Southeast African mangroves: an exceptionally young paleobotanical record

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Abstract

Mangroves are pantropical intertidal forests that maintain coastal biodiversity, provide a wide range of ecological services and represent the most efficient blue-carbon ecosystems for mitigating global warming. A recent global initiative aims to reconstruct the historical biogeography of mangroves using comprehensive paleobotanical datasets from biogeographically coherent regions. This approach has been applied to the Caribbean, Europe, the Middle East and western Africa. Here, the same methodology is used to investigate the paleobiogeography and evolution of Southeast African (SEAF) mangroves, including those of the Western Indian Ocean (WIO) islands. Unlike previous regional syntheses, which reconstructed mangrove history from the Late Cretaceous onward, the SEAF dataset contains only Middle-Late Pleistocene records, with no confirmed Cretaceous, Paleogene or Neogene occurrences. This pattern is consistent with molecular phylogeographic studies of SEAF true-mangrove taxa, which indicate that they originated and diversified in the Eastern Indian Ocean (EIO) before expanding into SEAF mainly during the Late Pleistocene. A comparable Cenozoic fossil gap has also been reported for the Madagascar fauna, suggesting that this pattern reflects a genuine biogeographical feature rather than methodological bias or an incomplete fossil record. If confirmed, SEAF mangroves would represent the youngest known mangroves worldwide by more than 70 million years. This finding challenges the assumption that major mangrove regions share a common Late Cretaceous–Cenozoic history and opens new perspectives on the assembly and evolution of tropical coastal biotas. Future work should focus on expanding the fossil record and improving the chronological calibration of molecular phylogenies.

Keywords

Mangroves, Southeast Africa, Pleistocene, biogeography, evolution, paleogeography, plant fossils

1. Introduction

Coastal mangroves are intertidal woody communities that occupy sheltered tropical and subtropical shorelines, with a nearly continuous distribution between about 30° N and 30° S (Spalding et al., 2010). By trapping sediments and attenuating wave energy, they stabilize coastlines, limit erosion, promote coastal accretion and create conditions favorable for adjacent coastal environments. They also form a dynamic interface between terrestrial and marine systems, supporting high biological diversity by providing habitat for terrestrial biota and breeding and nursery grounds for numerous aquatic species (Laegdsgaard & Johnson, 2001; Nagelkerken et al., 2008). Mangroves also provide a broad spectrum of provisioning, regulating, and cultural ecosystem services (Afonso et al., 2021) and are among the most efficient blue-carbon ecosystems, accumulating and preserving substantial amounts of organic carbon in waterlogged sediments, thereby contributing to climate-change mitigation (Nellemann et al., 2009; McLeod et al., 2011; Fest et al., 2022). Despite these ecological and societal benefits, mangrove forests continue to decline worldwide owing to natural and anthropogenic pressures, making their conservation and restoration a global priority (Duke et al., 2017; Worthington et al., 2020).

Mangrove communities are built around a relatively small group of highly specialized plant species from diverse evolutionary lineages that have independently evolved similar adaptations to survive in saline, waterlogged and oxygen-poor intertidal environments. Species restricted to mangrove habitats are known as true mangroves and are divided into major and minor elements. Major elements are the canopy-forming trees that define the forest structure, whereas minor elements are restricted to mangroves but usually occur as subordinate components. In contrast, associate elements also occur in other coastal environments (Tomlinson, 2016).

The composition of true-mangrove floras differs markedly across the tropics, defining two major biogeographic regions: the Atlantic–East Pacific (AEP) and the Indo–West Pacific (IWP), separated by the African continent (Fig. 1). The IWP supports 54 true-mangrove species in 17 genera, whereas the AEP contains only 11 species in six genera. Despite this contrast, the canopy-forming genera *Rhizophora* (Rhizophoraceae) and *Avicennia* (Acanthaceae) occur in both regions, although they are represented by different species. Among the minor true-mangrove elements, only the fern genus *Acrostichum* (Pteridaceae) is pantropical (Tomlinson, 2016; Duke, 2017).

