennia* since the Early Eocene is known, but this information is missing for other mangrove taxa. Here, we evaluate the diversity of past mangroves with respect to latitude during three Cenozoic thermal maxima (PETM: 56 Ma; EECO: 54–49 Ma; MMCO: 17–14 Ma).

Location: North Atlantic, Mediterranean.

Taxa: *Avicennia*, other mangrove taxa (Rhizophoraceae, *Nypa*, *Xylocarpus*, *Pelliciera*, etc.).

Method: We collected well-dated marine sediments along a Northern Hemisphere latitudinal transect and we analysed their pollen content in order to compare the past distribution of mangrove taxa with the present. The analysis of 89 samples (PETM: 13; EECO: 31; MMCO: 45) was performed and interpreted using a robust botanical background for identification of pollen grains and their representativeness in marine sediments.

Results: During the Early Eocene, two palaeolatitudinal thresholds at 65–70°N and 35°N, respectively, delimited the *Avicennia*-only mangrove from a diversified but scrawny mangrove and finally from a diversified and well-developed mangrove. The *Avicennia* threshold was selective at 40°N during the Mid-Miocene. The *Avicennia* range limit was up to 10–15° poleward of the limit for other mangrove taxa during the Early Eocene and the Mid-Miocene compared with 9° at present.

Main conclusions: A buffer zone characterised by a diversified but scrawny mangrove co-occurring with a few megathermal plants occurred in the Early Eocene between 35°N and 65–70°N. This finding questions the relative influence of a more ‘equable’ climate and/or the ability of some taxa to expand towards areas with cooler conditions in the past. Mangrove provincialism, which was established progressively after the Early Eocene, was probably forced by plate tectonics. The taxonomic impoverishment of the Atlantic East Pacific province was probably caused by successive periods of global cooling. These results support the Tethyan origin of the mangroves.

KEYWORDS

Avicennia, Climate change, Eocene–Miocene, Mangrove, Range limit, Thermal optimum.

1 INTRODUCTION

Inter-tropical mangrove vegetation comprises major trees such as *Avicennia*, Rhizophoraceae (*Rhizophora*, *Bruguiera*, *Ceriops*, *Kandelia*), *Nypa*, *Sonneratia*, and other less abundant plants such as *Excoecaria*, *Xylocarpus*, *Pelliciera*, *Aegialitis*, *Heritiera*, *Scyphiphora* and *Brownlowia* (Tomlinson, 1986). Mangrove distribution today reveals latitudinal differences between different geographic areas partly due to the influence of marine currents and partly to plant sensitivity to different air and water temperatures (Figure 1; Tomlinson, 1986; Duke, 1992; Duke et al., 1998; Kao et al., 2004; Osland et al., 2017). If >1,000 mm, annual rainfall is also an important factor affecting the distribution, stature and diversity of mangroves (Osland et al., 2017; Bardou et al., 2020). Mangrove establishment is closely linked to hydrodynamics and, particularly, to sea-level changes (Woodroffe et al., 2016).

Avicennia occurs in a slightly wider latitudinal range than *Rhizophora*, but the generally observed latitudinal difference between these genera (median value 1.8°) is 8–9° in northern New Zealand and southern Australia (Quisthoudt et al., 2012). Although the lowest temperature limits tolerated by *Avicennia*, (e.g., 8.1°C minimum air temperature,

12.7°C minimum water temperature) differ significantly from those tolerated by *Rhizophora* (e.g., 13.1°C minimum air temperature, 16.4°C minimum water temperature), the difference is not enough to explain the observed differences in latitude distribution (Quisthoudt et al., 2012). Freezing appears to be a critical factor in limiting mangrove expansion (Stuart et al., 2007) while resistance to freezing may drive the northward expansion of North American mangrove in response to current climate warming (Cook-Patton et al., 2015; Bardou et al., 2020).

Avicennia and *Rhizophora* are emblematic mangrove genera because they occur in both the Atlantic East Pacific (AEP) and Indo-West Pacific (IWP) provinces although they are represented by different species (Figure 1; Tomlinson, 1986; Duke et al., 1998; Ellison et al., 1999). Some genera only occur in one of the provinces (*Pelliciera* to the west; *Sonneratia*, *Xylocarpus* and *Nypa* to the east; Figure 1).

The discovery of mangrove vegetation consisting of only *Avicennia* inhabiting the Mediterranean shorelines during the Miocene (Bessedik, 1981a) advanced our knowledge of mangrove history (Plaziat et al., 2001; Srivastava & Prasad, 2019). More recently and surprisingly, *Avicennia* was recorded up to Arctic latitudes and even near the North Pole during the Early Eocene (Suan et al., 2017; Salpin et al., 2019; Suc et al., 2020). Accordingly, the following question arose: did the poleward limit of *Avicennia* compared with that of the other mangrove taxa increase or decrease after the Early Eocene? To answer this question, pollen records containing mangrove taxa from three Cenozoic thermal maxima were selected for comparison with present-day mangrove distribution: Palaeocene–Eocene Thermal Maximum (PETM: 56 Ma; Westerhold et al., 2015), Early Eocene Climatic Optimum (EECO: 54–49 Ma; Westerhold et al., 2020), and Mid-Miocene Climatic Optimum (MMCO: 17–14 Ma; Zachos et al., 2001). The Early Eocene pollen records in which *Avicennia* is the only mangrove tree are limited to the Arctic domain (Suan et al., 2017; Salpin et al., 2019; Suc et al., 2020), and the Mid-Miocene pollen records in which *Avicennia* is the only mangrove tree are limited to the Mediterranean domain (Bessedik, 1981a, 1981b, 1984; Jiménez-Moreno & Suc, 2007; Jiménez-Moreno et al., 2008). Hence, we chose to focus on the North Atlantic by analysing new locations and using earlier data (Table S1). The results of this work may inform potential future distribution and diversity of mangroves in response to current climate warming with the need to provide increasing protection against anthropic damage (Giri et al., 2011).

2 MATERIALS AND METHODS

The pollen records concerned are shown on the palaeogeographic maps in Figure 2 (PETM and EECO) and Figure 3 (MMCO) and listed in Table S1. They were aligned along an Atlantic latitudinal transect (including the Mediterranean region for the MMCO) to enable us to locate the threshold which separates the diversified mangrove from impoverished mangrove containing only *Avicennia*. The study concerns clayey sediments which are usually excellent deposits for pollen preservation.

The pollen data from each location have been dated independently, most often by micropalaeontology, as specified in Table S1. We selected the pollen spectra that indicated the warmest conditions in the selected records where the expected warming event is diffuse. The duration of each pollen record was appraised by fitting the pollen assemblages and their variations to the reference oxygen isotope curve within the originally defined biostratigraphic interval (see Figure S1 and explanation herein).

Palaeolatitude estimates were deduced from the global Eulerian rotation poles database from Torsvik et al. (2012), using the Paleolatitude.org online toolbox (van Hinsbergen et al., 2015) and then compared to regional maps. Uncertainties vary from ± 2 to ± 3 latitude degrees. For location 1 in the PETM (Figure 2) uncertainty might be higher due to the

uncertain position of the Lomonosov Ridge prior to the Eurasian Basin opening but conservative reconstructions place it north of Greenland since 70 Ma (Gion et al., 2017). The 76°N and 78°N palaeolatitudes are probably minimum estimates for PETM and EECO at location 1, respectively (Table S1). The computed position of location 3 (Figure 2) during the EECO is consistent with recent regional palaeogeographical reconstructions (Table S1; Eberle & Greenwood, 2012). For European sites and the Tethyan realm, computed palaeolatitudes are systematically 6° to 7° lower than those mentioned in regional reconstructions (Meulenkamp & Sissingh, 2003). This discrepancy is mainly explained by the northward rotation of extra-Alpine stable Europe since 50 Ma at least (Torsvik et al., 2008). For the MMCO, as locations 2, 8 and 9 are situated in unconstrained mobile regions, their palaeolatitude was deduced from latitude changes at adjacent locations.

