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Eocene/Oligocene global disruption and the revolution of Caribbean mangroves

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Abstract. In a recent paper, the author demonstrated that, in contrast with the prevailing view of eventual gradual regional differentiation from a hypothetical Cretaceous pantropical mangrove belt around the Tethys Sea, the Caribbean mangroves originated de novo in the Eocene after the evolutionary appearance of the first mangrove-forming tree species known for the region, the ancestor of the extant *Pelliciera*. This paper represents a second step in the analysis of the evolution of Caribbean mangroves dealing with the most important change experienced by these communities, occurring across the Eocene–Oligocene transition (EOT), which is termed here the Caribbean mangrove revolution. This shift consisted of the disappearance of the primeval *Pelliciera* mangroves and their replacement by mangrove communities dominated by *Rhizophora*, a newly emerged mangrove tree that still dominates extant Caribbean mangroves. This paper first reviews the available literature on the EOT global disruption (tectonic and paleogeographic reorganizations, ocean circulation, cooling, Antarctic glaciation, sea-level fall) and its regional manifestations in the study area, along with the corresponding biotic responses. This provides the paleoenvironmental framework with which to analyze the EOT mangrove revolution using the nearly 80 pollen records available for the region. In the circum-Caribbean region, cooling of 3-6 °C and a sea-level fall of 67 m were recorded between 33.8 and 33.5 Ma, which led to significant shifts in dispersal pathways and barriers, as well as in marine paleocurrents. Late Eocene mangroves were dominated by the autochthonous *Pelliciera* (up to 60% of pollen assemblages), while *Rhizophora*, which likely arrived from the Indo-Pacific region by long-distance dispersal, was absent or very scarce. After the EOT, the situation was radically different, as the mangroves were widely dominated by *Rhizophora,* and *Pelliciera*, when present, was a subordinate mangrove element (<10%). At the same time, *Pelliciera*, which had been restricted to a small patch (Central America and NW South America or CA/NWSA) during the Eocene, expanded its range across the Caribbean and beyond, always as a minor component of *Rhizophora* mangroves. The dominance shift could have been due to the cooling, by favoring the expansion of the euryclimatic and vagile *Rhizophora* over the stenoclimatic *Pelliciera*, of limited dispersal ability. This is considered a case of competitor coexistence by niche segregation. In addition, *Rhizophora* could have facilitated the expansion of *Pelliciera* by providing refuge against environmental and biotic stressors, notably light intensity and salinity. The Eocene *Pelliciera* mangroves never returned, but this species survived to the present as a minor element and experienced significant range shifts along three main phases, namely, EOT–Miocene expansion to the whole neotropics, Mio-Pliocene contraction to the southern Caribbean margin and Pliocene to recent reorganization to the original Eocene CA/NWSA location. The potential role of Neogene and Pleistocene climatic shifts and human activities in these biogeographical loops (taxon cycles) is discussed, with an emphasis on precipitation. The paper ends by suggesting some prospects for future research.

Keywords. Eocene/Oligocene boundary, Neogene, climatic change, paleogeography, sea level, mangroves, evolution, biogeography, Caribbean, Neotropics

*This paper is dedicated to Jan Muller for his contribution to Paleogene and Neogene Neotropical palynology.

1. Introduction

Mangroves are unique forested ecosystems that dominate the intertidal fringe of tropical and subtropical coasts worldwide and occupy a total of nearly 140,000 km^2 (Lugo & Snedaker, 1974; Bunting et al., 2018). Mangrove forests are usually dominated by a few mangrove-forming tree species that provide the structural basis for the development of these characteristic ecotonal land–sea communities (Chapman, 1976; Tomlinson, 2016), which are instrumental in the maintenance of terrestrial and marine biodiversity and play a key role in the functioning of global biogeochemical cycles (Saenger, 2002; Nagelkerken et al., 2008; Nizam et al., 2022). Mangroves are highly sensitive to climatic changes, sea-level shifts and human pressure (Gilman et al., 2008; Spalding et al., 2014; Biswas & Biswas, 2019; Wang & Gu, 2021) and are currently among the world's most threatened ecosystems (Worthington et al., 2020).

Biogeographically, mangroves display a global asymmetric biodiversity pattern with maximum species richness (up to 47 species) in the Indo–West Pacific (IWP) region and minimum diversity (up to 12 species) in the Atlantic–Caribbean–East Pacific (ACEP or AEP) region, along with important specific disjunctions within the most relevant genera (Ellison et al., 1999; Tomlinson, 2016; Duke, 2017) (Fig. 1). This pattern has been explained assuming a hypothetical continuous pantropical mangrove belt along the coasts of the Cretaceous Tethys Sea that would have been disrupted after the closing of this sea by the African barrier, which would have promoted regional evolutionary differentiation in the eastern and western hemispheres (McCoy & Heck, 1976; Sowunmi, 1986; Ellison et al., 1999; Plaziat et al., 2001; Duke, 2017; Srivastava & Prasad, 2015, 2018). However, this view has recently been challenged by a review of palynological evidence that did not support the assumed Cretaceous precursors of Caribbean mangroves and, instead, found robust evidence for a de novo Mid-Eocene (Lutetian) origin of these Neotropical ecosystems (Rull, 2022a). The key evolutionary innovation for the origin of Caribbean mangroves was the unexpected evolutionary appearance of the oldest known mangrove-forming tree represented by form-species *Lanagiopollis crassa*, the fossil pollen representative of the modern genus *Pelliciera*, which provided the structural basis for the development of mangrove ecosystems, without which these communities would not have existed. These findings were possible thanks to the quantitative analysis of pollen evidence using a community assemblage approach instead of the formerly used qualitative approach based on the presence/absence of individual fossil taxa with botanical affinity to modern mangrove species (Rull, 2022a).

Modern Caribbean mangroves, however, are very different in composition and are not evolutionary descendants of their Mid-Late Eocene counterparts. Indeed, *Pelliciera*, which was of Neotropical distribution during the Eocene, went abruptly extinct in most of its range in post-Eocene times, and the remaining extant representative, *P. rhizophorae*, is now restricted to a relict spot around the Panama Isthmus, where it plays a subordinate role within mangrove communities dominated by other tree species (Dangremond et al., 2015; Duke, 2020). Extant Neotropical mangroves are dominated by mangrove trees of the genera *Rhizophora*, *Avicennia* and *Laguncularia* (Tomlinson, 2016), belonging to disparate families and even orders with no direct phylogenetic relationships among them or with *Pelliciera* (Table 1 and Fig. 2). Relevant examples of the corresponding phylogenies can be found in Schwarzbach & Ricklefs (2000), Schwarzbach & McDade (2002), Andergerg et al. (2002), Geuten et al. (2004), Schönenberger et al. (2004), Tripp & McDade (2014), Fonseca (2021) and Maurin et al. (2021). This means that extant Caribbean mangroves, as communities, are structurally and ecologically similar to

Eocene mangroves but are organized around tree species belonging to distant evolutionary lineages. Thus, the habit, architectural features and physiological traits of Caribbean mangrove trees are examples of the evolutionary convergence of non-closely

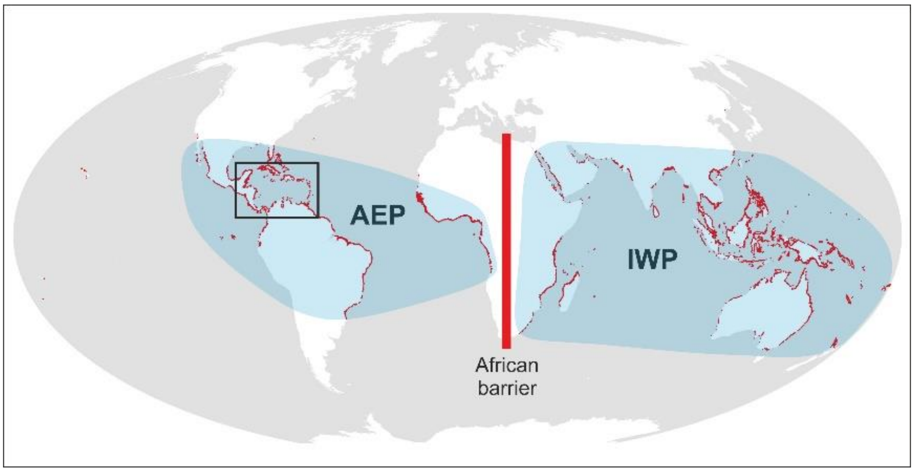


Figure 1. World distribution of mangroves (red fringes) showing the Atlantic-East Pacifc (AEP) and the Indo-West Pacific (IWP) biogeographical regions. The Caribbean region is highlighted by a black box. Base map downloaded from the World Atlas of Mangroves (https://data.unep-wcmc.org/datasets/5).

related taxa, resulting from adaptation to intertidal saline environments. Therefore, the appearance of modern-like mangrove ecosystems represented a second evolutionary surprise linked, once more, to the emergence of new mangrove-forming trees within unexpected taxonomic groups, rather than to the phylogenetic progress of already existing mangrove species.

Table 1. Extant Caribbean mangrove-forming tree species grouped by order and family, to emphasize their high phylogenetic diversity (see also Fig. 2). The most abundant and characteristic species are indicated by an asterisk. The number of worldwide mangrove species within each genus (spp) is also provided for comparison. Distribution range: AEP, Atlantic-East Pacific region (Fig. 1); Af, Africa; Am, America. Raw data from Tomlinson (2016) and Duke (2017).

Family (Order)	**Genus**	**Range**	**spp**	**Caribbean**	**Range**
Malpighiaceae (Malpighiales)	*Rhizophora*	Pantropical	6	*R. mangle**	AEP (Af-Am)
				R. racemosa	AEP (Af-Am)
Acanthaceae (Lamiales)	*Avicennia*	Pantropical	8	*A. germinans**	AEP (Af-Am)
				A. bicolor	AEP (Am)
				A. shaueriana	AEP (Am)
Combretaceae (Myrtales)	*Laguncularia*	AEP	1	*L. racemosa**	AEP (Af-Am)
	Conocarpus	AEP	1	*C. erectus*	AEP (Af-Am)
Tetrameristaceae (Ericales)	*Pelliciera*	AEP	1	*P. rhizophorae*	AEP (Am)

According to the available fossil evidence (Fig. 3), the evolutionary replacement of Eocene mangroves by modern-like Caribbean mangroves took place in the Eocene–Oligocene transition (EOT), a geological boundary characterized by global and intense environmental and biogeographical disruptions (Prothero & Berggren, 1992; Coxall & Pearson, 2007). Therefore, the evolution of Caribbean (and, by extension, of Neotropical) mangroves has been punctuated by two main abrupt and unexpected events, namely, (i) the dawn of the primeval Eocene *Pelliciera* mangrove communities and (ii) their post-Eocene collapse and replacement by modern-like mangrove forests. After the EOT, a trend toward increasing species richness with no apparent extinctions characterized the evolution of post-Eocene mangrove forests, in the shaping of the extant taxonomic and biogeographical patterns of Caribbean mangroves

(Graham, 1995). The first event (i) was analyzed in detail by Rull (2022a), and the second (ii) is the main target of this review.

An early attempt to review the potential influence of EOT global disruptions on the evolution of Neotropical mangroves was made by the author of this paper (Rull, 1998a), who concluded that the global cooling and drying reversals in the EOT could have affected the taxonomic and

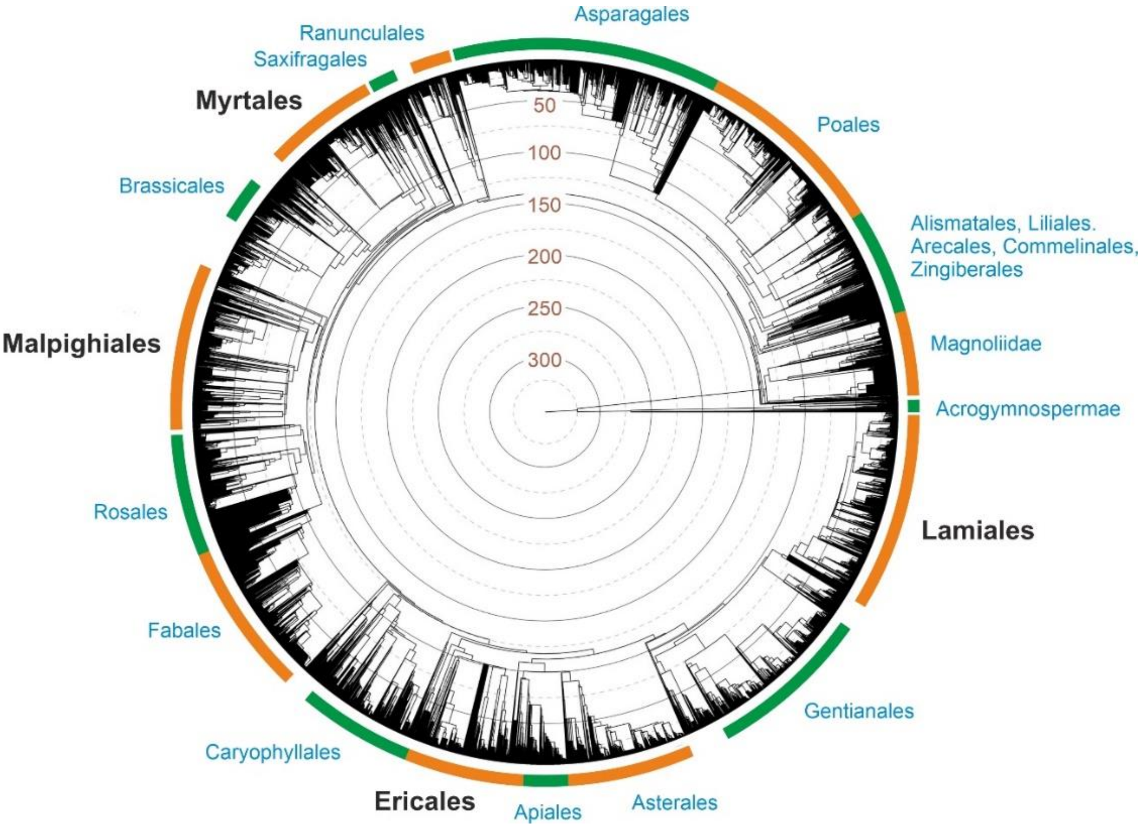


Figure 2. Dated angiosperm phylogeny, based on global molecular genetic and phylogenetic data from GenBank and the Open Tree of Life project (Smith & Brown, 2018), showing the disparate phylogenetic and chronological features of the orders with extant Caribbean mangrove-forming tree genera: Myrtales (*Laguncularia* and *Conocarpus*; Combretaceae), Malpighiales (*Rhizophora*; Rhizophoraceae), Ericales (*Pelliciera*; Tetrameristaceae) and Lamiales (*Avicennia*; Acanthaceae). Numbers are divergence ages in million years.

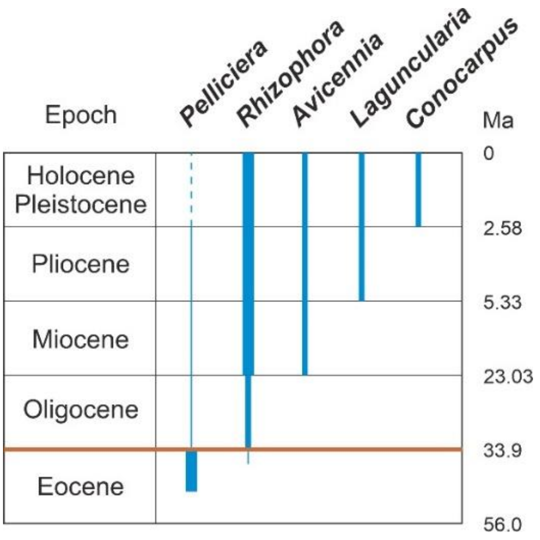


Figure 3. Stratigraphic ranges of the fossil pollen taxa representing the modern genera of Caribbean mangrove trees. Redrawn from Rull (2022a) after raw data from Muller (1981), Frederiksen (1985), Lorente (1986), Mullet et al. (1987), Thanikaimoni (1987) and Graham (1995, 1999a). Boundary dates after Cohen et al. (2013).

biogeographical turnover observed in the mangrove pollen record. However, only qualitative (presence/absence) fossil evidence was used on that occasion, which is insufficient to reconstruct the origin and evolution of mangrove ecosystems (Rull, 2022a). In addition, molecular phylogenetic studies for Caribbean mangrove taxa were still unavailable in the 1990s, and their recent development has been instrumental in reconstructing their evolution (Graham, 2006; Duke, 2017). Additionally, new and meaningful paleoenvironmental and paleogeographic information on the EOT has been produced and modeled in recent decades that was unavailable at the time of the first review on the subject (compare, for example, Prothero & Berggren, 1992, with Hutchinson et al., 2021). Finally, the review by Rull (1998a) was written in Spanish, which limits access for those unable to read in this language. Therefore, the need for an updated English review on the possible influence of EOT events on Caribbean mangrove evolution that considers relevant and previously unavailable multiproxy information seems evident, and providing such a review is the main aim of the present paper.