The samples analysed in this work, plus those analysed earlier by our team (Table S1), were processed using a standard protocol: acid digestion (HCl, HF), concentration using ZnCl₂ (at density 2.0), and sieving through a 10-µm nylon mesh. A 40 µl volume of residue was mounted between the coverslip and microscope slide using glycerol.

The major methodological and conceptual contribution of this study is the use of a botanical approach for the Palaeogene samples. This approach was made possible by considering all the morphological characters of the pollen instead of just a few (often secondary). Details on *Avicennia* and other mangrove taxa are provided in Supporting Information (Figures S1–S10). In addition, we performed pollen counts (at least 100–150 pollen grains per sample excluding over-represented taxa such as *Pinus*), which is another novelty. Pollen data are shown in synthetic pollen diagrams (Figures 4–6) where the taxa are grouped according to both their present-day ecological significance and to their behaviour during the Cenozoic (Table S2; Suc et al., 2018, 2020).

Taxa are mainly grouped according to the thermal classification of Nix (1982) with some emphasis on the woody mangrove: *Avicennia*; other mangrove taxa; other megathermal plants which require a mean annual temperature (MAT) higher than 24°C; mega-mesothermal plants that require a MAT between 24°C and 20°C; mesothermal plants that require a MAT between 20°C and 14°C; *Pinus* plus indeterminable Pinaceae devoid of thermal significance because of their low level in botanical identification; meso-microthermal plants that require a MAT between 14°C and 12°C; microthermal plants that require a MAT under 12°C; plants of no significance because of their cosmopolitan status at the family or genus level; Cupressaceae *p.p.* (*Cupressus-Juniperus* type); herbaceous plants. A complete list of the identified taxa and additional details on the ecological groups of plants are provided in Table S2.

Some reconstructed terrestrial palaeoclimate parameters taken from pollen records are used to discuss our results. These data come from the Climatic Amplitude Method (Fauquette et al., 1998), which, based on comparison with >6000 present-day pollen records distributed worldwide, relies on the relationship between the relative abundance of each taxon and the climate. To obtain more refined estimates, this method accounts not only for the occurrence/absence criterion but also for pollen grain percentages. The reconstructed climatic values concern the low-elevation vegetation, meso-microthermal and microthermal taxa being excluded from the process. *Pinus*, which inhabits different vegetation belts, from the lowest to the highest belts, especially in the Mediterranean region, was also excluded from the calculation.

The advantage of applying this ‘Quaternary–Neogene’ palynological approach to the Palaeogene samples is that it not only provides reliable information on the palaeo-ecosystems but also helps to establish robust homogeneous data.

Marine pollen records are reliable indicators of the occurrence of mangrove vegetation along the shoreline whether they are supplied by air or fluvial transport as demonstrated by studies on modern pollen sedimentation (Hooghiemstra et al., 1986; Caratini et al., 1987; Poumot, 1989; Somboon, 1990; Bengo, 1996; Phuphumirat et al., 2016). For some of the study areas, the distance travelled by mangrove pollen grains is more than a few kilometres, indeed even after several dozen kilometres percentages can be 5-10% of the pollen sum (Hooghiemstra et al., 1986; Caratini et al., 1987; Bengo, 1996). Such data are of great importance for the reliability of our past mangrove records, all located relatively close to the land (Figures 2–3). In addition, some modern pollen records show high variability in mangrove pollen percentages with respect to the whole pollen flora: the highest percentages are recorded in front of large mangroves, the lowest percentages in front of weakened mangroves (Hooghiemstra et al., 1986; Caratini et al., 1987; Bengo, 1996) or dwarf mangroves (Willard et al., 2001). It will be recalled that in these modern records, *Avicennia* pollen is usually under-represented in comparison with other mangrove taxa, particularly Rhizophoraceae (e.g., Somboon, 1990).

3 RESULTS

3.1 Palaeocene–Eocene Thermal Maximum

Avicennia was the only mangrove taxon we recorded in the Arctic pollen floras (locations 1–2; Figures 2, 4). These floras were also very poor in megathermal plants, as they are only represented by two taxa, both at very low percentages (Figure 4; Table S2). In southern Greenland (location 5; Figure 2), larger quantities of *Avicennia* were recorded than in Arctic samples, along with a small number of other mangrove taxa (Rhizophoraceae, *Xylocarpus*, *Brownlowia*) and small percentage of a few megathermal plants (Figure 4; Table S2). At Noirmoutier (location 7; Figure 2), *Avicennia* was rarely recorded but small percentages documented three other mangrove trees (Rhizophoraceae, *Xylocarpus*, and *Nypa*) and megathermal plants (Figure 4; Table S2). In the North Pyrenean Gulf (location 8; Figure 2), *Avicennia* pollen was found in small quantities with high percentages of *Nypa* and moderate amounts of a few megathermal plants (Figure 4; Table S2). Offshore northwestern Africa (location 11; Figure 2), *Avicennia* was found abundantly along with several other mangrove trees (Rhizophoraceae, *Excoecaria*, *Xylocarpus*, and possibly *Sonneratia*-type – see comment in Supporting Information) in equal quantities and with significant percentages of some megathermal plants (Figure 4; Table S2).

3.2 Early Eocene Climatic Optimum

As in the PETM, *Avicennia* was the only mangrove tree recorded in the Arctic pollen floras during the EECO (locations 1 and 3; Figures 2, 5). These floras were also very poor in megathermal plants which were only represented by very small percentages of six taxa (Figure 5; Table S2). We found *Avicennia* pollen in significantly larger quantities with low percentages of other mangrove taxa (Rhizophoraceae, *Xylocarpus*, *Brownlowia*, *Scyphiphora*, *Excoecaria*, cf. *Heritiera*, and possibly *Sonneratia*-type) offshore northwestern Europe and offshore southern Greenland (locations 4 and 5; Figures 2, 5). A similar pollen flora characterised the Belgium Basin (location 6; Figure 2) where *Avicennia* was accompanied by Rhizophoraceae, *Nypa* and *Sonneratia*-type and an increasing number of megathermal plants (Figure 5; Table S2). Small to moderate quantities of *Avicennia* pollen were observed in the North Pyrenean Gulf (locations 9–10; Figure 2), along with a large quantity of *Nypa* and several other woody mangrove taxa (Rhizophoraceae, *Pelliciera*, *Xylocarpus*, *Aegialitis* and *Sonneratia*-type); the

accompanying megathermal plants were abundant and present at significant percentages (Figure 5; Table S2).

3.3 Mid-Miocene Climatic Optimum

The northernmost known pollen flora consisting of only *Avicennia* indicating mangrove vegetation, occurred together with very few megathermal taxa, was located at 45°N palaeolatitude (location 1; Figures 3, 6). *Avicennia* was commonly recorded south of 41°N (locations 4–7), usually at a low percentage except at locations 4 and 7, and with no other mangrove taxa (Figures 3, 6; Tables S1, S2). Megathermal plants were diversified at locations 4 and 7 but at relatively low percentages (Figures 3, 6; Table S2). In contrast, location 10 (Figure 3) contained neither *Avicennia* pollen nor megathermal plants, despite being at an almost similar palaeolatitude to locations 4–6 on the Atlantic side (Figure 6; Table S2).

4 DISCUSSION

Three thermal optima were chosen as periods during which climatic conditions favoured maximum spreading of *Avicennia*, and possibly other mangrove taxa accompanied by diverse megathermal taxa, towards high latitudes. In addition, the distribution and diversity of past mangroves during particularly warm periods can be compared to the present-day context characterised by climate warming. The results we obtained from our analyses of pollen floras located along a latitudinal transect in the Northern Hemisphere in both the Atlantic and Mediterranean regions provide new insights into several aspects including (1) the occurrence of latitudinal thresholds leading to successive steps in mangrove development, (2) the spread of the latitudinal limit of *Avicennia* in relation to other mangrove taxa, (3) the onset of the present mangrove provinces, and (4) location of mangrove refuges during colder periods. But before interpreting our results, we review the representativeness of the occurrence/absence of mangrove pollen grains and the significance of their variations in abundance.

4.1 Representativeness of mangrove pollen and implications of its quantitative variations

The three past warm intervals studied correspond to episodes with high global sea level characterised by major elevations (up to 80 m in the PETM and 60 m in the EECO and MMCO; Miller et al., 2020). During the longer climatic optima such as EECO and MMCO, the global sea level fluctuated somewhat (50 m in the EECO, 40 m in the MMCO) under the direct forcing of global temperature variations (Miller et al., 2020). Variations in mangrove pollen in our long pollen records in the EECO (Site M0004A, Caribou Hills, Kallio 027E148) and MMCO (Göllersdorf, Narbonne V. Hugo College, La Rierussa) may, according to their correlation with the oxygen isotope curve (Figure S1), have been caused by these secondary changes in sea level, which, in any case, resulted from global temperature changes. The same interpretation could be applied to the other locations of shorter duration.

The available reconstructed palaeoclimatic conditions indicate that the annual rainfall was higher than 1,000 mm at many locations:

- In the PETM: Faddeevsky (Suan et al., 2017), Site M0004A (Suc et al., 2020), Calavanté 1 (Fauquette, in progress);
- In the EECO: Caribou Hills (Salpin et al., 2019), Site M0004A (Suc et al., 2020), Morlaàs 1 and Gan (Fauquette, in progress);
- In the MMCO: Göllersdorf (Jiménez-Moreno et al., 2008), Estagel (Fauquette et al., 2007), Narbonne V. Hugo College (Fauquette, in progress).

Only the MMCO records from La Rierussa and Alboran A1 indicate annual precipitation slightly lower and significantly lower than 1,000 mm, respectively (Fauquette et al., 2007). This low precipitation does not seem to have affected the abundance of *Avicennia* pollen in La Rierussa. This can be compared to the modern distribution of *Avicennia* in the sub-desertic Red Sea region. Conversely, it could be the cause of the small quantity of *Avicennia* pollen in the Alboran A1 well. Accordingly, annual precipitation does not seem to have played a critical role in the distribution and development of mangroves during the three climatic optima considered here, except at the southernmost location in the Mediterranean in the MMCO.

The reconstructed mean temperature of the coldest month is evidence for the absence of freezing episodes during the PETM and EECO in the Arctic domain (Suan et al., 2017; Salpin et al., 2019; Suc et al., 2020). In this region, the first appearance of ephemeral continental ice seems more recent than 38 Ma (see: Suc et al., 2020). Similarly, the reconstructed mean temperature of the coldest month for the northernmost *Avicennia* locations during the MMCO suggests a lack of freezing episodes (Fauquette, unpublished data).

We conclude that, at the macroecological (geographical and chronological) scales of our study, sea and land temperatures were the main factors that controlled the development and diversity of the mangrove forests during the Palaeogene and Neogene climatic optima.

4.2 Latitudinal thresholds in the Northern Hemisphere separated diversified mangroves from *Avicennia*-only mangroves

4.2.1. PETM and EECO

The abundance of pollen records in the EECO allowed us to reconstruct an almost continuous latitudinal gradient of mangrove distribution in the North Atlantic region (Figures 2, 5; Table S1). A first palaeolatitudinal threshold was identified, at about 58–73°N, delimiting the transition from a mangrove ecosystem with only *Avicennia* (locations 1, 3) to a diversified mangrove ecosystem. A second palaeolatitudinal threshold was identified at about 32–40°N which separated pollen records where the abundance of the other mangrove taxa was less than 5% with little diversity of megathermal plants (locations 4–6) from pollen records where the abundance of the other mangrove taxa was higher than 5% with a relatively high diversity of megathermal flora (locations 9–10) (Figure 5). The value of 5% of other mangrove taxa allowed us to define a scrawny though diversified mangrove between 32°N and 40°N and a well-developed diversified mangrove below 32°N. The same palaeolatitude thresholds were inferred for the PETM, at about 55–76°N and 32–35°N, respectively (Figure 4). The large amount of *Avicennia* pollen recorded at location 5 may be explained by the existence of a protected area offshore southern Greenland (Figure 2).

Mangrove expansion depends on air temperatures but chiefly on sea temperatures. Today, *Avicennia* species are generally limited to coastal areas characterised by a warm climate with sea surface temperatures (SSTs) around 22.6°C (Quisthoudt et al., 2012) and cannot tolerate extremely cold air temperatures (below -4°C; Cavanaugh et al., 2014). However, thanks to warm marine currents, *Avicennia* is the only mangrove plant that is not limited to the tropics and can occur at SSTs as low as 15.6°C at its coldest limit in New Zealand and eastern Australia (Quisthoudt et al., 2012). *Rhizophora* requires slightly higher SSTs, even at its coldest limit (SSTs > 20.8°C; Quisthoudt et al., 2012). Model simulations of the sea surface (SSTs) and terrestrial mean annual temperatures (MATs) realised for the PETM and EECO along Earth's latitudinal range give too low temperature estimates and do not provide any evidence for a significantly reduced equator-to-pole temperature gradient (e.g., Huber & Caballero, 2011; Hollis et al., 2012; Lunt et al., 2012;

Zhu et al., 2020). The only one consistent with the palaeoclimate estimated through tetraether lipids (Weijers et al., 2007) and pollen records (Suan et al., 2017; Suc et al., 2020), although SSTs and MATs estimated north of 70° are also too low, reveals a sharp drop in the SST curve between palaeolatitude 65°N and 70°N (Figure 7; Sagoo et al., 2013) that could limit the distribution of the more thermophilous mangrove taxa such as Rhizophoraceae as evidenced in our pollen data (Table 1). Moreover, the inversion of MATs and SSTs curves at ~37°N (Sagoo et al., 2013) corresponds in our data to the transition from diversified but scrawny mangrove to diversified and well-developed mangrove at about 35°N (Figure 7, Table 1). These inflexions in the marine and atmospheric temperature curves may record Early Eocene mangrove distribution and diversification in the Northern Hemisphere. Evidence for a similar threshold is shown in the Southern Hemisphere at palaeolatitude 65°S characterised by the occurrence of an Early Eocene scrawny mangrove with only *Nypa* in Tasmania (Table 1; Pole & Macphail, 1996). These thresholds should be taken into account to review the so-called Early Eocene 'equable' climate (Sloan & Barron, 1990).

Two challenging-correlating interpretations can be proposed:

- (1) Are the coupled climate models affected by insufficient performance under greenhouse conditions? It is now generally accepted (e.g., Sagoo et al., 2013);
- (2) Are temperature estimates from proxies exaggerated? Do tetraether lipids over-estimate temperatures or are the temperature requirements attributed to *Avicennia* in estimations based on pollen, too warm? This is possible, but the results based on kaolinite content of sediments in New Siberia (Suan et al., 2017), by MAT estimated in Antarctica (Pross et al., 2012) and TEX86-derived SSTs in Tasmania (Bijl et al., 2009) are in line with pollen-based estimates.

To answer these questions, we need to understand the process and magnitude of Arctic temperature amplification, especially seasonality, which is observed in the present global warming (Riboldi et al., 2020) and is believed to have been intense during the PETM and EECO (Huber & Caballero, 2011; Lunt et al., 2012; Frieling et al., 2017).