In this review, mangrove communities are reconstructed using the community approach based on quantitative evidence (usually percentages), and the evolution of their main components, the mangrove-forming tree taxa, is approached with the aid of molecular phylogeographical methods or spatial projections of dated phylogenies. These methods provide robust reconstructions of spatiotemporal trends in mangrove communities that are compared with paleoenvironmental and paleogeographic trends, as deduced from independent proxies, to establish potential chronological correlations that suggest possible causal relationships. To facilitate reading and understanding, the paper is subdivided into four main parts. The first part is a summary of the main EOT events, aimed at providing a general paleoenvironmental, paleogeographical and biogeographical framework for this particular boundary. This part is of global scope, and the main topics reviewed are climate change and its potential causes, biotic responses and global mangrove evolution, with emphasis on *Pelliciera* and *Rhizophora*. The second part is focused on the Caribbean region and is a summary of the physical (tectonics, paleogeography, paleoclimates, paleocirculation, sea-level shifts) and biogeographical features of this region during the EOT. Once the general and Caribbean physical and biological frameworks have been outlined, the third part analyzes in detail the qualitative and quantitative fossil palynological evidence of mangrove evolution during the Eocene and the Oligocene, with emphasis on the transition between these two geological epochs. The main aim of this part is to discuss mangrove evolution and the potential environmental and biotic drivers involved in the shift from *Pelliciera*-dominated to *Rhizophora*-dominated mangroves during the EOT in the Caribbean region. A summary of the main Neogene trends is also provided for reference, but they are not analyzed in depth, as Mio-Pliocene evolution shaped present-day Caribbean mangrove communities and this topic deserves specific treatment by itself. The fourth part of the analysis is an account of the range shifts of *Pelliciera* from the Eocene to the present and their possible causes, which are addressed using a novel biogeographical framework provided by the fossil evidence gathered here. Finally, a conclusions section aims to provide a take-home message by highlighting the main findings, with emphasis on novel approaches to classical issues, and suggests some possible future research directions. It is important to note that this paper considers the whole circum-Caribbean region as a biogeographic unit (Fig. 4).

2. The Eocene–Oligocene transition

Initially, the EOT was defined as a phase of accelerated climatic and biotic change that began at the Eocene/Oligocene (E/O) boundary (33.9 Ma) and lasted ~500 kyr (Coxall & Pearson, 2007). Further studies led to a slightly different scenario, with the EOT ranging from 34.4 Ma to 33.7 Ma, with a duration of ~800 kyr (Hutchinson et al., 2021). The first compilation of the available evidence was published by Prothero & Berggren (1992) in a seminal multidisciplinary book. More recently, Coxall & Pearson (2007) and Hutchinson et al. (2021) updated the review, accounting for the addition of new methodological developments on paleoclimatic proxies and the outstanding contribution of the Ocean Drilling Program (ODP; https://www.iodp.org/) to the characterization of the EOT. The same authors reviewed the potential causes for the climatic shift, as well as the potential consequences of these events for terrestrial and marine biotas.

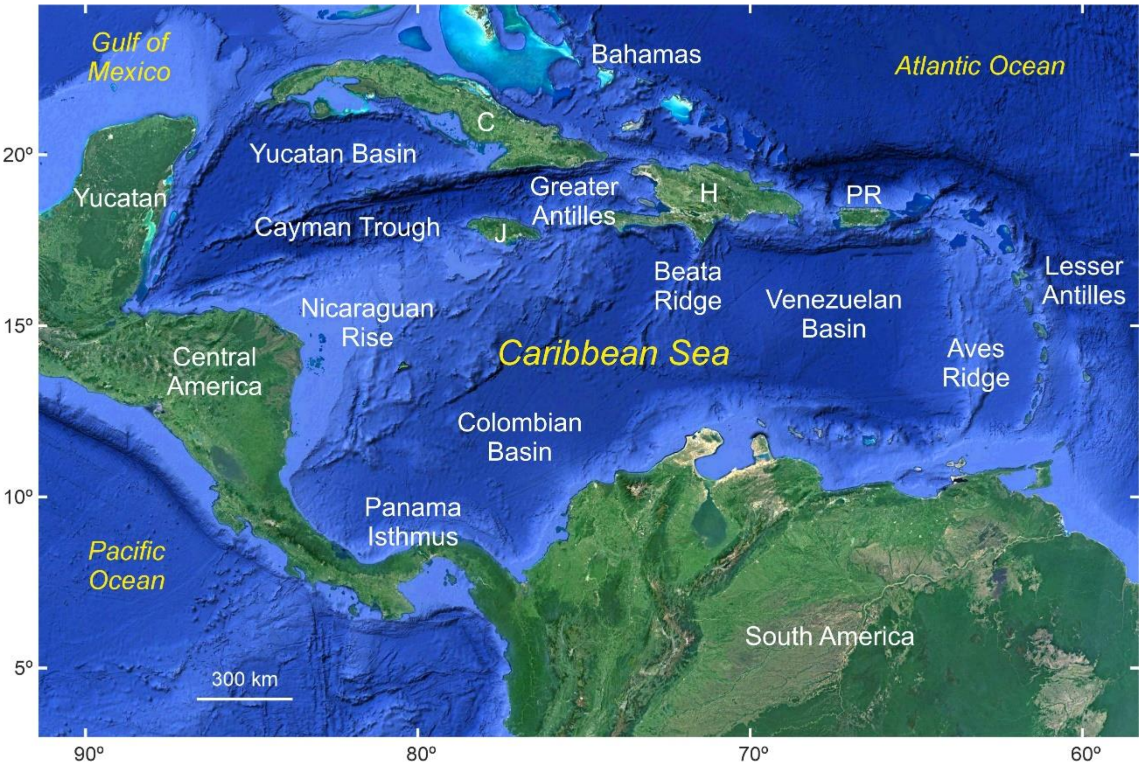


Figure 4. Google-Earth map of the circum-Caribbean region considered in this paper. Greater Antilles: C, Cuba; H, Hispaniola, J, Jamaica; PR, Puerto Rico,

2.1. Climatic and sea-level change

Presently, there is consistent and widespread evidence for global EOT cooling, as recorded by oxygen isotopic ($^{18}\delta O$) records of benthic foraminifera from deep-sea marine cores retrieved worldwide by the Ocean Drilling Program (ODP) (Diester-Haas & Zhan, 1996; Zachos et al., 1996; Coxall et al., 2005; Coxall & Pearson, 2007; Pearson et al., 2008; Coxall & Wilson, 2011; Bohaty et al., 2012; Wade et al., 2012; Borrelli et al., 2014; Langton et al., 2016) (Fig. 5). This global cooling represented the end of Cenozoic greenhouse climates that dominated Earth until the Eocene and the onset of Cenozoic icehouse climates, which persist today. A prominent consequence of the EOT cooling was the glaciation of Antarctica, which remained unglaciated until the Eocene (Katz et al., 2008; Young et al., 2011). There is no comparable evidence for the Northern Hemisphere, and it is accepted that only Antarctica was glaciated during the Oligocene (Zachos et al., 2001; Westerhold et al., 2020). Evidence for Northern Hemisphere glaciation is not available until the Late Miocene (11-6 kyr BP) in Greenland (Larsen et al., 1994; Helland & Holmes, 1997; Maslin et al., 1998; Bierman et al., 2016; Pérez et al., 2018), with outstanding intensification across Greenland, Eurasia and North America around the Pliocene/Pleistocene boundary (2.6 Ma) (Shackleton, 1984; Raymo, 1994; Ehlers & Gibbard, 2007; De Schepper et al., 2014).

The EOT cooling was also responsible for the establishment of strong latitudinal temperature gradients, which has suggested that this phenomenon was the precursor of present-day Earth's global climatic zonation (Pagani et al., 2011; Straume et al., 2022). During the Eocene, a low-temperature gradient existed, manifested as high-latitude temperatures 20-40 °C higher than those today and tropical temperatures only 5-10 °C above present ones (Huber & Sloan, 2000; Huber, 2008; Bijl et al., 2009; Huber & Caballero, 2011), along with the occurrence of frost-intolerant flora and fauna at high latitudes (Greenwod & Wing, 1995). A number of continental biotic records also suggest a trend toward aridification in the EOT, but it is still unclear whether this may be considered a global phenomenon (Coxall & Pearson, 2007; Hutchinson et al., 2021). Not only climate but also sea levels abruptly shifted across the E/O boundary. The available evidence points toward a general sea-level fall of ~70 m (Miller et al., 2008; Houben et al., 2012; Wilson et al., 2013), likely linked to Antarctic glaciation, which led to marine disconnections that affected circulation patterns (Coxall et al., 2018; Hutchinson et al., 2019).

The EOT cooling and the glaciation of Antarctica have been linked to the interplay of three main mechanisms, namely, a significant reduction in global atmospheric CO_2 concentration, the establishment of the Antarctic Circumpolar Current (ACC) and ice sheet growth (DeConto & Pollard, 2003; Hutchinson et al., 2021; Straume et al., 2022). During the EOT, $p\mathrm{CO}_2$ values experienced an outstanding decline from ~1000 ppm in the Priabonian to 700-800 ppm in the Rupelian, which significantly reduced the greenhouse effect. The use of several modeling approaches suggested that this could have been the main cooling driver (Hutchinson et al., 2021). In addition, the Late-Eocene tectonic opening of Southern Ocean pathways in the Drake Passage and the Tasman (or Tasmanian) Gateway (Fig. 5) would have facilitated the establishment of the ACC circulation leading to the thermal isolation of Antarctica and accelerating its glaciation (Barker & Burrell, 1977; Barker & Thomas, 2004). The Drake Passage opening was already open before the Late Eocene, but it was too shallow to sustain the ACC (Livermore et al., 2007; Markwick, 2007). The appearance of a deep (>500 m) opening across the Tasman Gateway occurred at 33.5 Ma, close to the E/O boundary (Stickley et al., 2004; Scher et al., 2015), and both pathways would have been suitable to support the ACC by 30 Ma (Hutchinson et al., 2021). Recently, it has also been suggested that connections between the Arctic and North Atlantic through the Fram Strait and the Greenland–Scotland Rise (Fig. 5) could have played a role in EOT cooling and Antarctic glaciation by regulating the southward flow of cold Arctic freshwaters (Straume et al., 2022). According to the available modeling outputs, albedo-driven changes in radiative forcing due to the growth of the Antarctic ice sheet would have played a secondary role (Hutchinson et al., 2021).

2.2. Biotic responses

The E/O boundary was a time of intense biotic turnover due to enhanced Eocene extinction and Oligocene radiation rates, as well as major biogeographical reorganizations, which have been linked to rapid EOT cooling and sea-level fall and to the establishment of permanent icehouse conditions. Although these biotic changes did not attain the magnitude of the "Big Five" mass extinctions (Sepkoski, 1986; Jablonsky & Chaloner, 1994), they significantly affected Earth's terrestrial and marine biotas (Coxall & Pearson, 2007). Relevant extinctions appear in marine microfossils that are used as chronostratigraphic markers. One of the most characteristic examples is the planktonic foraminiferal family Hantkeninidae, whose last occurrence is the E/O marker in the Global Stratotype Section of this boundary (Premoli Silva &

Jenkins, 1993). In general, the EOT transition is characterized by the extinction of warm-loving tropical planktonic foraminifera, which has been attributed to the rapid cooling recorded in this transition (Boersma & Premoli Silva, 1986; Keller et al., 1992). Similar examples can be found in benthic foraminifera, calcareous nannoplankton, radiolarians, dinoflagellates, diatoms, ostracodes and shallow-marine invertebrates (Balfauf, 1992; Berggren et al., 1995; Schellenberg, 1998; Dockery & Lozouet, 2003; Nebelsick et al., 2005; Van Mourik & Brinkhuis, 2005; Funakawa et al., 2006).

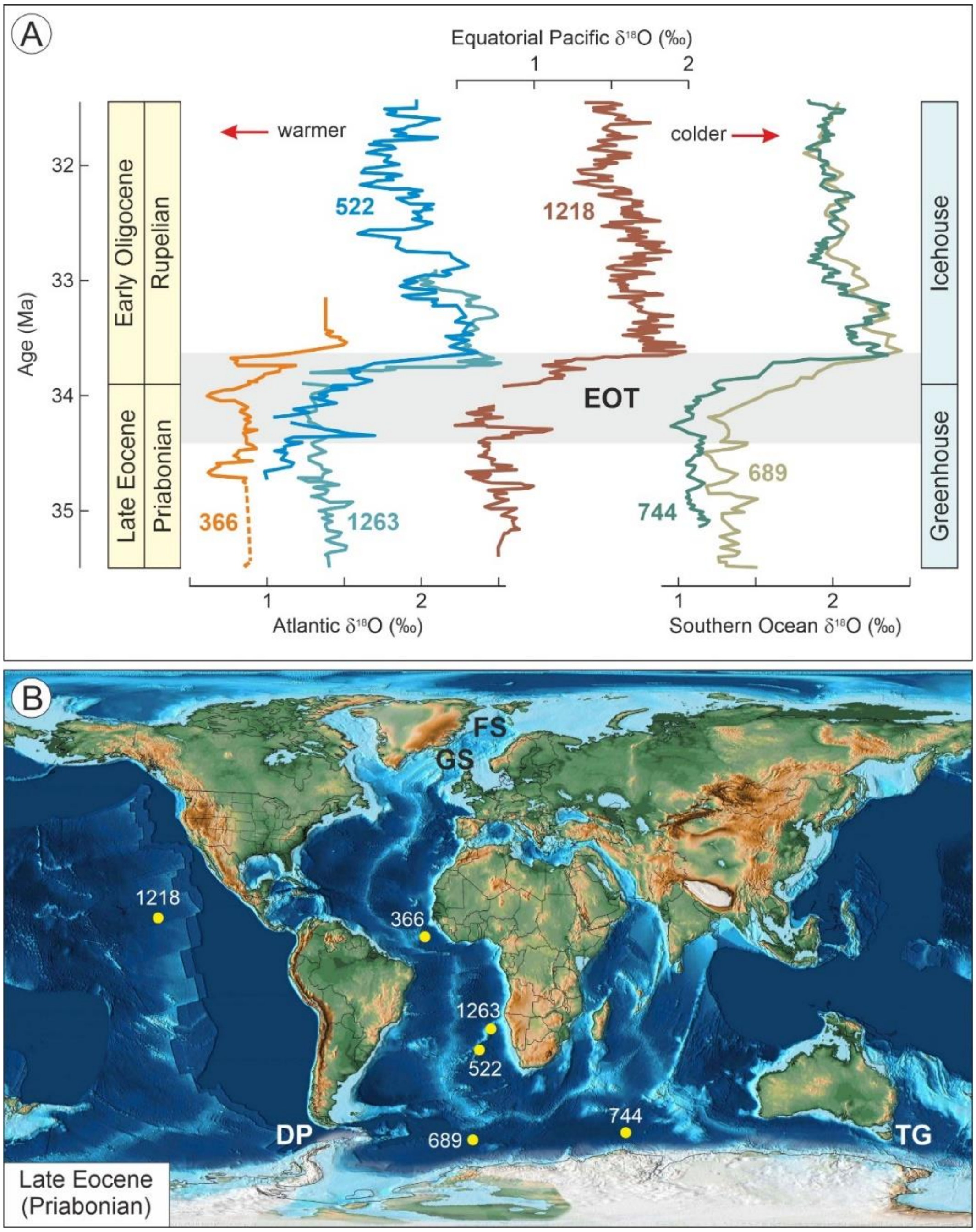


Figure 5. EOT paleoclimatic trends. A) Cooling (gray band) as recorded in the oxygen isotopic curves of benthic foraminifera from six deep marine ODP cores retrieved in different oceans and different latitudes (see B for location). Redrawn and simplified from Hutchinson et al. (2021). B) Late Eocene (Priabonian) paleogeography indicating the approximate location of ODP cores and the gateways regulating ocean circulation: DP, Drake Passage; FS, Fram Strait; GS, Greenland-Scotland Rise; TG, Tasman Gateway. Base map downloaded from PALEOMAP

PaleoAtlas for GPlates (https://www.earthbyte.org/paleodem-resource-scotese-and-wright-2018/, retrieved 10 August 2022).

In contrast with marine records, continental biotic turnover across the EOT shows substantial spatial variability (Sheldon et al., 2016). This is especially evident in mammal and plant records. In the case of mammals, a major Eurasian faunal turnover known as the "Grand Coupure", characterized by the extinction of many (up to 60%) endemic European species and their replacement by Asian immigrants, coincided with the onset of Oligocene glaciation (Hooker et al., 2004). These changes have been attributed to a combination of climate-driven extinction, competition and the opening of long-distance dispersal pathways due to sea-level regression. A similar major mammal turnover was recorded in Asia and was attributed mainly to climate change (Meng & McKenna, 1998), but no similar events have been found in North and South American mammalian faunas (Prothero, 2012; Woodburne et al., 2014), where continental evidence suggests heterogeneous responses.

This continental heterogeneity is also the main feature of vegetation responses to the EOT, as recorded in a recent worldwide study based on global pollen/spore databases (Pound & Salzmann, 2017). The authors attributed the heterogeneous patterns of vegetation response to the EOT to the combination of multiple drivers (tectonics, sea-level fall and declining greenhouse gas concentrations) and to the action of more local/regional factors, such as orogeny and precipitation regimes. This does not mean that vegetation did not experience significant shifts across the E/O boundary. On the contrary, major changes occurred on most continents, but the pattern of change varied from continent to continent and across latitudes (Coxall & Pearson, 2007). For example, in North America, widespread replacement of subtropical evergreen Eocene vegetation by cold-adapted deciduous Oligocene forms occurred, together with relevant regional extinctions, especially at higher latitudes (Liu et al., 2007). In the continental interior, increasing aridity could have been the main driver for the observed diversification of desert species (Yancey et al., 2003; Moore & Jansen, 2005). A shift from subtropical to temperate vegetation was also recorded in southern South America (Barreda & Palazzesi, 2007), but this shift was attributed later to long-term Eocene cooling rather than to an abrupt EOT shift (Quatrocchio et al., 2013). In the Neotropics, pronounced floral turnover was recorded at the E/O boundary, which has been linked to EOT cooling (Rull, 1998a; Jaramillo et al., 2006). Noteworthily, an important part of this evidence was recorded in and around the Caribbean region (Germeraad et al., 1968; Frederiksen, 1985; Mullet et al., 1987).