The inherent forcing of solar radiation should be examined as an outcome. Indeed, studying the Mid-Holocene latitudinal variation of insolation controlling the temperature gradient, Davis and Brewer (2009) provide evidence for a threshold at 47°N delimiting increased summer insolation at higher latitudes but reduced insolation at lower latitudes and a threshold between 60 and 70°N of the June insolation. Loutre et al. (2004) reconstruct global insolation for the Late Quaternary and provide evidence for a phase reversal at 43–44°N with prevalence of obliquity forcing over climate at higher latitudes and eccentricity at lower latitudes, the difference in mean annual irradiance being particularly marked above 70°N. An Early Eocene latitudinal reconstruction of insolation with the respective effect of winter vs. summer irradiance could allow to check if such thresholds forced the progressive diversity of mangrove ecosystems and the distribution of its major components.

4.2.2. MMCO

A threshold at about 40°N seems to have existed during the MMCO in the Mediterranean region, separating the *Avicennia* mangrove based on the abundance of *Avicennia* pollen and/or megathermal plants (Figure 6). The difference is particularly well expressed at locations 4 and 7 compared to location 1. Location 4 (Châteauredon) probably benefited from protected environmental conditions at the far end of a narrow gulf.

Our data concern the northern shorelines of the Mediterranean region where no other mangrove taxon was recorded. The lack of coeval pollen data from the southern Mediterranean shorelines does not allow us to hypothesise their occurrence a few

latitudinal degrees southward. In this direction (Fig. 3), the first available pollen data are those from La Herradura (location 15: Palacios Chavez & Rzedowski, 1993) and from the coastal area of Senegal (location 11: Médus, 1975). Unfortunately, these pollen floras are not really usable because of their chronological imprecision and unavailable pollen data. However, their abundant pollen illustrations support the occurrence of *Nypa* and *Pelliciera* at La Herradura and that of *Rhizophora* at both locations. In addition, observation of the pollen photographs published convinces us of the occurrence of *Avicennia* at the two locations (detailed in Supporting Information). Close to the palaeo-equator, location 12 (well M1 from the Niger Delta; Durugbo & Olayiwola, 2017) shows evidence of abundant *Rhizophora* and scarce *Avicennia* pollen grains during a stratigraphic interval attributable to the Mid-Miocene, the redrawing of which is provided in Figure 6 for comparison with the Mediterranean pollen floras. At location 16 (Lower Apaporis River; Fig. 3), Hoorn (2006) documents the occurrence of *Rhizophora* and *Mauritia* (Arecaceae). This comparison suggests that the diversity of the AEP mangrove was already significantly impoverished in the Mid-Miocene.

The MMCO has been modelled and sea surface and/or terrestrial temperature simulations are available (e.g.: You et al., 2009; Herold et al., 2011; Goldner et al., 2014). Herold et al. (2011) reconstructed terrestrial MATs that are characterised by strong dip variations between 30 and 35°N with a temperature gradient of 1.5°C per degree in latitude, which is significantly higher than the modern temperature gradient (0.6°C per degree in latitude) and very much higher than the temperature gradient obtained for the MMCO from pollen records in Western Europe (0.48°C per degree in latitude: Fauquette et al., 2007). In addition, the proposed terrestrial MATs for the latitudinal interval 30–42°N are significantly lower (11–17°C) than those estimated from pollen data in the Mediterranean domain (18.2–20.5°C; Fauquette et al., 2007; Jiménez-Moreno et al., 2008). Accordingly, there is a marked discrepancy in the MATs for the MMCO between the model simulation and pollen proxy, as in the SSTs between the model simulation and biomarker proxy (Salocchi et al., 2021), similarly to previous time periods. As hypothesised above, it is possible that too much weight was attributed to *Avicennia* and/or the few megathermal plants in the temperature reconstructions based on pollen records. However, it is well known that for the MMCO, like for the previous periods, climate models generally fail to reproduce the polar amplification and lead to over-estimation of the equator to pole temperature gradient (e.g., You et al., 2009; Goldner et al., 2014). It is also possible that, like today, the Mediterranean Basin was a particular climatic region that allowed *Avicennia* to survive in slightly lower thermal conditions and to develop in some propitious contexts (locations 4 and 7; Figure 6; Table S1). This assumption is supported by some evidence: (1) the unexpected very rare presence of *Avicennia* pollen in the southernmost pollen flora (location 9: Figures 3, 6); (2) the absence of *Avicennia* and of any megathermal taxon at location 10 on the Atlantic shoreline at a northwestern Mediterranean palaeolatitude (Figures 3, 6; Table S1); the absence of *Avicennia* and of any megathermal taxon at the West Atlantic locations 13 and 14 corresponding to southernmost Mediterranean palaeolatitudes.

4.3 Northernmost latitudinal limit of *Avicennia* distribution with respect to the diversified mangrove

Today, the northernmost distribution of *Avicennia* is limited to a latitude range of 1.8° of the diversified mangrove (Figure 1; Table 1; Quisthoudt et al., 2012). In the Middle Miocene (MMCO), this interval may have reached latitude range of about 15°, an interval that could be exaggerated considering the lack of data between palaeolatitudes 33°N (location 9) and 15°N (location 15) (Figures 3, 6–7; Table 1). During the Early Eocene

(PETM and EECO), this geographical difference in latitude would have been about 10–15° (Figures 2, 4–5, 7; Table 1). Obviously, the size of the gap is linked with warmth, even if the temperature may have been somewhat higher in the Mediterranean Basin, which was probably sheltered from cold air masses. Today, there is a latitudinal difference of about 9° in *Avicennia* distribution between mangrove consisting only of *Avicennia* and diversified mangrove in the South Hemisphere, illustrating the high potential thermal flexibility of the genus (Figure 1; Table 1; Quisthoudt et al., 2012).

To summarise, the maximum latitudinal gap for *Avicennia* distribution outside diversified mangrove could have been 15° during the three Cenozoic thermal maxima, which matches the 9° observed today and accounts for uncertainty in palaeolatitude estimates.

The simultaneous occurrence of several (PETM) and many (EECO) megathermal plants including mangrove taxa (represented by abundant pollen grains) (Figures 4–5; Table S2) marks diversified and well-developed mangrove. Considering the maximum latitudinal expansion of this mangrove, there is no or little latitudinal difference between the Early Eocene and today, which would be feasible in the case of an ‘equable’ climate during the Early Eocene (Figure 7; Table 1). However, a buffer zone between 35 and 65–70°N, where we recorded a diversified but scrawny mangrove with only few megathermal companions for the Early Eocene (Figures 4–5, 7; Table 1; Table S2), questions the relative influence of a more ‘equable’ climate and the ability of some taxa to invade cooler areas in the past. During the Middle Miocene, disregarding the probable peculiar environmental context of the Mediterranean domain (Figure 3), the moderate diversity in megathermal plants expressed by low pollen percentages (Figure 6; Table S2) suggests a transition between the buffer zone and the *Avicennia* mangrove, as witnessed during the Early Eocene, and signals the gradual withdrawal of the mangrove in Europe.

4.4 What is the relationship between the past *Avicennia*-only and diversified mangroves and the present mangrove provinces?

Avicennia comprises eight modern species (The Plant List, 2013) equally distributed in the AEP province (*A. bicolor*, *A. germinans*, *A. schaueriana*, *A. tonduzii*) and IWP province (*A. balanophora*, *A. integra*, *A. marina*, *A. officinalis*) (Dahdouh-Guebas, 2020). Some morphological characters make it possible to distinguish these species by their pollen (Thanikaimoni, 1987), as supported by our own observations (Figures S1–S3).

Precise observation of Early Eocene *Avicennia* pollen grains from the Arctic indicates the occurrence of several species, some specimens being very close to the modern species *A. germinans*, *A. marina* and *A. officinalis* (Figures S1–S2; Suan et al., 2017; Salpin et al., 2019; Suc et al., 2020). The same variety in *Avicennia* pollen morphology is observed in the other pollen records from the Early Eocene Atlantic latitudinal transect (Figure 2: locations 4–11; Figures S6–S9), suggesting similar specific diversity to that considered at the higher palaeolatitudes. According to the present geographical distribution of the three above-mentioned *Avicennia* species, it appears that no mangrove provincialism existed during the Early Eocene, in agreement with evidence at locations 4–11 (Figures 2, 4–5; Tables S1–S2), in addition to the Rhizophoraceae, of *Nypa* and *Xylocarpus*, currently restricted to the IWP province (Figure 1; Tomlinson, 1986). *Pelliciera*, now confined to the AEP province (Figure 1; Tomlinson, 1986), was already present in the Atlantic domain (location 9; Figures 2, 5; Tables S1–S2). These data are robust and support a Tethyan origin of mangroves, consequently, the regional taxonomic diversity resulted from the continental drift and not from an Indo-Pacific centre of origin (Ellison et al., 1999; Morley, 1999; Plaziat et al., 2001; Srivastava & Prasad, 2019).

A cluster of probably two *Avicennia* species inhabited the Mediterranean domain during the Middle Miocene with pollen indicating *A. marina* and *A. officinalis* (Figures S3, S10; Bessedik, 1981b). Today these species belong to the IWP province thereby contributing to the persistence of *Avicennia* in western Europe, favoured by large marine connections to the east while, at the same time, the eastern Atlantic shoreline is devoid of this taxon at similar palaeolatitudes (Figure 3). This could argue for provincial differentiation almost completely achieved during the Miocene, if not the ultimate occurrence of *Nypa* along the western Atlantic shoreline (location 15: Figure 3; Palacios Chavez & Rzedowski, 1993). The more restricted distribution of *Pelliciera* in the AEP province is confirmed by pollen flora found at location 15 (Figure 3; Palacios Chavez & Rzedowski, 1993).

These data lead us to conclude that mangrove provincialism progressively established itself after the Early Eocene warm period, probably forced by plate tectonics, the taxonomic impoverishment of the AEP province probably being caused by successive global colder periods (Plaziat et al., 2001; Srivastava & Prasad, 2019).

4.5 Persistence of mangrove during cooler periods between thermal optima

Our study focuses only on the three warmest episodes of the last 60 Ma but mangrove history obviously continued in the meantime. Here, we only recall or complete some items of this history, which was already summarised by Ellison et al. (1999), Plaziat et al. (2001) and Srivastava and Prasad (2019).

Considering its high expansion up to the northernmost latitudes during the PETM and EECO, logically *Avicennia* rarely occurred in the Arctic region up to the Mid-Eocene Climatic Optimum (MECO: 40 Ma; Suc et al., 2020). This late occurrence in the Arctic region also questions the potential ability of *Avicennia* to persist during cooler periods and/or its possible latitudinal shifts between the EECO and MECO, unless the thermal amplitude suggested by the $\delta^{18}\text{O}$ curves is over-estimated. Its southward retreat is illustrated by one last Early Oligocene occurrence (with no other mangrove taxon) at Site 345 (NW Norway; study in progress). Only *Avicennia* was present in the northwestern Mediterranean Oligocene (study in progress), where it persisted up to the earliest Serravallian (Bessedik, 1984; Jiménez-Moreno & Suc, 2007). The youngest record of *Avicennia* at similar palaeolatitude on the European side of the Atlantic belongs to the early Burdigalian. *Avicennia* persisted in the southern Mediterranean and Atlantic Morocco up to the late Messinian (Suc et al., 2018). The ultimate reliable record of *Avicennia* concerns the Early Pliocene in the southern Black Sea (Biltekin et al., 2015). *Avicennia* expansions and retreats very closely mirror increases and decreases in temperature, respectively, and were driven by the opportune opening or persistence of marine gateways.

The most recent evidence of a diversified and well-developed mangrove in the northwestern Mediterranean Basin was in the Bartonian (ca. 40 Ma) with, in addition to *Avicennia*, *Pelliciera*, *Bronlowia*, *Nypa*, *Heritiera* and *Aegiceras* (Cavagnetto & Anadón, 1995). A scrawny mangrove was still present during the Oligocene in northern Turkey, including *Avicennia*, *Pelliciera* and *Nypa* (Akgün et al., 2013). These data complete the information on the process of disjunction of the modern mangrove biogeographic provinces, which occurred during the Late Eocene and Oligocene and ended in the earliest Neogene.

5 CONCLUSION

A set of eleven pollen floras arranged along a North Atlantic latitudinal transect were analysed using a botanical approach and provide information on mangrove distribution and diversity during the warmest Palaeogene phases (PETM and EECO). Evidence is provided

for two palaeolatitudinal thresholds, at respectively 65–70°N and 35°N, separating the *Avicennia*-only mangrove (which reached 80°N) from a diversified but scrawny mangrove, and then from a diversified and well-developed mangrove. These thresholds, which moderate the so-called Early Eocene ‘equable’ climate hypothesis, were probably due to latitudinal changes in temperature and possibly in solar irradiation. The latitudinal gap between the northward expansion of *Avicennia* and diversified mangrove during the three Cenozoic thermal maxima (10–15°) could have been almost similar to the southward gap observed today in Australia (9°; Table 1). This mangrove organisation once more reveals significant discrepancies between models and proxies, unless the temperature estimates deduced from *Avicennia* and some mangrove and other megathermal plants have been somewhat exaggerated when these taxa only are represented by a few pollen grains. A similar expansion event occurred during the MMCO but chiefly concerned *Avicennia*, which benefited from propitious conditions in the Mediterranean Basin documented by nine pollen records, also suggesting *Avicennia*’s possibly greater adaptive ability in the past.

Our results concerning the Early Eocene North Atlantic and Arctic mangroves provide the missing link to robustly support the Tethyan origin of mangroves, the provincialism of which started in the Late Eocene probably forced by continental drift, and ended in the Early Neogene. The subsequent global colder periods probably played a key role impoverishing the Western mangroves.

Table 1. Latitudinal distribution and diversification of mangroves during three noteworthy thermal maxima compared to Present.

| PETM and EECO | | MMCO | | Present | | Hemisphere |
|----------------|---|----------------|---|-----------|---|-----------------------|
| Palaeolatitude | Mangrove type | Palaeolatitude | Mangrove type | Latitude | Mangrove type | |
| 70-80°N | <i>Avicennia</i> -only mangrove | | | | | N O R T H |
| 60-70°N | No data | | | | | |
| 35-60°N | Diversified but scrawny mangrove | | | | | |
| <35°N | Diversified and well-developed mangrove | 33-45°N | <i>Avicennia</i> -only mangrove | 30-31.8°N | <i>Avicennia</i> -only mangrove | |
| | | 15-33°N | No data | <30°N | Diversified and well-developed mangrove | |
| | | ?<20°N | Diversified and well-developed mangrove | | | |
| | | | | <30°S | Diversified and well-developed mangrove | S O U T H |
| | | | | 30-39°S | <i>Avicennia</i> -only mangrove | |
| 65°S | <i>Nypa</i> | | | | | |