In Europe, the EOT was characterized by a change to more seasonal temperate flora and the extinction of tropical and subtropical taxa (Collinson, 1992; Eldrett et al., 2009). However, the impact of the EOT was far from homogeneous, including shifts from subtropical to warm-temperate forests, deciduous mixed forests or more arid and seasonal biomes, along with no evident vegetation changes, depending on the region (Pound & Salzamann, 2017; Hutchinson et al., 2021). In Asia, synchronous floral and faunal turnover was recorded during the European Grand Coupure, characterized by a shift from warm-temperate forests and large-bodied perissodactyl faunas (Eocene) to dry-temperate forest-steppe vegetation with small-bodied rodents/lagomorphs (Sun et al., 2014). However, regional differences linked to local phenomena such as the Tibetan uplift and associated climatic changes also existed (Jin et al., 2017; Su et al., 2018). In Australia, the passage from the Eocene to the Oligocene was characterized by a trend toward lower diversity, higher seasonality and the expansion of cool-temperate flora (Sluiter et al., 2022). In Antarctica, the expansion of ice sheets was accompanied by the replacement of evergreen forests by shrubby and tundra vegetation (Francis & Poole, 2002; Galeotti et al., 2021).

To summarize, the EOT was not only a phase of profound environmental change leading to a modern climatic regime but also characterized by a deep biotic turnover that initiated a trend toward the establishment of modern biotas. In both the marine and terrestrial realms, enhanced E/O extinction and renewed Oligocene radiation seem to have been common features; however, biotic responses were significantly more heterogeneous in continental environments, where biogeographical reorganizations played a fundamental role (Coxal & Pearson, 2007; Hutchinson et al., 2021). Biotic change across the EOT has been attributed to global phenomena such as cooling, sea-level drop and declining atmospheric CO_2 concentrations, but other more local drivers such as tectonic and topographical reorganizations have also been important, especially in the case of changing precipitation regimes. Although insufficient to be considered a phenomenon of global extent, increasing aridity and/or precipitation seasonality has been suggested in a number of continental records, especially in interior environments, on the basis of paleontological evidence.

2.3. Mangroves and the EOT

This section analyzes the present distribution of mangrove tree genera with Caribbean representatives and the phylogeographic trends that may have led to these biogeographic patterns, with emphasis on the EOT. Two genera are of pantropical distribution (*Rhizophora* and *Avicennia*), but their species have disjunct AEP and IWP distributions. The other three genera (*Pelliciera*, *Laguncularia* and *Conocarpus*) are monotypic and restricted to the EAP region (Table 1, Fig. 6). In this review, the focus is on *Pelliciera* and *Rhizophora*, as the dominant Caribbean mangrove-forming trees of Eocene and Oligocene times, respectively (Graham, 1005; Rull, 1998). The other genera (*Avicennia*, *Laguncularia* and *Conocarpus*) emerged later, between the Miocene and the Pleistocene (Fig. 3), and will be addressed in a further review of Neogene mangrove evolution.

2.3.1. Fossil and biogeographical evidence

Before the recent development of molecular phylogeographic studies, biogeographical and evolutionary hypotheses were based mostly on theoretical inference, for example, the center-of-diversity and center-of-origin concepts, and fossil evidence. The AEP–IWP polarity was first explained using either dispersalist or vicarianist points of view. Dispersalists proposed that mangroves originated in the high-diversity IWP region and then dispersed to the ACEP region (Van Steenis, 1962). Vicarianists believed that mangroves evolved during the Late Cretaceous around the coasts of the continuous Tethys Sea and diversified later, when this sea was closed by the African barrier (McCoy and Heck, 1976). A fairly complete review by the time of macrofossil (leaves, wood, flowers, and fruits) and microfossil (pollen) evidence, as well as fossils of mollusks characteristic of the mangroves, was used to support the vicariance hypothesis (Ellison et al., 1999). Under this hypothesis, the timing of mangrove origin and the further split into the ACEP and IWP regions varied from author to author, ranging from Cretaceous to Oligocene (e.g., Sowunmi, 1986; Ellison et al. 1999; Plaziat et al., 2001; Duke, 2017; Srivastava and Prasad, 2015, 2018). Using fossil evidence, the E/O environmental disruption has been advocated as an important driver for the initial split between IWP and EAP biogeographical mangrove regions (Plaziat et al., 2001; Srivastava & Prasad, 2019), as well as for the replacement of *Pelliciera* by *Rhizophora* mangroves in the Neotropics (Rull, 1998a). However, no definite explanations have been provided for these events, and hence, no causal links have been established between the EOT global disruption and mangrove evolution on the basis of fossil and biogeographical evidence.

2.3.2. Molecular phylogenetics and phylogeography

Recent developments in molecular phylogenetics and phylogeography have provided more clues for understanding how extant mangrove biodiversity and biogeographical patterns have been shaped. Molecular phylogenetic studies on mangrove tree taxa with Caribbean representatives, notably *Rhizophora* and *Avicennia*, began in the late 1980s and have significantly increased since the 2000s (review in Triest, 2008). A full account of the results of these studies is beyond the scope of this paper, and only an overview of the main findings for the extant Caribbean mangrove-forming tree genera before and after the E/O boundary is provided. As mentioned above, *Pelliciera* and *Rhizophora* were the most important players in this transition and will be analyzed in more detail.

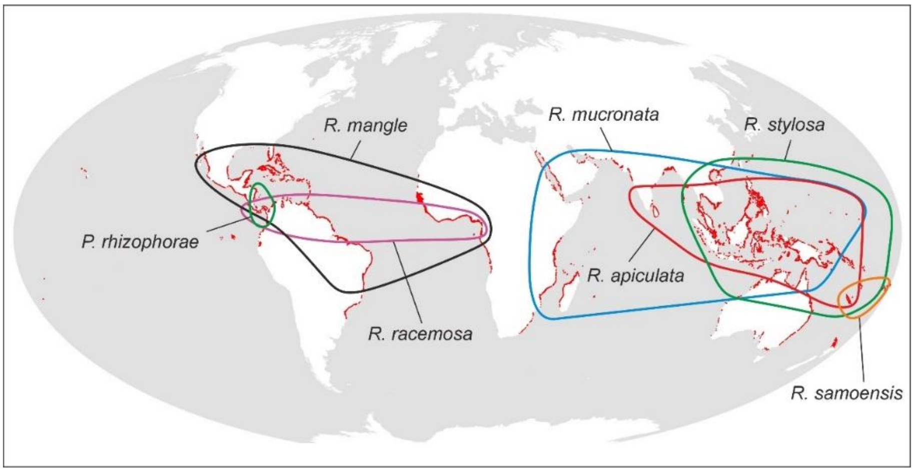


Figure 6. Geographical distribution of extant *Rhizophora (R)* and *Pelliciera (P)* species. Redrawn from Lo et al. (2014) and Duke (2017).

Pelliciera is a monotypic genus (but see Duke, 2020) with a very restricted geographical range and no close phylogenetic relatives in mangrove ecosystems worldwide, which hinders the establishment of phylogeographic relationships with evolutionary significance for these communities. The available phylogenetic studies for *Pelliciera* are essentially systematic and aimed at resolving its taxonomical placement within the family and the order to which this genus belongs (e.g., Anderberg et al., 2002; Bremer et al., 2002; Geuten et al., 2004; Schönenberger et al., 2004). Molecular phylogenetic data have also been used to evaluate potential incipient speciation trends within the extant species *P. rhizophorae* (Castillo-Cárdenas et al., 2014, 2015).

The case of *Rhizophora* is very different, as this genus has greater diversity, a worldwide distribution and clear biogeographical differentiation between the IWP and AEP mangrove regions (Fig. 6). Given its present biogeographical patterns and the antiquity of the oldest known fossils – 38-34 Ma (Late Eocene), according to Graham (2006) – phylogeographical trends of this genus have been used as a proxy for mangrove evolution and historical biogeography at a global level. Xu et al. (2017) estimated that mangrove members of the Rhizophoraceae family, including the IWP genera *Bruguiera*, *Ceriops*, and *Kandelia* and the cosmopolitan *Rhizophora*, separated from their non-mangrove counterparts of the same family by 55 Ma (Early Eocene), coinciding with the Paleocene/Eocene Thermal Maximum. The same study estimated that the genus *Rhizophora* emerged by 39 Ma (Late Eocene) and that the EAP species *R. mangle* diverged from its IWP sisters *R. apiculata*, *R. mucronata* and *R. stylosa* at some unspecified point in the Neogene. It should be noted that this phylogeny was calibrated with the above-mentioned Late Eocene fossil records (Graham, 2006); therefore, comparisons with the fossil record are hindered by the principle of circularity.

According to Takayama et al. (2021), the genus *Rhizophora* would have originated in the IWP region during the Eocene and was distributed worldwide by the Late Eocene, after dispersal to the EAP region through the Tethys seaway and possibly a southern route around Africa. This would have occurred between 50 Ma (Early Eocene) and 23 Ma (Oligo/Miocene). The same study situates the splitting between EAP and IWP *Rhizophora* species by 11 Ma (Late Miocene), favored by the Tethys closure and a cooling that would have limited dispersal across the Indian and Atlantic Oceans by the southern African corridor. Further diversification within the EAP and IWP regions would have occurred later, favored by the Mio-Pliocene global cooling. Again, these phylogenies were calibrated with the same fossil records. Former molecular phylogenetic studies obtained similar results regarding the IWP origin and further EAP dispersal of *Rhizophora* but situated the initial IWP–EAP diversification event in the Eocene, between 50 Ma and 34 Ma, and the intra-IWP diversification at the Oligocene/Miocene boundary (Lo et al., 2014). These authors concluded that neither vicarianist nor dispersalist explanations alone can account for the current biogeography of *Rhizophora* and that a combination of both is needed to understand present-day geographical patterns of mangroves. Based on these results and the available fossil record, Duke (2017) proposed the occurrence of two main radiations within *Rhizophora*; the first would have separated the IWP and EAP clades in the Oligocene (35-25 Ma), and the second would have been responsible for the Late Miocene (~15 Ma) intra-IWP and intra-EAP diversifications. The Oligocene radiation was linked to the Tethys closure, which would have terminated pantropical interchange, whereas the Miocene radiation coincided with the North Atlantic widening and the Australia/SE Asia collision.

In these studies, the EOT cooling and sea-level fall are rarely mentioned as drivers for mangrove evolution; only Lo et al. (2014) pointed out that "The ancestral Rhizophoras that once existed along the Tethys seaway, Mediterranean and Arabian coasts and Europe could have become extinct by the Cenozoic with its notable cooling and drastic environmental changes during the late Tertiary", citing the EOT papers by Pagani et al. (2005) and Liu et al. (2009). Therefore, the potential influence of EOT global disruption on mangrove evolution remains largely unexplored in the phylogeographical literature, and the preferred explanations regarding the historical biogeography of mangroves are related to the waxing and waning of dispersal pathways and barriers driven by continental drift (Dodd & Afzal-Rafii, 2002; Dodd et al., 2002; Duke et al., 2002; Triest, 2008; Duke, 2017; Van der Stocken et al., 2019).

3. The Caribbean region during the EOT

Before getting fully into the topic, it is necessary to highlight that this paper considers the Caribbean region in a wide sense, including all Caribbean coasts, from north (Greater Antilles) to south (northernmost South America) and from east (Lesser Antilles) to west (Central America) (Fig. 4). The inclusion of a number of presently interior localities (notably from South America) is necessary because these sites were on past proto-Caribbean coasts and now are more distant from this sea due to the highly dynamic nature of coastal configuration in the region. In this regard, it is worth mentioning that all localities with palynological information found in the literature have been included, without any a priori selection. The geographical imbalance among different areas, for example, the large number of South American localities in comparison with the lower amount of insular sites, reflect only differences in the intensity of research efforts.

3.1. Tectonic setting

From a tectonic point of view, the Caribbean is a very peculiar region owing to the existence of the Caribbean microplate, situated between the North American and South American plates, and the Pacific plates of Cocos and Nazca (Fig. 7). According to the current models, the Caribbean plate originated in the eastern Pacific and migrated eastward to its present position after the Triassic–Jurassic (210-140 Ma) breakup of Pangea and the subsequent seafloor spreading between the North American and South American plates, which created the Cretaceous (140-90 Ma) proto-Caribbean seaway (Pindell & Dewey, 1982; Pindell, 1990; Pindell et al., 2006; Mann et al., 2006; Pindell & Kennan, 2009). In the Late Cretaceous, (80-75 Ma), the incipient Caribbean plate front progressed northeastward and formed the Greater-Antilles arc that collided with the Bahamas carbonate platform and reoriented plate motion from northeastward to eastward during the Paleocene (60-44 Ma) (Pindell & Dewey, 1982; Pindell et al., 1988; Mann et al., 1995). This change in direction initiated the Cayman Trough as a pull-apart basin (Rosencrantz et al., 1988; Leroy et al., 2000). Eocene to Miocene (44-14 Ma) eastward migration led to the formation of the Aves arc and its further abandonment as the Aves Ridge, as a remnant arc, and the formation of the Lesser-Antilles arc (Aitken et al., 2011; Neill et al., 2013; Allen et al., 2019). The most updated review on the evidence that supports this model can be found in Romito & Mann (2020) and Mann (2021).

3.2. Paleogeography and paleocurrents

Paleogeographical changes are intimately linked to tectonic evolution and constitute the basis for reconstructing the waxing and waning of past migration/dispersal pathways and barriers, as fundamental traits for understanding biogeographical shifts. In this case, the main interest is the paleogeographic situation during the EOT when, according to the current models, the

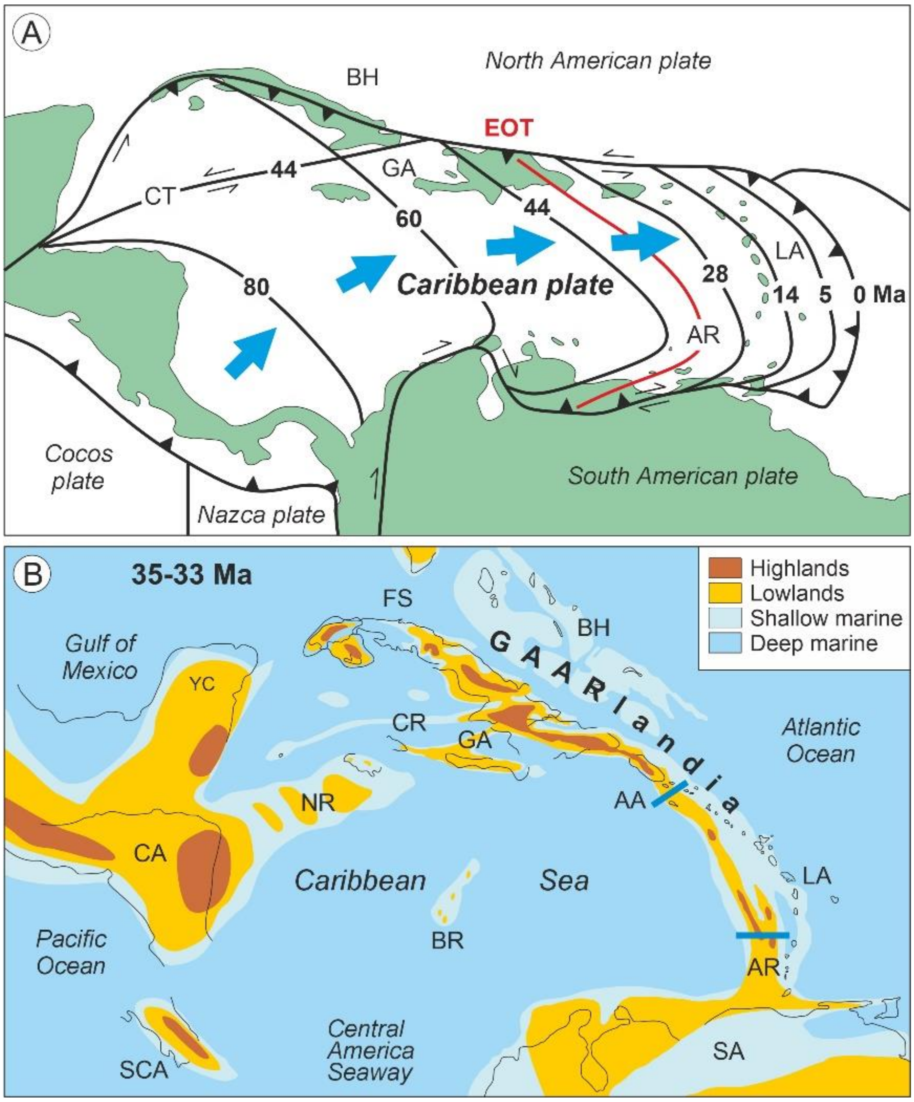


Figure 7. Tectonic evolution and paleogeography of the Caribbean region. A) Tectonic evolution of the Caribbean plate from Late Cretaceous to present. Numbered lines indicate the position of the leading edge of the Caribbean plate at the Late Cretaceous (80 Ma), Middle Paleocene (60 Ma), Middle Eocene (44 Ma), Middle Oligocene (28 Ma), Middle Miocene (14 ma), Early Pliocene (5 Ma) and the present (0 Ma). The approximate location of the advancing plate front during the EOT is indicated by a red line. The direction of the movement is indicated by blue arrows. Present-day continental and island configuration (green areas) are shown only for reference. Redrawn and simplified from Xie et al. (2010). B) Caribbean paleography at the Late Eocene/Early Oligocene transition (35-33 Ma), showing the exposure of the Greater Antilles-Aves Ridge arc (GAARlandia) due to lowered EOT sea levels. Black lines show the approximate location of present coasts. AA, Anguilla-Antigua passage; AR, Aves Ridge; BH, Bahamas carbonate platform; BR, Beata Ridge; CA, Central America; CR, Cayman Ridge; CT, Cayman Trough; FS, Florida Strait; GA, Greater Antilles; LA, Lesser Antilles; NR, Nicaraguan Ridge; SA, South America; SCA, southern Central America; YC, Yucatán. Redrawn from Iturralde-Vinent (2006) and Iturralde & MacPhee (1999).

advancing front of the Caribbean plate was close to the present-day eastern Greater Antilles and the Aves Ridge (Fig. 7). A number of paleogeographical reconstructions consider that, during the EOT, the Caribbean region was an open seaway that connected the Pacific and Atlantic Oceans, as the eastern and western plate boundaries were defined by volcanic island arcs open for marine circulation (e.g., Pindell & Kenan, 2006; Mann, 2021). Others, however, contend that the outstanding sea-level fall that characterized the EOT, combined with enhanced uplift, would have led to the emergence of a continuous land bridge between South America and the Greater Antilles, known as GAARlandia (Greater Antilles-Aves Ridge landspan) (Fig. 7), which blocked marine currents, except for a small opening in the Florida Strait

(MacPhee & Iturralde-Vinent, 1995; Iturralde-Vinent, 2006; Iturralde-Vinent & MacPhee, 1999) (Fig. 7). According to these authors, GAARlandia would have existed for a short time period (<3 million years), thus facilitating the interchange of terrestrial flora and fauna between South America and the Caribbean. The same authors suggest that, under these conditions, Caribbean waters may have been cooled by the combined action of the EOT cooling and the southward California current, entering the Caribbean by the southern seaway (today's southern Central America) (Figs. 7 and 8).