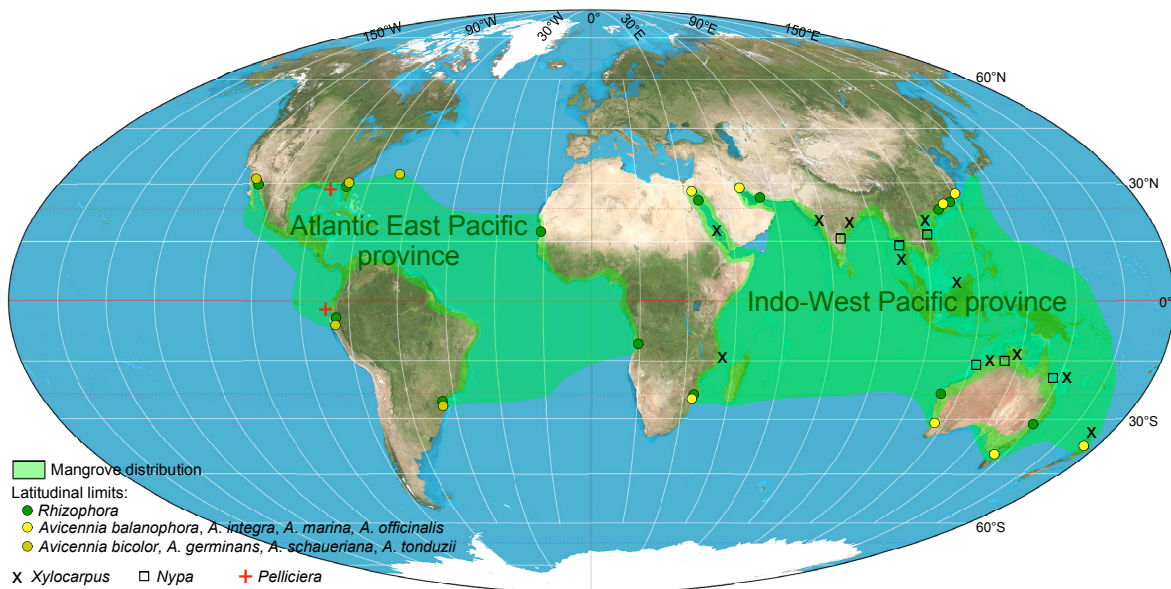


Figure 1. Present-day geographic distribution of mangroves with respect to their two provinces with information on occurrence of some taxa according to Tomlinson (1986) and latitudinal limits of *Avicennia* and *Rhizophora* according to Quisthoudt et al. (2012). The used geographic map is from Strebe, D. R. – CC BY-SA 3.0 (Mollweide projection equal-area), <https://commons.wikimedia.org/w/index.php?curid=16115320>.

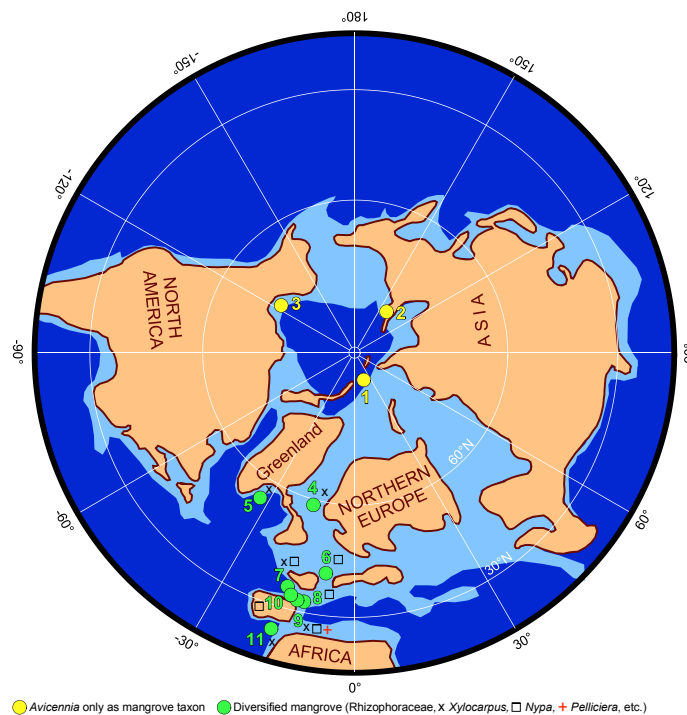


Figure 2. Palaeocene-Eocene (PETM) and early Eocene (EECO) mangrove pollen records (with information on the occurrence of some taxa) along a North-South transect. Palaeogeographical map with estimated palaeolatitudes (Polar orthographic Projection) is from Backman et al. (2006) and Eberle & Greenwood (2012), modified by Suc et al. (2020).

Locations: 1, Site M0004A; 2, Faddeevsky Island; 3, Caribou Hills; 4, Site 343; 5, Site 918; 6, Kallo 027E148; 7, Noirmoutier; 8, Calavanté 1; 9, Morlaàs 1; 10, Gan; 11, Site 547.

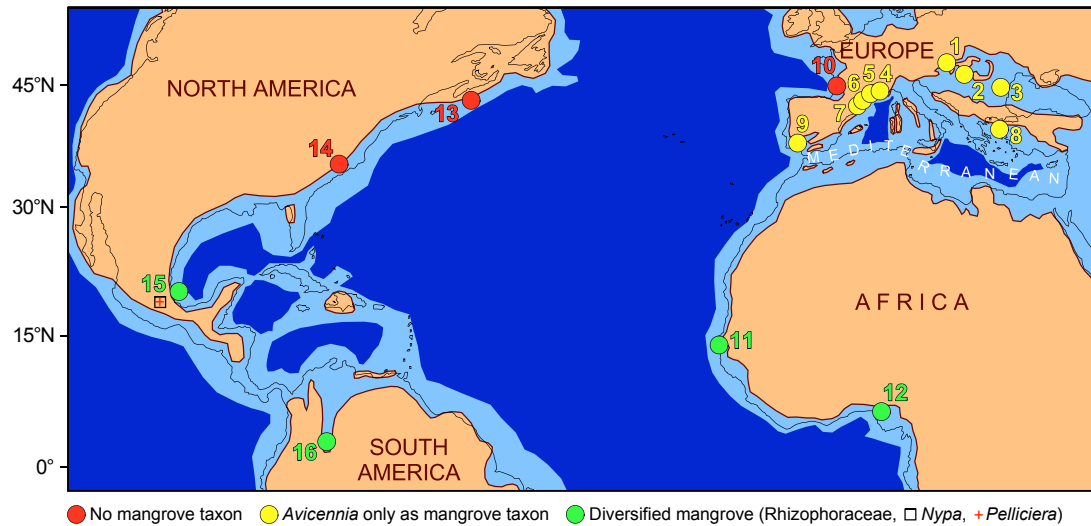


Figure 3. Mid-Miocene (MMCO) mangrove pollen records (with information on the occurrence of some taxa) along a North-South transect. Palaeogeography is from Rögl (1999) and Jolivet et al. (2006) for the Mediterranean region *s.l.* Atlantic–Pacific palaeogeography is from Herold et al. (2009), Scotese (2014), and Cao et al. (2017). The current geographic outline is from Strebe, D. R. – CC BY-SA 3.0 (Mollweide projection equal-area), <https://commons.wikimedia.org/w/index.php?curid=16115320>. The estimated palaeolatitude of each location is indicated in Table S1.

Locations: 1, Göllersdorf; 2, Herend 46; 3, Balgarevo C136A; 4, Les Mées 1, Châteauredon; 5, Estagel, Bayanne; 6, Narbonne V. Hugo College, Lespignan II, Montady, Saint-Géniès, Montagnac, Mèze, Loupian, Issanka, Poussan, Montbazin; 7, La Rierussa, Sant Pau d’Ordal; 8 Kultak; 9, Alboran A1; 10, Laborde 1D; 11, Bignona well; 12, Niger Delta well M1; 13, Site M00027; 14, Alum Bluff; 15, La Herradura; 16, Apaporis River.