The occurrence of the GAARlandia land bridge during the EOT could have been decisive for marine circulation and, therefore, for climatic and biogeographical patterns across the region. Presently, the dominant superficial current is the warm Caribbean Current, entering this sea from the equatorial Atlantic through the Lesser Antilles and progressing to the Gulf of Mexico via the Yucatan Current (Fig. 8). After loop circulation inside the gulf, waters flow outside through the Florida Current to join the Antilles Current and develop the Gulf Stream. Cold North Atlantic Deep Waters enter the Caribbean by the available passages in the Greater Antilles. This circulation pattern has been established since the closure of the Panama Isthmus in the Pliocene (~3 Ma; O'Dea et al., 2016). Before then, an open seaway existed in the south, the Central America Seaway (Kirilova et al., 2019; Öğretmen et al., 2020), which connected the proto-Caribbean with the Pacific circulation, at least since the Cretaceous. This seaway was open during the EOT, when two main circulation modes might have existed, depending on the occurrence or absence of GAARlandia. In the absence of this landspan, the proto-Caribbean would have been connected with both the Atlantic and the Pacific, thus allowing circulation between them. If GAARlandia actually existed, the Atlantic circulation would have been blocked, and the Caribbean would have been connected only to Pacific currents. Another possibility in the GAARlandia scenario is the occurrence of marine passages between the Greater and the Lesser Antilles – called here the AA passage for its location between the present Anguilla and Antigua banks – and the Aves Ridge (AR), which would have connected the Caribbean and the Atlantic circulation to some extent (Cornée et al., 2021; Garrocq et al., 2021).

3.3. Paleoclimates and paleo-sea levels

The few available oxygen isotope records from circum-Caribbean deep-sea marine cores and terrestrial outcrops including the E/O boundary show that global EOT cooling also occurred in the region (Fig. 9). Of these records, the Saint Stephens Quarry (SSQ) outcrop is the best constrained chronologically and has the highest resolution and has been one of the keystone sites used to characterize global EOT paleoenvironmental shifts (Keigwin & Croliss, 1986; Katz et al., 2008; Miller et al., 2008; Wade et al., 2012; De Lira Mota et al., 2020). In this record, three main events were recognized around the EOT (33.8-33.5 Ma), which demonstrated the stepwise, rather than continuous, nature of this transition (Katz et al., 2008). The first 2.5 °C cooling, as estimated from the Mg/Ca ratio of benthic foraminifera, occurred at 33. 8 Ma (EOT-1 event), accompanied by a minor 30 m relative sea-level fall (Fig. 9). After a return to pre-event conditions, a second step (EOT-2; 33.63 Ma) took place that is difficult to quantify in terms of temperature but occurred in a shallowing-upward sequence, indicating a sustained sea-level fall. The third event occurred in the early Oligocene (Oi-1; 33.545 Ma) and was characterized by a 2 °C cooling and a 105 m sea-level drop, which equates to a 67 m eustatic fall. Adding glycerol-dialkyl-glycerol-tetraethers (GDGTs) measurements of archaea as paleotemperature proxies in the same outcrop, Wade et al. (2012) estimated that, in the Gulf of Mexico, the overall EOT sea-surface temperature (SST) cooling was 3-6 °C, and thermal seasonality significantly increased in the Early Oligocene.

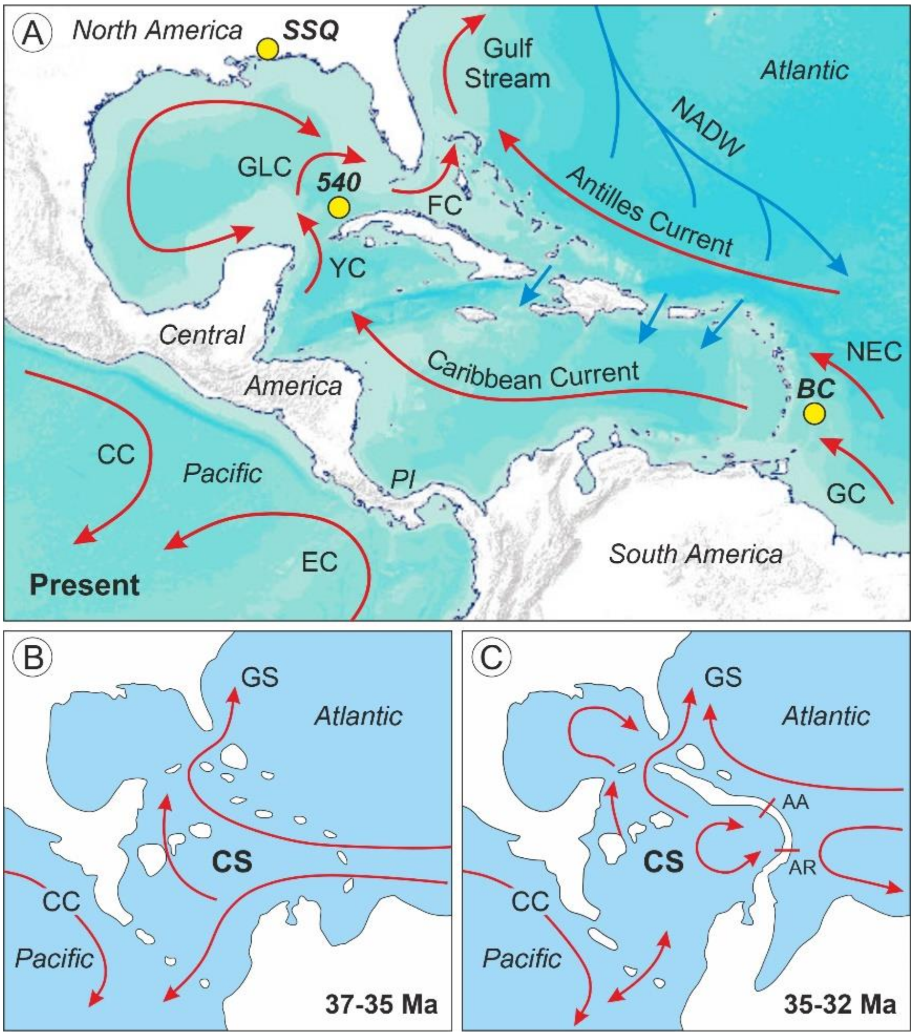


Figure 8. A) Present-day superficial (red arrows) and deep (blue arrows) marine currents of the Caribbean-Gulf of Mexico region. CC, California current; EC, Equatorial Countercurrent; FC, Florida Current; GC, Guiana Current; GLC, Gulf Loop Current; NADW, North Atlantic Deep Waters; NEC, North Equatorial Current; YC, Yucatan Current. Modified from Amador-Castro et al. (2021) and Öğretmen et al. (2020). The location of marine cores and terrestrial outcrops with EOT paleclimatological studies are indicates by yellow dots: BC, Bath Cliff outcrop; SSQ, St. Stephens Quarry outcrop; 540, DSDP Site 540 (marine core). B-C) Late Eocene to Early Oligocene paleocurrents with and without the GAARlandia land bridge. AA, Anguilla-Antigua passage (Cornée et al. 2021); AR, Aves Ridge passage (Garrocq et al., 2021); CS, Caribbean Sea. Redrawn from Iturralde-Vinent (2006).

3.4. Biogeography

The origin of the Caribbean biota has recently been discussed by Roncal et al. (2020), who considered four main, likely complementary, hypotheses for explaining the historical assembly of terrestrial Caribbean biogeographical patterns, with emphasis on plants: (i) Late Cretaceous vicariance, (ii) GAARlandia colonization, (iii) transoceanic dispersal, and (iv) in situ speciation. According to the Late Cretaceous vicariance (LCV) hypothesis, the Caribbean biota originated in a proto-Antillean land mass – which was the front of the migrating Caribbean plate and occupied a location similar to today's Central America between 80 and 70 Ma – and diversified by allopatric speciation following the eastward migration and the progressive fragmentation leading to the present Antilles (Rosen, 1975; Matos-Maraví et al., 2014). Critics argue that no proto-Antillean land masses existed before the Middle Eocene (40 Ma) (Iturralde-Vinent & MacPhee, 1999). These authors proposed the GAARlandia (GAA) hypothesis, according to which the colonization of the Antilles occurred later, in the Late Eocene/early Oligocene, and

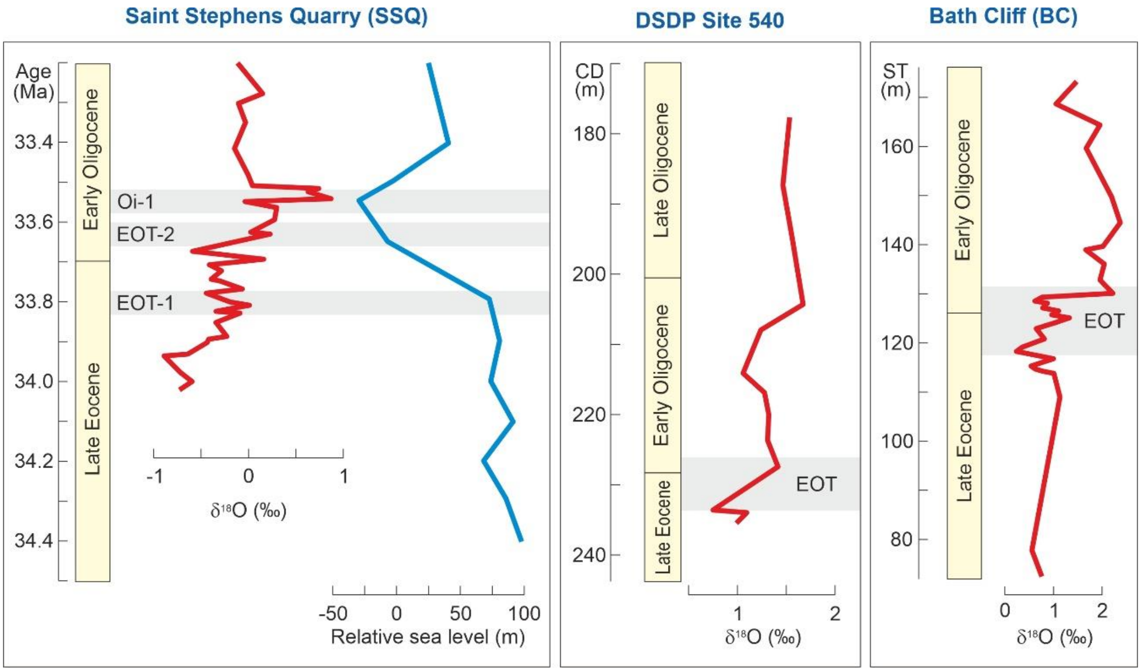


Figure 9. Circum-Caribbean oxygen isotope and sea-level records around the EOT (see Fig. 8 for the location of the study sites). The oxygen isotope curves are based on benthic foraminifera *Cibicioides* spp. (SSQ and DSDP 540) and *Oridorsalis umbonatus* (BC). Sea levels relative to today were estimated from the percentage of benthic foraminifera *Uvigerina* spp. SSQ section is represented in a chronological scale and the other sections are in core depth (CD; Site 540) and section thickness (ST; BC section) metric scales. Redrawn from Belanger & Matthews (1984), Saunders et al. (1984) and Katz et al. (2008).

proceeded from South America through the GAARlandia land bridge described above. The hypothesis of long-distance dispersal (LDD) from adjacent continents, especially South America, has been the preferred explanation for many decades (Darlington, 1983; Hedges et al., 1992; Regalado, et al., 2018). The main dispersal mechanisms would have been water currents flowing from South America to the Greater Antilles during the Cenozoic (Huber & Caballero, 2003; Sarnthein et al., 2009). Finally, the in situ speciation (ISS) hypothesis has been proposed to explain the origin and maintenance of high species richness and endemism characteristic of the region (Losos & Schluter, 2000).

All the above hypotheses have some empirical support in the geographical distribution and/or the phylogeographical patterns of particular taxonomic groups, but there is no conclusive evidence that favors one over the others. However, some general trends can be suggested from recent studies using molecular phylogenetic methods. A recent Caribbean-wide meta-analysis estimated the colonization time of nearly 90 endemic plant lineages and concluded that plants have repeatedly colonized the Antilles for the last 60 Ma (roughly the Cenozoic) from continental America, especially from Central and South America (Roncal et al., 2020). This does not support the LCV hypothesis. In addition, more than 80% of the colonization events occurred after the EOT, which questions the GAA hypothesis as a robust explanation for the origin of the Caribbean biota. More than half of the species studied colonized the Caribbean during the last 10 Ma, which coincides with the estimate from a former study by Antonelli et al. (2018), who reported an increase in the number of Neotropical dispersal events during the same time period, thus favoring the LDD hypothesis. The same meta-analysis failed to find a relationship between the colonization time and the number of species in each endemic clade, which is unsupportive of the ISS hypothesis. Based on these results, Roncal et al. (2020) supported the LDD hypothesis and highlighted the role of Central America as a potential source for Caribbean flora, as nearly 40% of the studied lineages were derived from this continental area.

As this review is concerned with the EOT, the most relevant point is the occurrence or absence of GAARlandia, which would have represented not only a dispersal pathway for terrestrial biota, as commonly emphasized in current biogeographical models, but also a barrier to marine dispersal between the Atlantic and Pacific oceans, as well as a major modifier of the internal Caribbean circulation (Fig. 8). It should also be noted that many studies on the origin of Caribbean biota are focused on island colonization, but within the scope of this review, continental coasts are equally important, as usual environments for the occurrence of mangrove ecosystems. Whether GAARlandia existed should be evaluated using direct geological and geophysical evidence and is beyond the scope of this review, which is focused on the biogeographical significance of the controversy. Indeed, although biogeography is at the root of the GAARlandia concept, it can provide indirect evidence – that is, evidence that is better understood in a GAARlandia scenario – but cannot demonstrate the actual existence of this landspan. This section concentrates on this type of evidence; the potential influence of a GAARlandia versus a non-GAARlandia scenario for the evolution of Caribbean mangroves will be evaluated after discussing the paleontological evidence from mangrove ecosystems.

The term GAARlandia was introduced by MacPhee & Iturralde-Vinent (1995) to explain the Early Miocene land mammal diversity of the Greater Antilles, specifically on the islands of Cuba and Puerto Rico. Shortly before, the same authors had already mentioned the potential occurrence of a continuous Oligocene subaerial pathway open to colonization by land vertebrates between South America and the Greater Antilles, but they still did not use the term GAARlandia to refer to it (MacPhee & Iturralde-Vinent, 1994). According to these authors, during the Late Eocene–Oligocene, the founder clades of the Antillean mammals were widely distributed across a “long-lasting positive topographic feature of the Caribbean basin” that they named GAARlandia, including “Cuba, Hispaniola, Puerto Rico, Virgin Islands, Aves Island, and some islands on the northern fringe of South America.” The disruption and fragmentation of this emerged land mass since the Late Oligocene would have led to the appearance of modern insular mammal faunas by vicariance and local extinction. By the time, the occurrence of GAARlandia was considered useful for explaining the distribution of a number of land faunal groups in the Greater Antilles (Borhidi, 1985; MacPhee & Iturralde-Vinent, 1994, 1995, 2000, 2005; Iturralde-Vinent & Mac Phee, 1996, 1999). Recently, this model has received support from molecular phylogeographic studies on a variety of taxonomic groups, including amphibians, mammals, insects, arachnids and plants (Fritsch, 2003; Dávalos, 2004; Van Ee et al., 2008; Moen & Wiens, 2009; Alonso et al., 2012; Bacon et al., 2012; Deler-Hernández et al., 2018; Pederneiras et al., 2018; Tong et al., 2019).

All the above considerations were based on biogeographical/phylogeographical patterns, and direct geological/geophysical evidence for the existence of GAARlandia remains inconclusive (Ali, 2012). The recent finding of geophysical (seismic) evidence for submerged environments in the Anguilla–Antigua banks and the Aves Ridge during the EOT (Cornée et al., 2020, 2021; Philippon et al., 2021; Garrocq et al., 2021) (Fig. 7) questions the existence of a continuous emerged land bridge from a physical perspective and has been used to dismiss the GAARlandia hypothesis (Ali & Hedges, 2021). However, the debate continues, and some researchers believe that, even in the absence of a continuous pathway for terrestrial organisms, biotic connection could have occurred via stepping stone dispersal (Pennington & Dick, 2004; Muellner-Riehl & Rojas-Andrés, 2022). In this hypothetical fragmented GAARlandia scenario, intra-Caribbean circulation and the colonization of continental coasts, two paramount features for water dispersal of mangrove trees, remain unknown. In the present state of knowledge, mangrove biogeography and evolution across the EOT should consider the two general paleogeographical scenarios represented in Fig. 8, which are abbreviated here as GAAR (with the variant frag-GAAR) and non-GAAR.

4. The EOT Caribbean mangroves

Once the tectonic, paleogeographic, paleoclimatic and biogeographical Caribbean context has been outlined, this section introduces the available qualitative and quantitative pollen records useful for discussing the major disruption experienced by mangrove communities during the EOT. More than 80 sites have been identified with palynological information suitable for reconstructing mangrove evolutionary history (Table 2). The majority of these localities are situated in today's countries of the southern Caribbean area (Fig. 10), notably Colombia and Venezuela, which could be linked to the higher development of exploration activities for natural resources, primarily oil and gas, in these countries. In the northern sector, only two sites from Puerto Rico and Jamaica contained fossil mangrove records useful for this study, whereas the other two from Cuba and Haiti (Hispaniola) hold pollen assemblages representing inland environments. The oldest of these inland Greater Antillean records (site 80) was from the Middle Eocene and suggested the occurrence of terrestrial vegetation of North American floral affinities growing under warm-temperate to tropical climates (Graham et al., 2000). The Haiti record (site 81) was Late Miocene in age and represented montane pine and cloud forests also of North American affinity and characteristic of warm and rainy climates (Graham, 1990). These records were used to dismiss the potential occurrence of arid climates (Graham, 2000) and to support that proto-Cuba/Hispaniola islands were part of the North American plate and were not directly connected to South America during the Cenozoic (Graham et al., 2000). This could have implications for the existence or absence of the GAARlandia land bridge that will be discussed in the next section.

Table 2. Eocene to Pliocene *Pelliciera* (represented by *Lanagiopollis crassa* and *Psilatricolporites crassus*) and *Rhizophora* (represented by *Zonocostites ramonae* and other species of this genus) records from the Neotropics, with indication of the relative abundance according to the original data reported in the corresponding papers (+ present, - absent or not mentioned). Numbers (N) correspond to localities depicted in Figs. 10 and 14. Age: Eo, Eocene; Oli, Oligocene; Mio, Miocene; Plio, Pliocene; E, Early; M, Middle; L Late. Countries: BRA, Brasil; COL, Colombia; CRI, Costa Rica; CUB, Cuba; GUA, Guatemala; GUY, Guyana; HAI, Haiti; JAM, Jamaica; MEX, Mexico; Guatemala; PAN, Panamá; PER, Perú; PUR, Puerto Rico; SUR, Surinam; TRI, Trinidad; VEN, Venezuela.

N	Site/area	Country	Age	*Pelliciera*	*Rhizophora*	References
1	Columbus	TRI	Plio	+	+	Lamy (1986)
2	Orinoco	VEN	Plio	+	+	Pocknall et al. (2001)
3	Talamanca	CRI	Plio	+	+(?)	Graham & Dilcher (1998)
4	Montañita	VEN	Plio	+	+	Lorente (1986)
5	Jocotán	GUA	Plio	-	≤100%	Graham (1998)
6	Barinas	VEN	Mio-Plio	+	+	Bermúdez et al. (2017)
7	Gatun	PAN	Mio-Plio	-	≤80%	Graham (1990b, 1991)
8	Urumaco	VEN	Mio-Plio	+	≤70%	Lorente (1986); Hambalek et al. (1994)
9	Tig-141X	VEN	L Mio	+	≤20%	Lorente (1986)
10	Veracruz	MEX	L Mio	-	≤96%	Graham (1975, 1976)
11	Zamuro-1X	VEN	L Mio	+	≤50%	Lorente (1986)
12	Guanipa-1X	VEN	L Mio	+	≤70%	Lorente (1986)
13	Hervidero-1X	VEN	L Mio	+	≤60%	Lorente (1986)
14	Cucaracha	PAN	M Mio	-	≤60%	Graham (1988b)
15	Yopal	COL	M Mio	-	+	Dueñas & Van der Hammen (2007)
16	TJ	VEN	E Mio	+	+	Rull (2001)
17	Sheroli	CRI	E Mio	-	≤5%	Graham (1987)
18	Gold Hill	PAN	E Mio	-	Common	Graham (1988a)
19	SZZ-119X	VEN	E Mio	-	≤60%	Lorente (1986)
20	SCZ-124X	VEN	E Mio	+	≤60%	Lorente (1986)
21	IZZ-100X	VEN	E Mio	-	≤20%	Lorente (1986)

22	Cascadas	PAN	E Mio	≤3%	70-90%	Graham (1989)
23	Saltarín	COL	E/M Mio	+	Abundant	Jaramillo et al. (2017)
24	NZZ-154/160	VEN	E/M Mio	+	≤80%	Lorente (1986)
25	Los Pobres-1	VEN	E/M Mio	+	≤40%	Lorente (1986)
26	Pariaguán-1X	VEN	E/M Mio	≤10%	≤90%	Lorente (1986)
27	Panchita-1X	VEN	E/M Mio	+	≤90%	Lorente (1986)
28	SDZ-117X	VEN	E/M Mio	-	≤30%	Lorente (1986)
29	LSJ-3310	VEN	E/M Mio	+	≤60%	Lorente (1986)
30	LS-992B	VEN	E/M Mio	+	≤40%	Lorente (1986)
31	LL-370	VEN	E/M Mio	+	≤30%	Lorente (1986)
32	Pozón-SX	VEN	E/M Mio	≤10%	-	Lorente (1986)
33	CO-85	TRI	Mio	+	Abundant	Germeraad et al. (1968)
34	B-188	VEN	E Mio	≤3%	≤80%	Lorente (1986)
35	Alliance	SUR	Mio	+	+	Wijmstra (1969)
36	SLA	VEN	Mio	-	Abundant	Rull (1992)
37	Culebra-1X	VEN	Mio	+	≤80%	Lorente (1986)
38	Catatumbo-1X	VEN	Mio	≤10%	≤40%	Lorente (1986)
39	OG-1X	VEN	Mio	+	≤80%	Lorente (1986)
40	Mariñame	COL	E/M Mio	+	≤70%	Hoorn (1994)
41	Chorros	COL	Mio	+	≤20%	Hoorn et al. (2022)
42	La Frontera	PER	Mio	+	-	Parra et al. (2020)
43	105-AM	COL	E/M Mio	+	+	Jaramillo et al. (2017)
44	Pará	BRA	Mio	≤2%	≤40%	Antonioli et al. (2015); Aguilera et al. (20217)
45	Amazon	BRA	Oli-Mio	+	+	De Boer et al. (1965)
46	Maranhão	BRA	Oli-Mio	+	+	Regali et al. (1974)
47	Banneirinhas	BRA	Oli-Mio			Regali et al. (1985)
48	Coastal Plain	SUR	Oli-Mio	+	+	Amstelveen (1971)
49	Falcón	VEN	Oli-Mio	-	Abundant	Rull & Poumot (1997)
50	Maturín	VEN	Oli-Mio	+	-	Helenes & Cabrera (2002)
51	Chama	VEN	Oli-Mio	-	Common	Rull (1997a, 2002)
52	Shelter Belt	GUY	Oli-Mio	≤5%	≤90%	Van der Hammen & Wijmstra (1964); Wijmstra (1968)
53	Planeta Rica	COL	L Oli-E Mio	-	Abundant	Dueñas (1980)
54	Chafurray	COL	Oli-Mio	+	Abundant	Germeraad et al. (1968)
55	Furrial	VEN	Oli-Mio	+	+	Fasola et al. (1991)
56	Simojovel	MEX	Oli-Mio	≤2.5%	>95%	Langenheim et al. (1967); Graham (1999b)
57	Carbón	VEN	Oli	≤25%	≤50%	Lorente (1986)
58	Friata-1X	VEN	Oli	+	+	Lorente (1986)
59	Lares	PRI	Oli	≤2%	≤95%	Graham & Jarzen (1969)
60	Pozón-SX	VEN	Oli	≤10%	-	Lorente (1986)
61	COT-1X	VEN	Oli	+	Common	Rull (2003)
62	Tig-141X	VEN	Oli	+	-	Lorente (1986)
63	Concentración	COL	L Eo/E Oli	≤47%	-	Ochoa et al. (2012)
64	Delicias	VEN	Eo/Oli	+	-	Colmenares & Teran (1993)
65	Bogotá	COL	L Eo	≤15%	+	Ochoa et al. (2012)
66	COT-1X	VEN	L Eo	Com	+	Rull (2003)
67	Alcalde Díaz	PAN	M/L Eo	≤11%	≤10%	Graham (1985)
68	Tarra	VEN	M/L Eo	Common	+	Rull (1997b)
69	Paz del Rio	COL	M Eo	Abundant	-	Germeraad et al. (1968)
70	VLC	VEN	M Eo	≤60%	-	Rull (1998b, 2002)
71	Chapelton	JAM	M Eo	Common	-	Graham (1977)
72	Sagu	COL	M Eo	Common	-	De la Parra et al. (2021)
73	Icotea	VEN	M Eo	Abundant	-	Germeraad et al. (1968)
74	Piñalerita	COL	M Eo	Common	+	Jaramillo & Dilcher (2001)
75	Boscán	VEN	M Eo	+	+	Colmenares (1988)
76	Rubio/Lora	VEN	E/M Eo	+	-	Germeraad et al. (1968); Pocknall & Erlich (2020)

77	Maracaibo	VEN	Eo	Abundant	-	Rull & Poumot (1997)
78	Nuevo Mundo	COL	Eo	Abundant	-	Rodríguez-Forero et al. (2012)
79	Maché	VEN	E Eo	Common	-	Rull (1999, 2000, 2002)
80	Maraguán	CUB	M Eo	-	-	Graham et al. (2000)
81	Mirebalais	HAI	Mio-Plio	-	-	Graham (1990a)

The available evidence on Caribbean mangrove paleocommunities is discussed here considering three main time intervals, namely, the Eocene, the Oligocene and the Neogene (Miocene and Pliocene) (Fig. 10). The Eocene mangroves will not be discussed in depth, as they were already analyzed and characterized in a former paper on the evolutionary origin of Caribbean mangroves (Rull, 2022a). Here, we will concentrate on the EOT and the replacement of the *Pelliciera* by the *Rhizophora* mangroves. It should be noted that a number of Oligocene records are reported in the literature as Oligo-Miocene records (Table 2) for several reasons, including the lack of sufficient chronological resolution or the transitional nature of the sequence studied, among others. In this review, these records are included in the Oligocene category, and only those clearly from the Miocene and Pliocene, as stated in the original references, are placed in the Neogene category. Although the focus of this paper is on the EOT, it has been considered that ignoring the Neogene, when *Rhizophora* mangroves attained their maximum development, would have left the account incomplete. Despite this, Neogene mangroves are not fully analyzed in terms of the ecological and evolutionary trends of their components and the communities they develop since they deserve special treatment, and as formerly stated, a more detailed analysis focused on the Neogene will be carried out in the future.

It should be noted that a number of doubtful *Pelliciera* records exist for Europe, Africa and North America (Germeraad et al., 1968; Machin, 1971; Elsik, 1974; Châteauneuf, 1980; Gruas-Cavagnetto et al., 1980). According to Frederiksen (1985), however, the accuracy of these identifications remains to be determined. Actually, *Pelliciera* is not mentioned in the extensive review by Graham (1999b) about the Late Cretaceous and Cenozoic history of North American vegetation, where mangrove dynamics and evolution are fully addressed. Therefore, this review concentrates on confirmed *Pelliciera* records without ruling out the possibility that future findings may offer new interpretations.

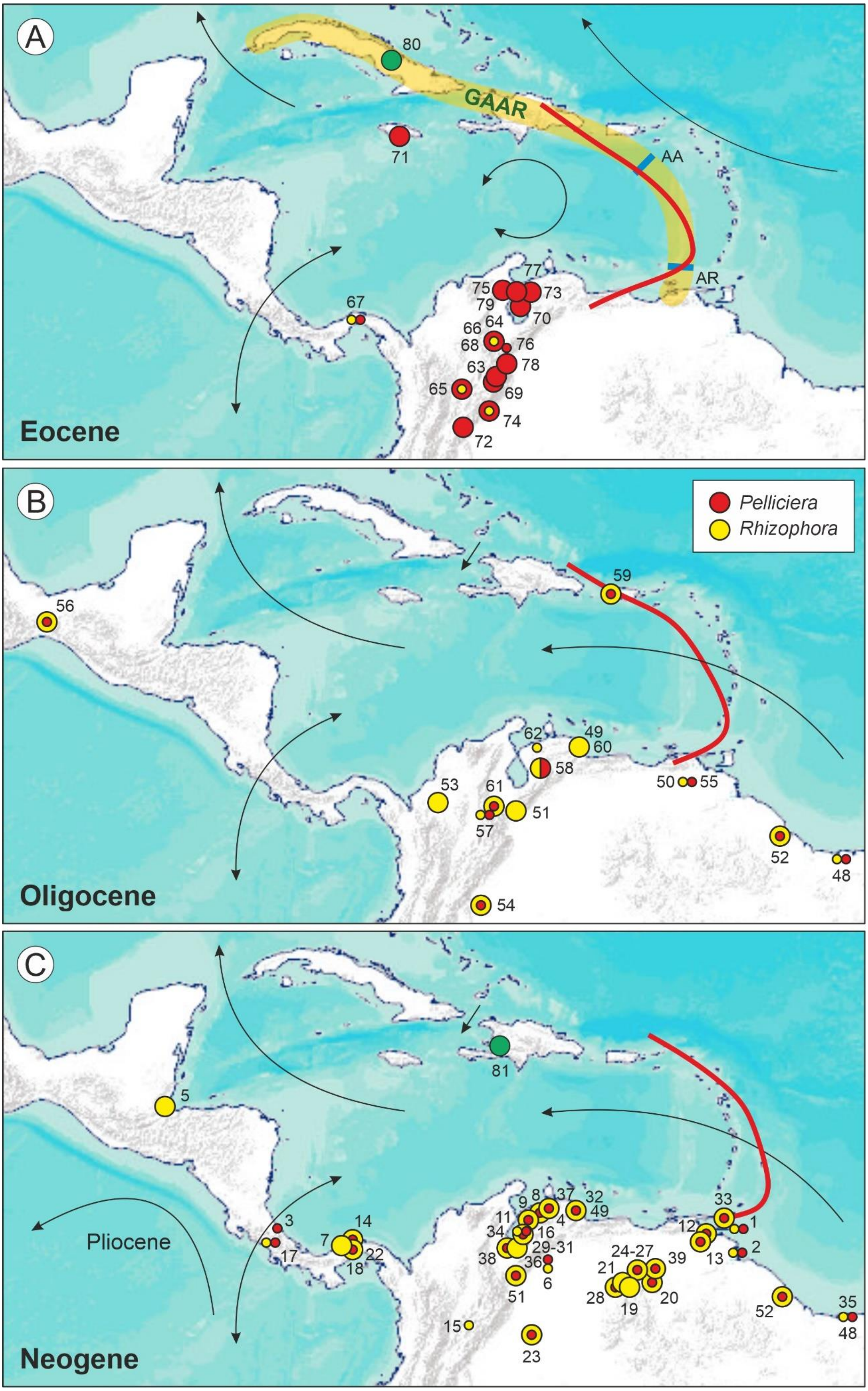
The representativity of pollen, in relation to its vegetation sources, is also a relevant parameter to be considered when discussing fossil records. The relationship between the amount and spatial patterns of sedimentary pollen and their parent plants is usually addressed by analogy with modern studies. In the case of *Rhizophora*, modern analogs show that its anemophilous (dispersed by wind) pollen is largely dominant in Caribbean mangrove assemblages due to its high pollen production and dispersal power. This pollen is locally very abundant on mangrove settings and decreases landward, but it remains abundant on shallow marine sediments in front of coasts with mangroves (Rull, 2022b). Therefore, *Rhizophora* pollen is a reliable indicator of coastal and shallow marine environments. The situation is less well known in the case of *Pelliciera*, due its restricted distribution and the scarcity of studies on its pollen dispersal. However, this plant is entomophilous (pollinated by insects) and its pollen is large and heavy (Duke, 2020), and hence, it is sedimented mostly locally, not far from the communities of its parent plant. Therefore, the presence of *Pelliciera* pollen, even in low quantities, can be considered a reliable indicator of the presence of in situ stands of this tree.

4.1. Eocene

A clear spatial pattern can be observed in the Eocene records that, with the exception of a single Jamaican record (site 71), are restricted to the present southern Caribbean margin (Fig.

10A). Noteworthily, all these records were situated west of the proposed GAARlandia emplacement during the Eocene, which could be used to support the actual existence of this landspan. In this scenario, *Pelliciera* mangroves would be considered isolated from the Atlantic circulation and, therefore, under the influence of Pacific mangroves in terms of dispersal and colonization. Indeed, modern studies have shown that the main dispersal agents for mangrove propagules are coastal currents (Van der Stocken et al., 2019) (Fig. 11), and GAARlandia would have acted as a barrier for Atlantic coastal continuity. All Eocene plate tectonic models agree that the western margin of the Caribbean plate was marked by a volcanic island arc open to Pacific circulation (Romito & Mann, 2020; Mann, 2021). Under the GAARlandia scenario, this may have important implications for mangrove dispersal, as only Pacific colonization would have been possible and, furthermore, the eventual Atlantic expansion of *Pelliciera* mangroves would have been prevented.