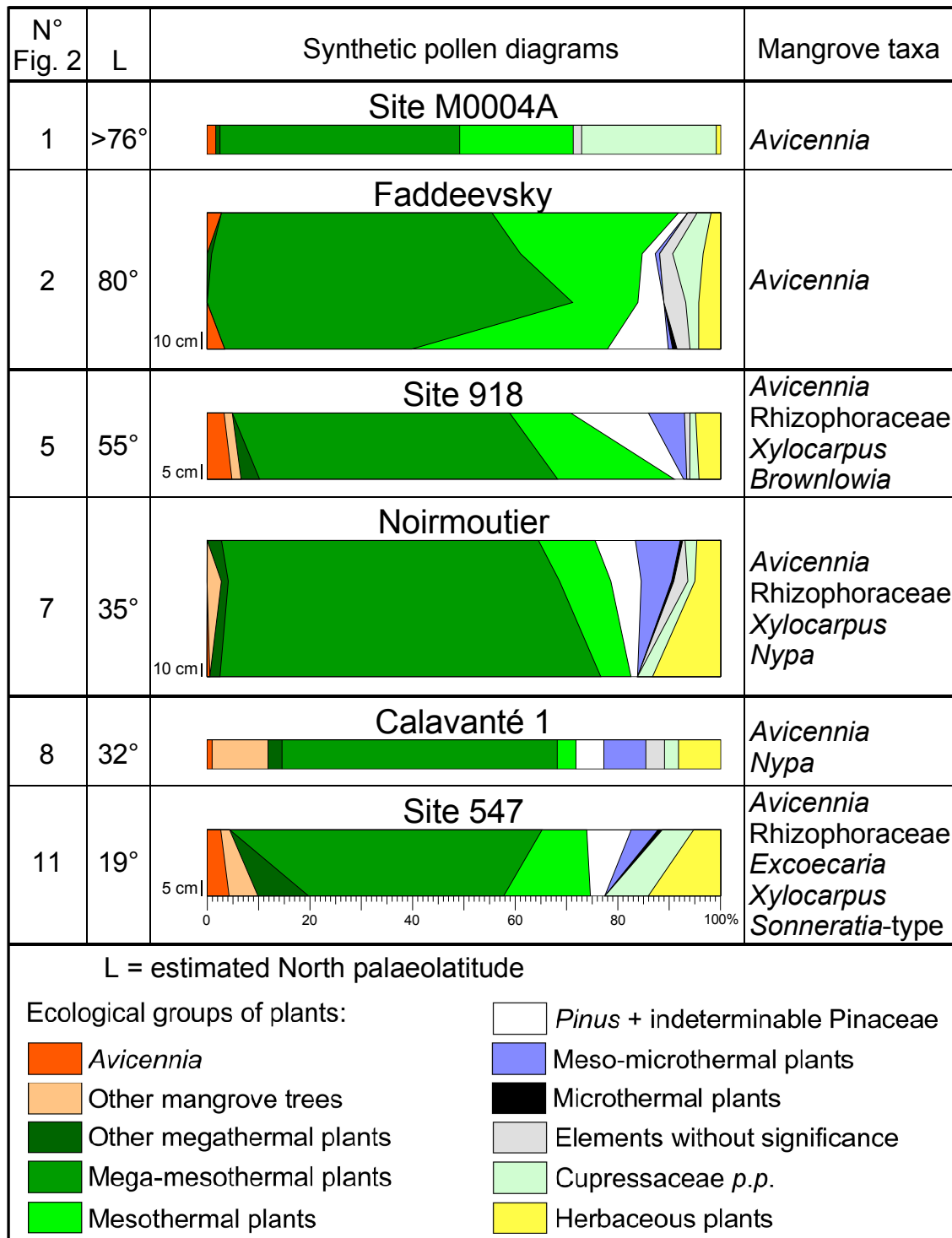


Figure 4. Synthetic diagrams of PETM pollen records arranged according to their estimated palaeolatitude with listing of their mangrove woody taxa. Site Number (No) refers to Figure 2.

Detail of taxa constituting the ecological groups of plants is given in Table S2.

For locations made of several samples, the thickness scale is indicated to the left of the diagram.

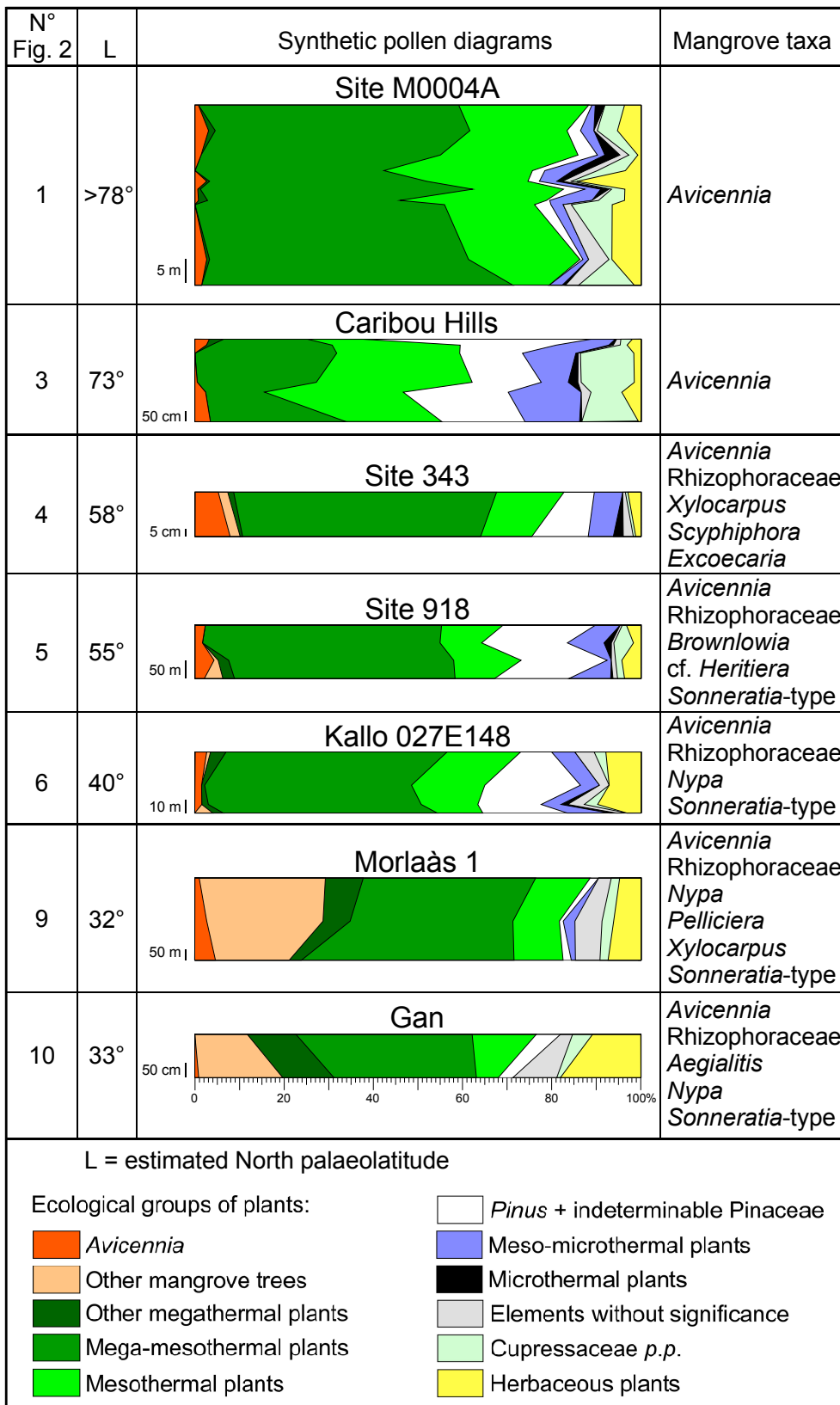


Figure 5. Synthetic diagrams of EECO pollen records arranged according to their estimated palaeolatitude with listing of their mangrove woody taxa. Site Number (No) refers to Figure 2.

For locations made of several samples, the thickness scale is indicated to the left of the diagram.

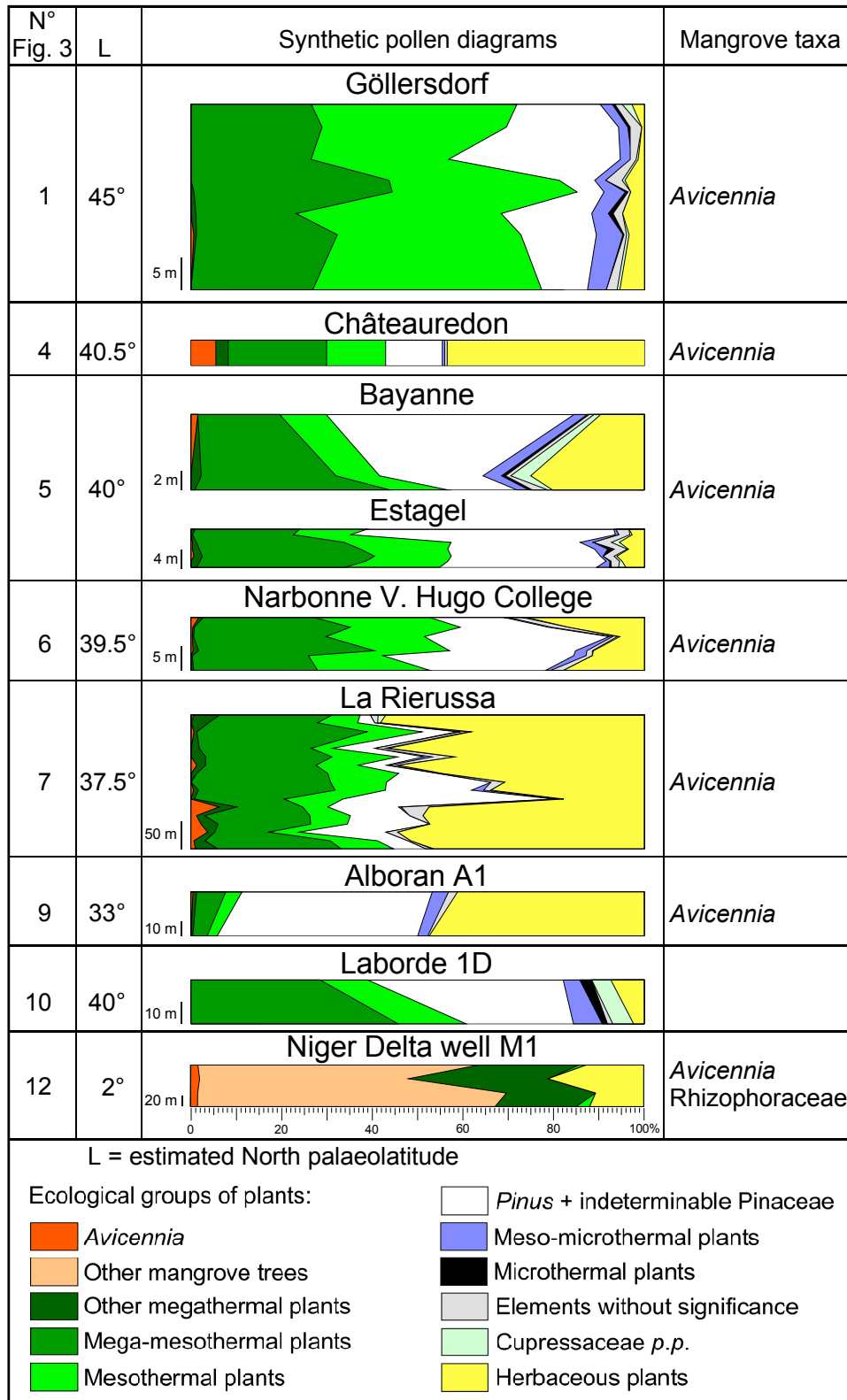


Figure 6. Synthetic diagrams of some selected MMCO pollen records arranged according to their estimated palaeolatitude with listing of their mangrove woody taxa. Site Number (No) refers to Figure 3.

For locations made of several samples, the thickness scale is indicated to the left of the diagram.

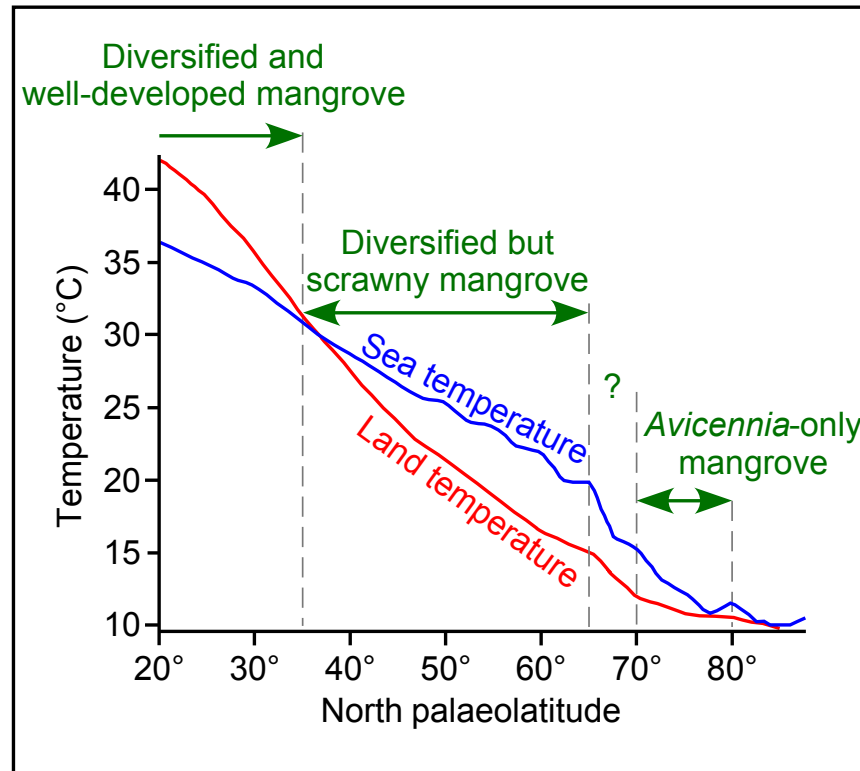


Figure 7. Sea surface temperature (SST) vs. land (air) mean annual temperature (MAT) and mangrove distribution and diversification in the North Hemisphere during the Early Eocene (simulation E17 from: Sagoo et al., 2013).

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

The detailed pollen data are stored in the Dryad repository (URL for the Miocene pollen records: <https://doi.org/10.5061/dryad.n02v6wwxn>; URL for the Eocene pollen records: <https://doi.org/10.5061/dryad.4j0zpc8bt>).

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BIOSKETCH

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Authors' Contribution: S.-M.P. & J.-P.S conceived the research, performed the Early Eocene pollen analyses, contributed to the Mid-Miocene pollen analyses, and wrote the first draft of the paper; S.F. contributed by specifying the thermal requirements of the mangrove plant ecosystems and performed the climatic data-model comparison; M.B. and G.J.-M. provided several unpublished Mid-Miocene pollen analyses; C.R. helped conceive the research; L.L. contributed by estimating the palaeolatitude of the study locations. All the authors contributed to improve the manuscript.

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