There are three possible objections to this view. One is that GAARlandia was relatively ephemeral – i.e., restricted to the last <3 million years of the Eocene epoch (Iturralde-Vinent,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Neogene

Figure 10. Eocene (A) Oligocene (B) and Neogene (C) *Pelliciera* and *Rhizophora* records from the Caribbean region (see Table 2 for site numbers and details). In some Oligocene sites, the distinction between Oligocene and Early Miocene was not possible (see Table 2). The dominant mangrove elements are indicated by larger dots and the scarcer mangrove components are represented by smaller dots. Green dots (sites 80 and 81) are localities with non-mangrove pollen assemblages (see text for details). The position of the advancing Caribbean plate boundary (thick red lines), the approximate location of the hypothetical EOT GAARlandia landspan (transparent yellow band) and the proposed marine connections AA and AR (blue strips) are indicated, following the chronological and paleogeographical frameworks of Fig. 7. Black thin lines indicate the main paleocurrents inferred from the paleogeographical reconstruction (see Fig. 8).

2006) – whereas *Pelliciera* mangroves emerged in the Early Eocene and flourished in the Middle Eocene (Rull, 2022a), when the Atlantic connection was open through the present Lesser Antilles (Fig. 8B) and, hence, they would have had many opportunities for in-and-out Atlantic dispersal. Another drawback is that no *Pelliciera* mangroves were recorded in extra-Caribbean regions prior to the Middle Eocene that could have acted as sources for Caribbean mangroves, which implies that the mangroves were most likely the result of in situ evolution rather than Pacific immigration (Rull, 2022a). Finally, the closure of GAARlandia would have been incomplete, as some degree of Atlantic influence could have been possible through the AA and AR passages (Cornée et al., 2012; Garroq et al., 2021). The full picture suggests that the eventual occurrence of a dispersal barrier such as GAARlandia could hardly have had a major influence on the biogeographical patterns of the Eocene *Pelliciera* mangroves, except for a relatively short Late Eocene time lapse.

During the Eocene, *Rhizophora* was mostly absent from the Caribbean region, with only scattered and rare occurrences, and when present, it was only a minor mangrove component, as already noted by Graham (1977) on the basis of qualitative records. This observation is reaffirmed here using the available qualitative and quantitative records summarized in Table 2 and Fig. 10. Indeed, of the 17 Eocene records reported (sites 63 to 79), *Rhizophora* was absent or not mentioned in 11, present in five and relatively frequent (up to 10%) in only one locality from Panamá (site 67). In this case, biogeographical patterns and processes are of a very different nature at both regional and global scales. Indeed, as suggested by phylogeographical studies, *Rhizophora* would have emerged in the IWP and then dispersed to the EAP during the Eocene using the Tethys seaway (Takayama et al., 2021). According to these results, *Rhizophora* would have arrived in the Caribbean via the Atlantic Ocean. Studies on modern dispersal pathways for mangroves show that the combination of intercontinental distance, predominant currents and floating propagule longevity makes the Atlantic a barrier for mangrove dispersal, even in the case of *Rhizophora*, whose propagules remain viable for a year or more when floating in salt water (Rabinowitz, 1978). In the Eocene, however, the Atlantic was less extensive, and coastal dispersal through the former pantropical Tethys Sea was still possible (Fig. 5). If we consider that the GAARlandia barrier, if it existed, was only present for a few million years close to the EOT, the dispersal of *Rhizophora* from the IWP to the Caribbean via the Atlantic pathway would have been theoretically possible during most of the Eocene.

One of the best quantitative examples of Eocene mangroves is from well VLC (site 70) in Venezuelan Lake Maracaibo, where *Pelliciera* was the dominant mangrove-forming tree during the Middle Eocene (Lutetian), associated with the palm *Nypa* (now restricted to the IWP; Pocknall et al., 2022), whereas *Rhizophora* was absent (Rull, 1998b) (Fig. 12). Examples with similar quantitative data are available from sites 69 (Paz del Rio, Colombia), 73 (Icotea, Venezuela), 74 (Piñalerita, Colombia) and 76 (Rubio Road and Rio Lora, Venezuela) (Germeraad et al., 1968; Jaramillo & Dilcher, 2001; Pocknall & Erlich, 2020). At other sites, only qualitative (presence/absence), semi-quantitative (abundant, common) or single-sample quantitative (percentage) information is available (Table 2).

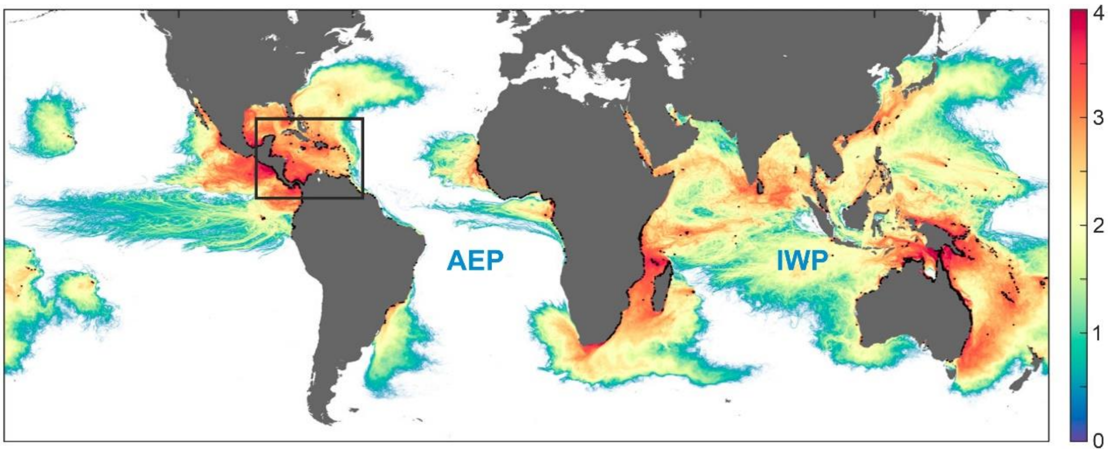

Figure 11. Present-day mangrove dispersal pathways represented as the simulated propagule trajectory density across the global ocean. The model combines the prevailing patterns of ocean currents with the viability of mangrove propagules during floating periods. Higher dispersal probability is represented by red tones and lower dispersal probability by blues tones, white represents zero probability. The Caribbean area is highlighted by a black box. Modified from Van der Stocken et al. (2019).

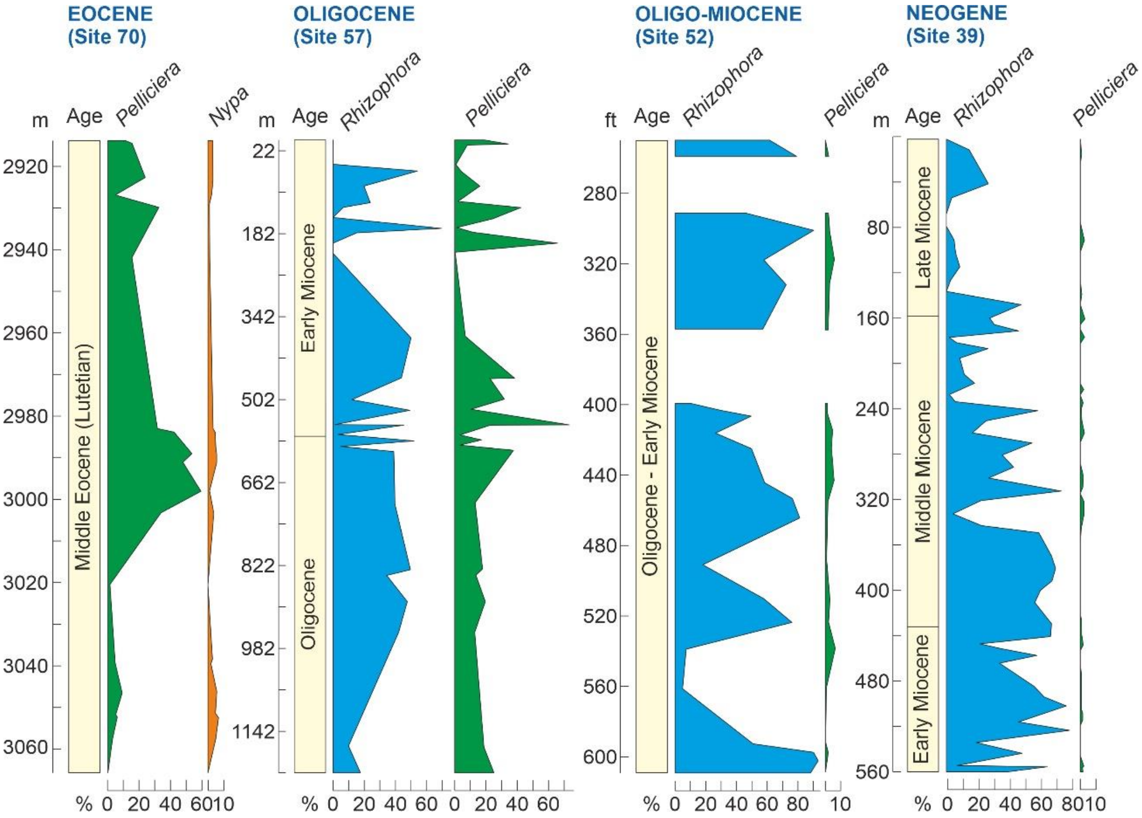

Figure 12. Eocene to Miocene representative Caribbean pollen diagrams showing the percentage trends of *Pelliciera* and *Rhizophora*. Depth scales in meters (m) and feet (ft); in sites 57 and 39, the depth scales are in relation to the top of the Miocene section. Redrawn from Van der Hammen & Wijmstra (1964), Lorente (1986) and Rull (1998b).

4.2. Oligocene

During the Oligocene, *Rhizophora* and *Pelliciera* expanded their geographical range beyond the proto-Caribbean Sea, reaching the northernmost plate boundary in the Greater Antilles (site 59), Central America (site 56) and the Atlantic Guianan coasts (sites 48 and 52) (Fig. 10B). The expansion of these mangrove trees, however, was of a radically different nature. Indeed, while

Rhizophora spread was accompanied by a general population increase that made this species dominant in mangrove communities, *Pelliciera* expansion involved significant population reductions that turned this tree into a subordinate component of mangrove vegetation. In some places (sites 52, 56 and 59), *Rhizophora* accounted for up to 90-95% of pollen assemblages (Van der Hammen & Wijmstra, 1964; Graham & Jarzen, 1969; Graham, 1999b), whereas in others (site 57), *Rhizophora* represented up to half of pollen counts (Lorente, 1986) (Fig. 12). The decline of *Pelliciera* was also somewhat heterogeneous, but its pollen frequency was always below 10%, except in one case (site 57), where it reached 25% of the assemblage (Lorente, 1986). According to qualitative and semi-qualitative records, *Pelliciera* is present in nine cases and absent/not mentioned in three (Table 2). The whole picture is consistent with a general expansion of Caribbean mangroves linked to the replacement of *Pelliciera* by *Rhizophora* as the dominant tree.

Both Atlantic and Pacific pathways were open for dispersal through the corresponding volcanic island arcs (Mann, 2021), which can help explain the Oligocene mangrove expansion. However, it could be asked why Caribbean mangroves did not experience a similar expansion during the Eocene, when similar marine circulation conditions existed (except for the possible short GAARlandia interval). The answer may be related to the EOT dominance shift and the ecological requirements of the taxa involved. First, it should be noted that the dispersal capacity (vagility) of *Rhizophora* is clearly superior to that of *Pelliciera*, as the *Rhizophora* propagules first can float in salt water for several months and are able to maintain their viability for a year or more, whereas the *Pelliciera* propagules have a maximum flotation period of barely a week and a maximum viability period of 70 days (Rabinowitz, 1978). This could help explain the expansion of Oligocene *Rhizophora* mangroves compared to Eocene *Pelliciera* mangroves. However, the dispersal capacity alone is insufficient to explain why *Pelliciera* also expanded in the Oligocene, together with *Rhizophora*. One possibility could be related to the phenomenon of ecological facilitation, in which a species provides refuge to another in the face of environmental stress, predation or competition, thus allowing survival under suboptimal conditions (Boucher et al., 1982; Callaway, 1995; Stachowicz, 2001; Bruno et al., 2003). This possibility is supported by recent studies on modern mangroves from Central America, as explained below.

Extant *Pelliciera rhizophorae* is highly sensitive to light intensity and salinity, and the combination of high levels of these environmental stressors leads to increased mortality, lower photosynthesis rates and reduced growth. When this species grows under shade conditions, however, it can tolerate high salinities, which suggests that light intensity is the main limiting factor for *P. rhizophorae*. As a result, this species is unable to establish in sites with an open canopy and grows in the understory beneath the canopy of other tree species that, in the case of Central America, is provided by *Rhizophora mangle*, which is more tolerant to environmental stressors (Dangremond et al., 2015). Interspecific competition with *Rhizophora* had been proposed in the past as a possible cause for the post-Eocene decline of *Pelliciera* (Jiménez, 1984; Graham, 1977). The study by Dangremond et al. (2015) demonstrates that, on the contrary, *Rhizophora* could have facilitated the survival of *Pelliciera* by providing protection against harmful environmental drivers. The possibility of plant competition relaxation in favor of facilitation relationships under biotic and abiotic stress cannot be disregarded, as demonstrated by modern ecological studies worldwide (He et al., 2013).

Other environmental factors, such as temperature, rainfall and sea-level changes, have also been proposed as potential causes for *Pelliciera* reduction (Fuchs, 1970; Graham, 1977, 1995). The chronological coincidence of *Pelliciera*-dominated and *Rhizophora*-dominated mangroves with global EOT cooling and sea-level fall (sections 2.1 and 3.3) is noteworthy, but any causal explanation should rely on the ecology of these taxa, which is unknown and can only be addressed by comparison with their modern counterparts. Comparisons of this type are not unusual in paleoecological reconstructions and are based on the principle of niche conservatism over time, which is especially useful in the case of long-lasting ecosystems such as mangroves (Wiens & Graham, 2005; Hadly et al., 2009; Wiens et al., 2010).

Climatically, *Rhizophora* is eurytopic (euryclimatic), as it lives under a variety of conditions with a relatively wide range of temperature and precipitation values and regimes, including tropical, subtropical, arid and temperate climates (Fig. 13, Table 3). In contrast, *Pelliciera* is stenotopic (stenoclimatic), as it is restricted to a small patch of equatorial climates characterized by high temperature and precipitation values and low seasonality. Typical values measured in modern *P. rhizophorae* studies are ~27 °C for average temperatures (minimum ~18 °C and maximum ~33 °C) and 1650-3050 mm of total annual precipitation (Castillo-Cárdenas et al., 2015; Dangremond et al., 2015). Under these conditions, a temperature drop like the EOT cooling is expected to have a greater influence on a stenothermic tree like *Pelliciera* than on a more eurythermic one like *Rhizophora*. In theory, *Pelliciera* mangroves could have adapted – in an evolutionary sense, that is, by experiencing genetic change – to the new climates or migrated toward more equatorial latitudes along the Pacific coasts, but none of this is observed in the fossil record. Instead, severe population reductions and local extinctions are documented at most sites (Fig. 10), likely due to the combined effects of stenothermy and low vagility. In contrast, *Rhizophora* not only accommodated the cooler Oligocene climates but also increased its geographical range and the size of its populations, thus becoming dominant in the mangrove communities, thanks to its higher phenotypic plasticity indicated by its wider environmental tolerance and greater dispersal capacity. The new *Rhizophora* mangrove ecosystems could have provided shelter for *Pelliciera* survival, as explained above.

Whether EOT cooling was accompanied by a shift toward aridification and/or enhanced seasonality in the Neotropics remains unclear, but, whatever the case, *Rhizophora* would have also been more efficient in withstanding these changes, if we consider the variety of precipitation regimes in which it is able to live at present (Fig. 13). In a climatic context, it is difficult to escape the idea that *Rhizophora* could have outcompeted *Pelliciera* in the EOT, in which case the proposal that *Rhizophora* mangroves could have provided refuge for *Pelliciera* survival and range expansion would seem contradictory. However, in ecology, it is well known that competition does not necessarily lead to extinction, and the coexistence of competing species is possible by niche segregation, which is essential for the maintenance of biodiversity (MacArthur & Levins, 1967; Violle et al., 2011; Kosicki, 2022). Niche segregation can occur by spatiotemporal and/or functional divergence, and a variable degree of overlap may exist. In the case of EOT mangroves, *Rhizophora* and *Pelliciera* would have differentiated in features such as dominance or autecological requirements (functional segregation), maintaining the same habitat (spatial overlapping).

Working on oceanic island vegetation, Fernández-Palacios et al. (2021) found that the dominant species of major plant communities, which they called “ecological winners”, usually are non-diversified immigrant species. In contrast, species that successfully evolve in situ by radiation, the so-called “evolutionary winners”, are abundant only in marginal habitats and are therefore considered “ecological losers”. Oligocene Caribbean mangrove communities could be considered to have some parallelisms with this situation, with *Rhizophora* – likely arriving by long-distance dispersal from the AEP region – as an ecological winner and *Pelliciera* – which evolved in situ and was replaced by *Rhizophora* as the dominant species – as an evolutionary winner but an ecological loser. In this case, however, the situation is more complex, as the ecological winner was precisely the one that provided the ecological loser the microhabitat conditions for becoming an evolutionary winner. Indeed, *Pelliciera* lost its dominance in favor of *Rhizophora* but obtained not only a microhabitat more protected from environmental

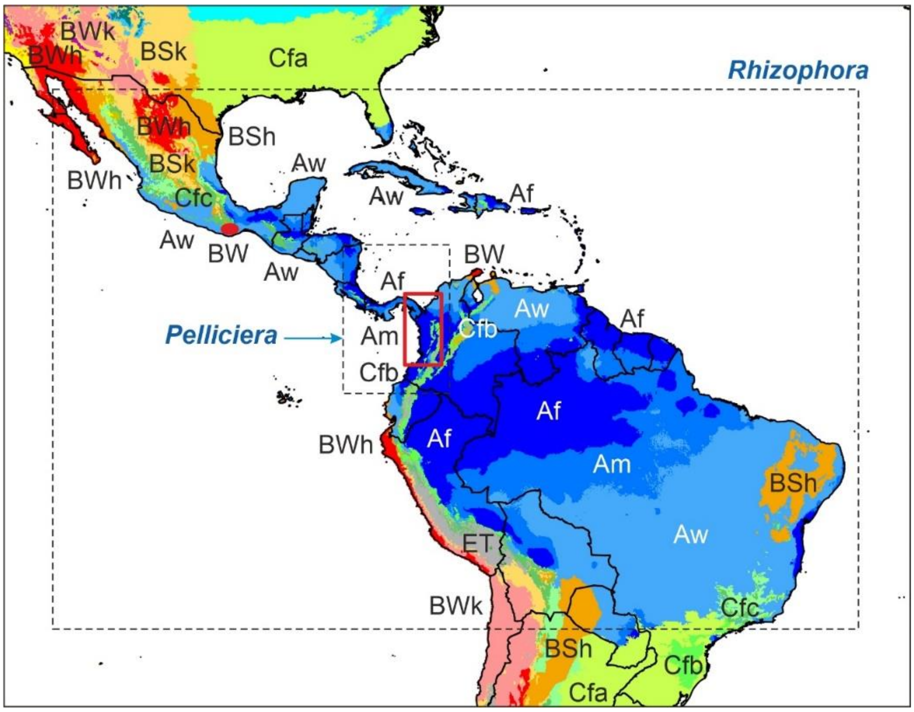

Figure 13. Approximate longitudinal and latitudinal amplitude of *Rhizophora* and *Pelliciera* species' distribution in the Neotropics (see Fig. 6), in relation to the climatic types according to the Köppen-Geiser classification (Table 3). The Chocó region, one of the wettest places on Earth (~13,000 mm y-1; Yepes et al., 2019), is highlighted by a red box. Base map from Peel et al. (2007).

Table 3. Description of Köppen-Geiger climate types represented in Fig. 13 and defining criteria (Kottek et al., 2006; Peel et al., 2007). MAP, mean annual precipitation; MAT, mean annual temperature; Th, temperature of the hottest month; Tc, temperature of the coldest month; T10, number of months where the temperature is above 10; Pd, precipitation of the driest month; Pt (threshold) varies according to the following rules: if 70% of MAP occurs in winter then Pt = 2 x MAT, if 70% of MAP occurs in summer then Pt = 2 x MAT + 28, otherwise Pt = 2 x MAT + 14. Temperature in °C and precipitation in mm.

1	Description	Criteria
Af	Tropical, rainforest	Tc≥18, Pd≥60
Am	Tropical, monsoon	Tc≥18, not Af, Pd≥100-MAP/25
Aw	Tropical, savanna	Tc≥18, not Af, Pd<100-MAP/25
BWh	Arid, desert, hot	MAP<5Pt, MAT≥18
BWk	Arid, desert, cold	MAP<5Pt, MAT<18
BSh	Arid, steppe, hot	MAP≥5Pt, MAT≥18
BSk	Arid, steppe, cold	MAP≥5Pt, MAT<18
Cfa	Temperate, no dry season, hot summer	Th>10, 0<Tc<18, Th≥22
Cfb	Temperate, no dry season, warm summer	Th>10, 0<Tc<18, not a, T10≥4
Cfc	Temperate, no dry season, cold summer	Th>10, 0<Tc<18, not a/b, T10<4
ET	Polar, tundra	0<Th<10

stressors but also a formerly non-existent agency for expanding its geographical range. In ecological terms, competition would have led to mutualistic and facilitative relationships mediated by functional niche segregation with a degree of physical overlap.

In addition to rapid cooling, the EOT sea-level fall also could have had an influence on mangrove replacement. As mentioned in sections 2.1 and 3.3, a sea-level drop of ~70 m has been proposed at both global and regional (Caribbean) scales, which would have exposed shallow marine shelf environments. Beyond the existence or absence of GAARlandia, which is discussed in sections 3.2 and 3.4, this sea-level fall would have increased the extension and connectivity of coastal areas suitable for mangrove establishment and dispersal (Fig. 7B), which would have favored the mangrove expansion documented for the Oligocene (Fig. 10B). This would have facilitated the expansion of generalist mangrove elements with high dispersion capacities, such as *Rhizophora*, over the more specialized and less vagile *Pelliciera*, which would have contributed to the EOT mangrove revolution by magnifying the effect of temperature decline.

4.3. Neogene

A brief comment on Miocene and Pliocene records is necessary to understand the full and, for the time being, irreversible replacement of *Pelliciera* by *Rhizophora* mangroves, as well as for the further analysis of *Pelliciera* range shifts leading to its present-day biogeographical patterns. Neogene records are concentrated in the southern Caribbean region, with new localities in Central America and northern South America (Colombia and Venezuela). Most of the communities represented are *Rhizophora* mangroves with *Pelliciera* as a subordinate element (Fig. 10). Marine circulation patterns were similar to those of the Oligocene, except for the last ~3 million years (Pliocene), when the Pacific connection disappeared after the closure of the Panamá Isthmus (O'Dea et al., 2016). A high proportion of Mio-Pliocene records are quantitative (Table 2) and collectively show dominance by *Rhizophora*, whereas *Pelliciera* attains a frequency up to 3-10% in a few samples and is barely present in most of the others. A representative example is from site 39 (Venezuela), where *Rhizophora* shows abundance values up to 80% and *Pelliciera* shows scarce and discontinuous occurrences (Fig. 12). These Miocene *Rhizophora* mangroves were the direct ancestors of present-day ones, which emerged after progressive Neogene diversification with no evident extinction or significant range shifts (Graham, 1995). Detailed analysis of this process using quantitative pollen evidence remains to be addressed and will be the target of a third article, in addition to Rull (2022a) and this paper, on the origin and evolution of Caribbean mangroves.

5. *Pelliciera* range shifts and potential causes

A favorite topic in the study of Neotropical mangrove evolution has been the contraction of the geographical range of *Pelliciera* from the Miocene to the present and its potential causes, which include those already mentioned in the former section for the EOT replacement of *Pelliciera* by *Rhizophora* mangroves (Wijmstra, 1968; Fuchs, 1970; Graham, 1977, 1995; Jiménez, 1984; Rull, 1998a, b, 2001a). However, the *Pelliciera* range shifts initiated well before and did not consist of a single monotonous contraction trend. Using the evidence gathered in this paper, the biogeographical history of *Pelliciera* has been subdivided into three main phases (Fig. 14). The first phase (I) began in the EOT and was characterized by the geographical expansion of *Pelliciera* accompanied by the significant reduction of its populations. The term "dilution", which would seem ideal to describe this phenomenon, has already been used to refer to a different biogeographical concept (Keesing et al., 2006, 2010). Here, this phenomenon, which extended until the Miocene, will be labeled "thinning expansion". The second phase (II) was the contraction of the widespread Miocene range, which encompassed a substantial part of the Neotropics, to a narrower latitudinally restricted band situated along the southern Caribbean margin. This is the Mio-Pliocene range contraction. The third phase (III) took place between the Pliocene and the present and consisted of the reorganization of the southern Caribbean Pliocene band to attain the current *Pelliciera* distribution in Mesoamerica and NW South America. This is called the Plio-Pleistocene reorganization.

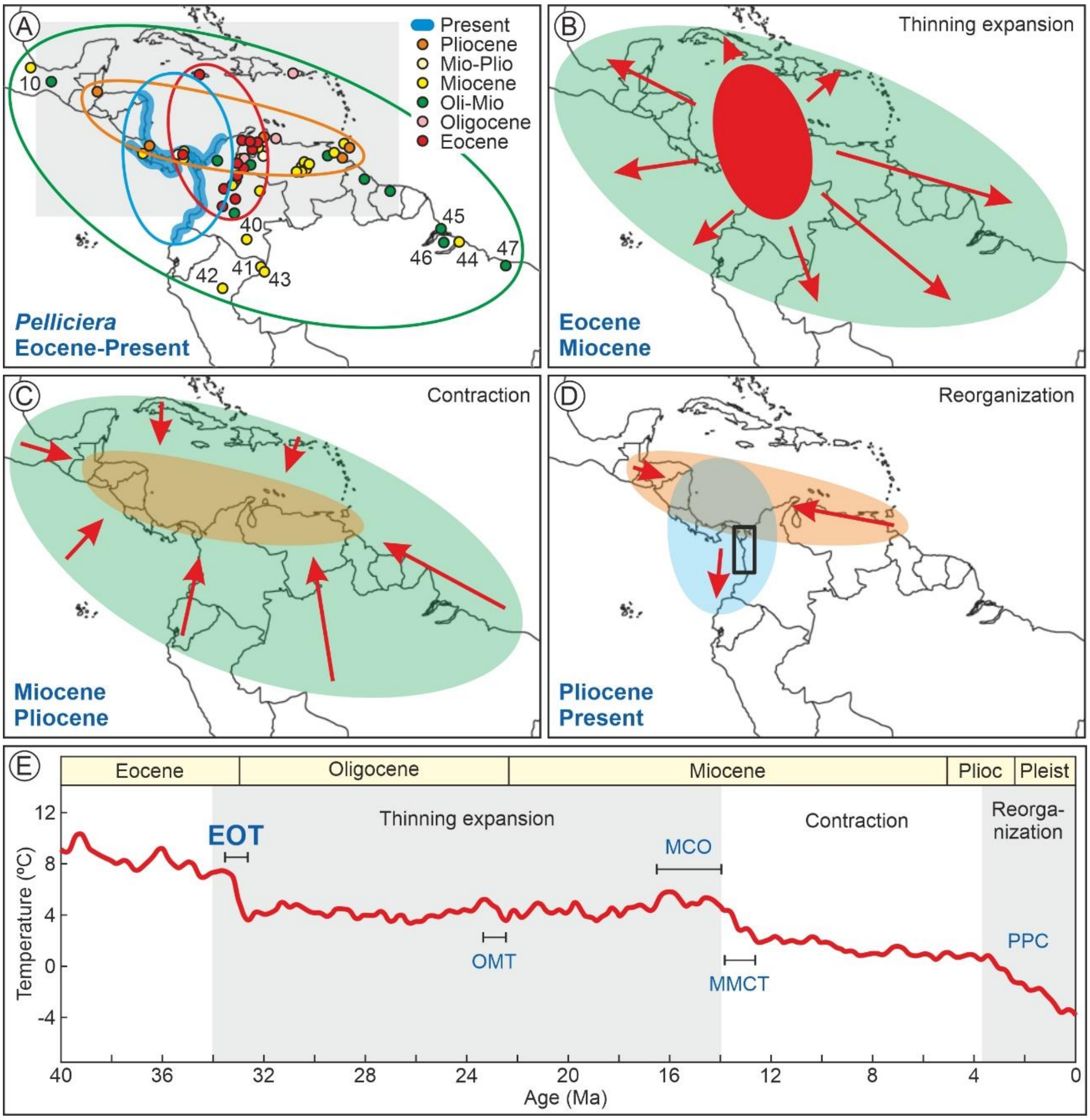

Figure 14. Eocene to present distribution of *Pelliciera* (A) and range shifts experienced by this mangrove tree during this time lapse (B to D), compared with the average global temperature trends expressed as the difference to today (E). The Caribbean region represented in Fig. 10 is highlighted by a gray box (A) and the Chocó region is marked by a black box (D). The localities already mapped and labelled in Fig. 10 are depicted but not named, only the sites beyond the Caribbean region are identified using the numbers of Table 2. OMT, Oligo-Miocene Transition; MCO, Miocene Climate Optimum; MMCT, Middle Miocene Climate Transition; PPC, Plio-Pleistocene Cooling. Temperature curve and climatic events from Westerhold et al. (2020).

5.1. EOT–Miocene thinning expansion

The potential causes of Eocene–Miocene thinning expansion have already been discussed, and EOT cooling has been considered a potentially important climatic driver (section 4.2). It could be added that the biogeographical outcome, that is, the spreading of tiny *Pelliciera* populations within a matrix of dominant *Rhizophora* mangroves, is similar to the concept of diffuse microrefugia, where small stands of a given species are able to thrive in favorable microhabitats under generally unfavorable macroenvironmental conditions (Rull, 2009, 2010).

5.2. Miocene–Pliocene contraction

The Mio-Pliocene contraction occurred during a phase of extended climatic stability after the Middle Miocene Climate Transition (MMCT), and the Pliocene–present reorganization took place during the Plio-Pleistocene cooling (PPC), which included the Pleistocene glaciations. Therefore, a coincidence between *Pelliciera* range shifts and the most relevant temperature drops is apparent, although a causal explanation is elusive, as the same climatic shift (i.e., cooling) is linked to disparate biogeographical events (i.e., expansion, contraction, and reorganization). It should also be noted that *Pelliciera* range shifts were not paralleled by similar episodes in Neotropical *Rhizophora* mangroves, which were experiencing a continuous expansion and diversification process since the EOT, as shown in sections 4.2 and 4.3 – see also Graham (1995) and Rull (1998a). Therefore, the *Pelliciera* range shifts can be regarded as specific to this mangrove tree rather than consequences of community-scale biogeographical phenomena. It is possible that environmental shifts overcame the narrow environmental tolerance of *Pelliciera* and that the buffering provided by *Rhizophora* mangroves was insufficient to guarantee survival in certain areas, thus leading to local extinction. This would be valid for explaining the Mio-Pliocene range contraction but not the EOT–Miocene range expansion, and the fact that both occurred after coolings of similar magnitude (Fig. 14E) seems to argue against temperature as the main driver. In addition, Mio-Pliocene range contraction was a centripetal trend toward the southern Caribbean margin rather than latitudinal displacement toward the equator, as would be expected if temperature was the main environmental forcing.

The possibility of precipitation – or hydrological balance (i.e., the precipitation/evaporation ratio) – being an important forcing for *Pelliciera* range shifts is difficult to evaluate because of the lack of information on precipitation patterns in the Caribbean region during the period of study. Once more, analogies with present conditions could provide some clues. As quoted above, *Pelliciera* is restricted to nearly equatorial warm and wet climates with little or no seasonality (Fig. 13, Table 3). Actually, the current distribution area of this mangrove tree is centered on one of the wettest regions of Earth, the Chocó region, with huge and unparalleled precipitation values on the order of 13,000 mm per year (Yepes et al., 2019). This suggests that the present distribution of *Pelliciera* is heavily influenced by precipitation. Using the principle of niche conservancy and considering the strong stenoclimatic nature of *Pelliciera*, it could be assumed that the threshold response for this tree to precipitation shifts would be easily attained and, hence, its distribution patterns would be affected even by small rainfall declines. For example, looking at the Pliocene distribution area (Fig. 14C), it could be hypothesized that the southern Caribbean sector would have remained perhumid during this geological epoch, whereas the surrounding areas would have been under rainfall regimes insufficient for *Pelliciera* survival. However, given the present state of knowledge, this type of reasoning is circular and, as in the case of temperature, cannot explain why the same taxon responds differently to the same climatic forcing. Regarding past precipitation seasonality, the same constraint of lack of information applies, but it would be interesting to consider this parameter in future paleoclimatic studies, especially in relation with the potential influence of relatively short-term (~20,000-100,000 yr period) Milankovitch cycles (Bennett, 1997).

Whether precipitation would have influenced *Pelliciera* in a straightforward manner or indirectly by affecting salinity, or both, is still difficult to assess, but this possibility should not be disregarded, as rainfall and soil salinity are inversely related and modern studies have demonstrated that *P. rhizophorae* is highly sensitive to salinity increases (Dangremond et al., 2015). In contrast, temperature and salinity are directly related to evaporation rates, and hence, salinity is higher in warmer climates. Therefore, salinity maximizes in hot/arid climates and minimizes under cold/humid conditions. Mangroves are mostly tropical ecosystems that do not grow in cold climates, but the range of moisture variation is extreme, ranging from deserts such as the Sahara to perhumid zones, such as the Chocó. In this range of conditions, precipitation is more critical than temperature for defining salinity patterns, and therefore, the salinity of mangrove soils, which is a major limiting factor for *Pelliciera*, is more strongly linked to aridity than to temperature. This reinforces the idea that past range shifts of this mangrove tree would have been heavily influenced by moisture changes. Unfortunately, with the available information, it is still difficult to relate the direction of biogeographical shifts (i.e., range expansion or contraction) with eventual moisture changes in a manner supporting a causal explanation.

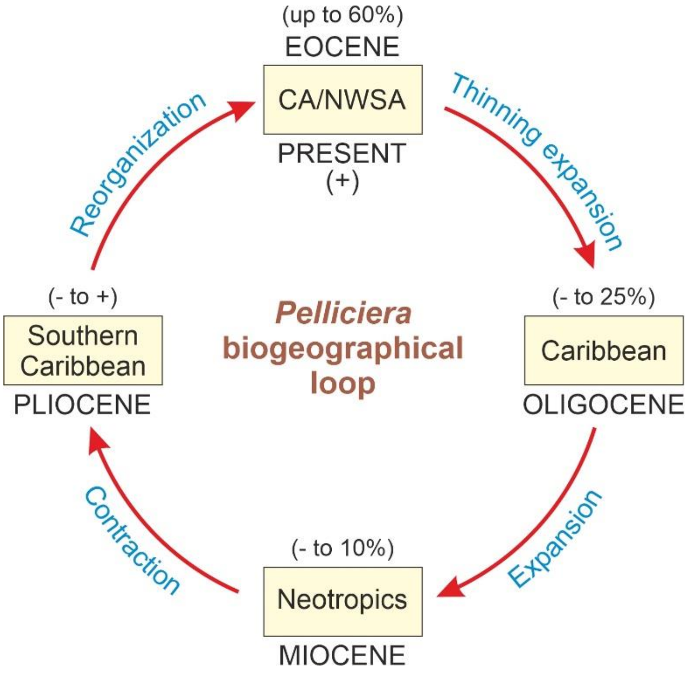

Figure 15. *Pelliciera* biogeographical cycle starting and ending with approximately the same distribution area around Central America and northwestern South America (CA/NWSA) but with reduced population density and dominance loss. The distribution range is inside the yellow boxes, whereas the age and the occurrence patterns (in brackets) – in pollen abundance (%), presence (+) and absence (-) – are indicated above and below the boxes.

5.3. Pliocene–present reorganization

The Pliocene to present reorganization is different from previous range shifts, as it combines a longitudinal contraction around Central America with a latitudinal displacement toward the equator (Fig. 14D). This latitudinal range migration could be linked to the effect of the global Pliocene cooling and the ensuing Pleistocene glaciations (Lisiecki & Raymo, 2005), whose magnitude far exceeded the intensity of EOT and MMCT coolings, and would have promoted the southward migration of *Pelliciera* populations to warmer equatorial climates. The longitudinal contraction is more difficult to explain with the available evidence, but the absence of a longitudinal temperature trend suggests that moisture, which is more irregularly distributed, could have been more influential than temperature. It has been suggested that, in the Neotropics, Pleistocene glaciations were characterized by arid climates, and the precursors of presently highly diverse rainforests, which required wetter climates, occupied refugia in favorable areas that were isolated among them, thus favoring allopatric speciation. This idea emerged from the study of the Last Glacial Maximum (LGM), which occurred ~21,000 yr BP, in combination with the current patterns of biodiversity and endemism (Prance, 1982; Whitmore & Prance, 1987), and was further extrapolated to the former Pleistocene glacial phases. This refuge hypothesis has been either supported or severely criticized on the basis of paleoecological evidence (Colinvaux et al., 2000; Van der Hammen & Hooghiemstra, 2000), and the debate is ongoing (Rull, 2008, 2011, 2020b). A number of potential LGM plant refuge areas have been identified in northern South America that fall within the Pliocene *Pelliciera* range (e.g., Steyermark, 1979), but no specific studies exist on the response of this mangrove tree to Pleistocene glaciations. Quaternary *Pelliciera* records are restricted to the Holocene, where it is present but at very low abundances (+ in the notation of Table 2) in surface sediments (Horn, 1985; Jaramillo & Bayona, 2000); no Pleistocene records are available for comparison with Pliocene and present spatial patterns. Again, the available evidence is indirect and insufficient for a sound assessment.

During the last millennia, human activities could have influenced mangrove distributions. Removal and range fragmentation are among the most common biogeographical consequences of anthropogenic disturbance for mangrove forests. This has deeply affected mangrove distributions, as a global loss of mangrove area of nearly 50% has been estimated for the last 50 years, with significant acceleration since the beginning of the 21st century (Giri et al., 2011; Wang et al., 2019; Goldberg et al., 2020; Toosi et al. 2022). Cultivation and aquaculture are among the main human activities responsible for global mangrove reduction, whereas the most influential natural hazards are coastal erosion, extreme climatic events and sea level rise (Goldberg et al., 2020). *P. rhizophorae* has been listed as Vulnerable – that is, under a high risk of extinction in the wild due to its small (500-2000 km^2) and fragmented distribution area – on the IUCN (International Union for Conservation of Nature) Red List of Threatened Species (Polidoro et al., 2010; Blanco et al., 2012; Bhowmik et al., 2022). Urban expansion has been recognized as a major threat for *Pelliciera* populations, which are being heavily fragmented and threatened by habitat loss (Blanco-Libreros & Ramírez-Ruiz, 2021). Good regeneration prospects have been reported for some extant *Pelliciera* populations that would encourage eventual restoration and reforestation actions (Gross et al., 2014; Alvarez-León, 2019; Madrid et al., 2019). However, urgent conservation actions, such as the creation of protected areas to control urban expansion, are still needed. From a biogeographical perspective, the available evidence suggests that, rather than shrinking the distribution area of *Pelliciera* as a whole, human activities have caused its severe fragmentation, which affects population viability and increases sensitivity to extreme events and global warming (Blanco-Libreros & Ramírez-Ruiz, 2021). To extent to which prehistoric societies would have affected the distribution area of *Pelliciera* remains unknown due to the scarcity of paleoecological records.

5.4. The *Pelliciera* biogeographical loop

It seems pertinent to point out that the biogeographical history of *Pelliciera* is a complex subject that may have been influenced by a variety of factors, and none of the potential causal relationships discussed above can be considered, by itself, the ultimate explanation. Rather, the coupling of a variety of environmental, ecological, evolutionary and anthropogenic drivers and their eventual interactions, feedbacks and synergies should be taken into account depending on the spatiotemporal context under consideration. The long-term persistence of *Pelliciera* despite the competitive superiority of *Rhizophora* seems surprising. However, it is known that eurytopic generalist species are better able to live under a wide range of environmental conditions whereas stenotopic specialized species are more efficient within the restricted set of conditions in which they can develop (Futuyma & Moreno, 1988). Therefore, *Rhizophora* could have displaced *Pelliciera* from a large part of its Miocene distribution area. However, once *Pelliciera* occupied the optimum setting within its niche in the Pliocene, it was ecologically more efficient and able to endure *Rhizophora* competition.

During the Plio-Pleistocene, optimum conditions for *Pelliciera* would have shifted in the way suggested above, but the range would have remained approximately the same size, which is also similar to the Eocene range. Indeed, the present and Eocene *Pelliciera* ranges are very similar in size and position except for a few sites (Fig. 14), with the main differences lying in population size and dominance relationships. Hence, after more than 35 million years of ecological and evolutionary dynamics, environmental change and paleogeographic reorganizations, *Pelliciera* has returned to its ancestral distribution area, but this time as a subordinate, rather than a dominant, mangrove tree (Fig. 15). This biogeographical loop may be an example of the "taxon cycle" concept introduced by Wilson (1961), who postulated that "a taxon maintains its headquarters in a given land mass indefinitely, expanding and contracting cyclically, or else declines to extinction" (p. 191). In the case of *Pelliciera*, the "headquarters" would be the Central America/NW South America (CA/NWSA) region, where it originated in the Eocene and lives today. Wilson (1961) defined the taxon-cycle concept while working on ants from the IWP region and proposed that "the taxon cycle dated no further back than the early Tertiary, when the radiation of modern ant genera began" (p. 189). This was deduced from geological evidence indicating that the Melanesian archipelagos under study were of Cenozoic origin and, hence, the modern ant faunas of these islands could not be older than that.

The estimated duration of taxon cycles was further addressed by Ricklefs & Bermingham (2002), who applied this model to Greater Antillean bird evolution and found that intervals between expansion phases have characteristic times on the order of 0.1 to 10 my, as deduced from molecular phylogenetic studies. Using similar methods, estimated taxon cycle durations of ~5 my were found for Indo-Pacific birds (Jønsson et al., 2014; Pepke et al., 2018). As these periodicities did not fit with Pleistocene glacial/interglacial cycles, which occurred at 0.02-0.1 my periods (Hays et al., 1976), these authors invoked other higher-rank phenomena, such as tectonic events (plate collision, orogenesis), as potential causes for taxon cycles (Pepke et al., 2018). Evidence for taxon cycles comes primarily from animal research; therefore, chronological comparisons with plants such as *Pelliciera*, with different life history traits and ecological/evolutionary patterns, are still premature. However, it is interesting to note that *Pelliciera* expansion initiated in the EOT (~34 Ma), which roughly coincides with the maximum ages for taxon cycles as proposed by Wilson (1961), and was characterized by profound tectonic, climatic and paleogeographical reorganizations.

Whether the biogeographical loop documented here for *Pelliciera* is a recurrent feature is hard to establish with the available information, as this taxon originated in the Eocene and no previous records of Caribbean mangroves are available before those dates (Rull, 2022a). However, the Eocene/Oligocene extinction event has been considered to be part of a Phanerozoic cyclic extinction series with a period of 26-30 my (Raup & Sepkoski, 1984; Melott & Bambach, 2014), which is in the range of possible durations of the *Pelliciera* loop. This means that the initial expansion of *Pelliciera* was linked to a cyclic phenomenon, but whether the biogeographical loop reported here for this taxon is a recurrent feature can only be known in ~34 my. This does not preclude, however, qualifying the event as a taxon cycle sensu Wilson (1961). Therefore, the *Pelliciera* biogeographical loop could be considered empirical evidence for such a concept, which was initially a hypothesis erected by evolutionary inference on the basis of present-day biogeographical patterns.

6. Conclusions and prospects for future research

The main topics discussed in this review and the contributions made to the knowledge of the EOT revolution of Caribbean mangroves can be summarized as follows:

6.1. Global

- The EOT was characterized by rapid (0.5-0.8 my duration) worldwide cooling that caused the glaciation of Antarctica and represented the end of Cenozoic greenhouse climates and the onset of the present icehouse state of Earth. Whether this cooling was accompanied by a global trend toward aridification remains unclear, although the available evidence suggests this possibility at a regional level. A global sea-level fall of ~70 m, on average, has been estimated for the EOT, which has been linked to the Antarctic glaciation.
- The EOT cooling and Antarctic glaciation have been attributed to the interplay of three main mechanisms: a global reduction in atmospheric CO_2 concentration (from ~1000 ppm to 700-800 ppm), the establishment of the Antarctic Circumpolar Current (after the opening of the Drake Passage and the Tasman Gateway) and the albedo effect of ice sheet growth.
- The EOT was characterized by intense biotic turnover due to cooling, sea-level fall and paleographical reorganizations. Globally, marine organisms (foraminifers, radiolarians, calcareous nanoplankton, dinoflagellates, diatoms, and ostracods) were the most affected by extinction, whereas terrestrial extinction rates exhibited strong spatial variability, especially in plants and mammals. These Eocene extinctions combined with increasing Oligocene speciation initiated the trend toward the establishment of modern biotas.
- On the basis of fossil evidence, mainly pollen, the EOT global disruption has been considered to be an important driver of the initial split between the Indo-West Pacific (IWP) and Atlantic-East Pacific (AEP) mangrove biotas, as well as for the replacement of *Pelliciera*-dominated by *Rhizophora*-dominated Neotropical mangroves.
- Recent molecular phylogeographic studies suggest that *Rhizophora* would have originated in the IWP region during the Eocene and migrated to the EAP region, attaining its current worldwide distribution in the Late Eocene. Modern EAP *Rhizophora* species would have emerged between the Late Miocene and the Pliocene. The same studies have shown that neither vicarianist nor dispersalist explanations alone can account for mangrove biogeography, and both are needed to understand the present-day patterns of these coastal ecosystems.

6.2. Caribbean region

- During the Eocene/Oligocene boundary, the Caribbean microplate, situated between the North American and South American plates, was migrating to the east, with the advancing front situated between the present eastern Greater Antilles in the north and the Aves Ridge in the south. The Lesser Antilles had not yet appeared.
- Most paleogeographical reconstructions show that, during the EOT, the Caribbean region was an open seaway that connected the Pacific and Atlantic Oceans, as the eastern and western plate boundaries were defined by volcanic island arcs open for marine circulation. However, some have proposed that an ephemeral (<3 my duration) land bridge, named GAARlandia, would have existed that connected the Greater Antilles with northern South America. This landspan would have been due to the combination of lowered sea levels and tectonic uplift and would have blocked the Atlantic–Pacific marine connection.
- Circum-Caribbean paleoenvironmental records suggest that the EOT occurred between 33.8 and 33.5 Ma and was a stepwise event characterized by three short stages, with an overall cooling of 3-6 °C and a total eustatic sea-level fall of 67 m.
- The EOT has been considered an important phase for the origin of present-day Caribbean biotic patterns. Some researchers favor long-distance dispersal using marine currents from Central and South America as the main source for the Caribbean biota, whereas others believe that terrestrial migration from South America via GAARlandia was the main

dispersal pathway. The potential influence of the EOT cooling and sea-level drop is rarely mentioned.

- Most Caribbean biogeographical studies are focused on the origin of the island biotas, especially in the Greater Antilles; therefore, emphasis is placed on dispersal pathways from the continent. However, mangroves grow on continental and island coasts, and understanding their biogeographical patterns and processes is a more complex task.
- More than 80 qualitative (presence/absence), semi-quantitative (abundance classes) and quantitative (percentages) fossil pollen records have been reviewed, ranging from the Eocene to the Pliocene, with emphasis on the Eocene/Oligocene transition. Neogene records have also been listed but not analyzed in depth, as they deserve special treatment.
- The Eocene mangroves were dominated by the autochthonous *Pelliciera* with pollen abundances up to ~60%, accompanied by the palm *Nypa* in the intertidal zone and other back-mangrove elements, such as the fern *Acrostichum* (brackish waters) and the palm *Mauritia* (freshwaters). *Rhizophora* was mostly absent or very scarce.
- *Rhizophora* could have arrived in the Late Eocene from the IWP by long-distance dispersal through the Atlantic, which is supported by the high dispersal ability of its propagules and the modeling of worldwide ocean currents.
- Under the GAARlandia hypothesis, *Pelliciera* mangroves would have been isolated from the Atlantic influence and connected only to the Pacific coasts. Likewise, the arrival of *Rhizophora* from the Atlantic would have been hindered by the GAARlandia barrier. However, this hypothetical land bridge was ephemeral, and the Atlantic connection would have existed for most of the Eocene. Therefore, GAARlandia could hardly have had a major influence.
- The Oligocene mangroves were dominated by *Rhizophora,* and *Pelliciera* was a subordinate element with pollen abundances below 10% and absent in some cases. Therefore, the EOT witnessed a general and abrupt replacement of *Pelliciera* by *Rhizophora* mangroves across the whole Caribbean region. This dominance shift was accompanied by expansion from the original mangrove patch, situated in the Central America/NW South America sector (CA/NWSA), to the whole circum-Caribbean region.
- The Oligocene mangrove expansion was led by *Rhizophora*, whose propagules can float for months and remain viable for a year or more, whereas those of *Pelliciera* have a maximum floating period of barely a week and a viability of a couple months. Despite this, *Pelliciera* also expanded its range, likely facilitated by *Rhizophora*, which would have provided protection against biotic and abiotic stress, as occurs in modern mangroves.
- The EOT mangrove dominance shift from *Pelliciera* to the newly arrived *Rhizophora* could have been influenced by the recorded cooling. *Rhizophora* is euryclimatic, as it can live under a wide range of temperature and moisture conditions, whereas *Pelliciera* is stenoclimatic and restricted to warm and wet/perhumid climates. The EOT cooling would have been withstood by *Rhizophora* due to its high climatic tolerance but not by *Pelliciera*, whose survival was guaranteed only by occupying protected microhabitats within the *Rhizophora* canopy. This EOT mangrove revolution could be considered an example of ecological competition with no exclusion, as it favored the coexistence of the competing species by niche segregation.
- Eocene-like *Pelliciera* mangroves never returned, but this species survives today as a minor mangrove component, having experienced significant range shifts subdivided into three main phases: EOT–Miocene expansion, Miocene–Pliocene contraction and Pliocene–present reorganization. The maximum extent of the *Pelliciera* range (the whole Neotropical area) was attained in the Miocene and was followed by significant Pliocene contraction to the southern Caribbean margin, possibly linked to climatic causes. The ensuing range reorganization could have been influenced by both Pleistocene glaciations and, during the last millennia, human activities.

- Long-term biogeographical shifts of *Pelliciera* are characterized by successive expansion, contraction and reorganization trends that define a loop starting and ending in the same geographical area, i.e., the Central America/NW South America (CA/NWSA) region, thus defining a taxon cycle of ~34 my duration. Whether this taxon cycle is of a recurrent nature remains unknown.

6.3. Future research

A number of issues remain to be clarified and should be addressed with future research. Among them, the following points can be highlighted:

- While the EOT cooling has been unequivocally documented worldwide, the occurrence of global patterns of moisture conditions is uncertain, especially in reference to eventual trends toward aridity and/or enhanced seasonality.
- Phylogenetic and phylogeographic studies should pay special attention to the potential influence of EOT on the global patterns of mangrove evolution.
- More studies on DSDP and ODP Caribbean cores are needed to reconstruct EOT climates and marine circulation in the region.
- Caribbean biogeographical and phylogeographical studies have traditionally been concentrated on island biotas, especially in the Greater Antilles, and more focus is needed on continental coasts for a better understanding of mangrove evolution.
- More conclusive geological and geophysical evidence is needed to verify the existence of the GAARlandia land bridge. Inferences based on biogeographical and phylogeographical patterns are indirect and may lead to circularity.
- A detailed taxonomic review and more pollen records are needed to clarify the potential occurrence of *Lanagiopollis crassa* (=*Psilatricolporites crassus*), the fossil representative of *Pelliciera* in Africa, Europe and North America during the Paleogene and Neogene.
- In pre-Quaternary palynological studies, emphasis should be placed on quantitative records as the best way of reconstructing past communities.
- More ecological studies on *Pelliciera* are needed to better define its niche and clarify its ecological relationships with *Rhizophora*, with emphasis on the interplay between competition and facilitation processes.
- More Holocene paleoecological surveys are needed in the present distribution area of *Pelliciera* to unravel the potential influence of human activities during the last millennia.
- A detailed study of the *Pelliciera* biogeographical loop as a potential taxon cycle deserves special attention as a contribution to ecological and biogeographical theory.

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