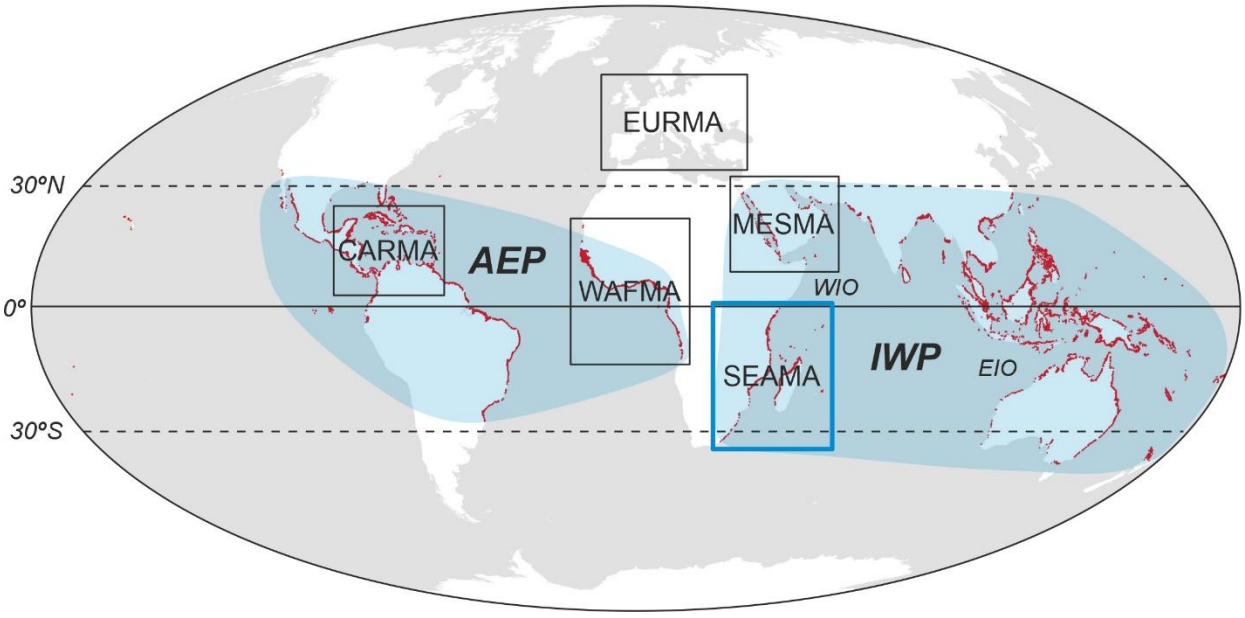

Figure 1. Worldwide mangrove distribution (red fringes) highlighting the Atlantic-East Pacific (AEP) and Indo-West Pacific (IWP) biogeographic regions (blue shading). The study area (SEAMA) is indicated by a blue box, while regions previously studied using the same methodology (EURMA, CARMA, MESMA and WAFMA) are denoted by black boxes. Base map from Rull (2022), downloaded from https://data.unep-wcmc.org/datasets/5 (last accessed April 15, 2026). EIO, Eastern Indian Ocean; WIO, Western Indian Ocean.

Two contrasting hypotheses have traditionally been proposed to explain the global biogeography of mangroves. Under the dispersalist model, the exceptional diversity of the IWP is interpreted as evidence that this region was the principal center of origin from which mangrove taxa subsequently expanded to other tropical coastlines (Van Steenis, 1962). In contrast, the vicariance model postulates that ancestral mangrove lineages were once broadly distributed along the Tethyan margins and that the present-day floristic differences arose through geographic isolation associated with the progressive closure of the Tethys Sea (McCoy & Heck, 1976; Ellison et al., 1999). Estimates for the biogeographic separation between the IWP and AEP mangrove floras range from the Paleocene to the Oligocene (Ellison et al., 1999; Plaziat et al., 2001; Duke, 2017; Srivastava & Prasad, 2019). More recent molecular phylogenetic studies of widespread mangrove genera, including *Rhizophora* and *Avicennia*, indicate that neither hypothesis alone adequately explains current distribution patterns, which instead reflect the combined influence of vicariance and long-distance dispersal (Lo et al., 2014; Li et al., 2016; Takayama et al., 2021).

The mangroves of the southeastern African coasts constitute a well-defined isolated area in the western Indian Ocean within the IWP region (Fig. 1). As in many other mangrove-bearing areas, comprehensive syntheses based on critically assembled datasets are unavailable. Furthermore, SEAF is absent from most global fossil mangrove reconstructions (e.g., Germeraad et al., 1968; Muller, 1981; Thanikaimoni, 1987; Ellison et al., 1999; Morley, 2000; Plaziat et al., 2001; Duke, 2017; Popescu et al., 2021; Srivastava & Prasad, 2019; Pocknall et al., 2023), although it is unclear whether this reflects a genuine lack of available data or the selection criteria and geographical coverage of these studies.

A recently established research strategy reconstructs the evolutionary history of mangroves by compiling critically evaluated regional databases from biogeographically coherent areas using only original published fossil records. Rather than relying on heterogeneous global compilations, this framework produces independent regional syntheses that preserve the spatial and temporal context of the primary evidence while remaining fully compatible with broader global analyses. Taxonomic identifications, stratigraphic assignments and biogeographic interpretations are standardized at the regional level before integration into larger datasets, minimizing inconsistencies and providing a more robust basis for investigating mangrove origin, diversification and historical biogeography.

This framework has so far been implemented in four biogeographically coherent regions: the Caribbean (CARMA), Europe (EURMA), the Middle East (MESMA) and tropical western Africa (WAFMA). These syntheses have substantially revised previous interpretations of mangrove history. For example, in the Caribbean, the fossil record indicates that Neotropical mangroves were established independently during the Middle Eocene and acquired their modern floristic structure after the Eocene/Oligocene transition (Rull, 2022, 2023a, 2024). In Europe, mangrove assemblages originated through the convergence of lineages dispersed from the IWP, taxa that evolved locally, and others derived from the southern Tethyan realm (Rull, 2026a). The Middle East emerged as an important evolutionary center rather than merely a dispersal route (Rull, 2026b), whereas tropical western Africa shows long-term progressive floristic enrichment largely unaffected by the major disruptions recorded elsewhere in the AEP and IWP (Rull, 2026c).

This paper extends the regional synthesis initiative to the SEAF coasts through the development and analysis of the SEAMA (SouthEast African MAngroves) dataset (Fig. 1). Consistent with the outcomes of previous regional studies, the resulting database is expected to reveal previously unrecognized aspects of mangrove evolution while contributing robust evidence to broader reconstructions of the origin, paleobiogeography, and evolutionary history of mangroves worldwide. In addition, the SEAMA results will be particularly valuable for elucidating the biogeographic and evolutionary history of the westernmost IWP region and evaluating its potential role as a dispersal route for IWP mangrove taxa into the AEP region via the southern African corridor, much as the Middle East dataset (MESMA) revealed the importance of the northern Tethyan pathway.

2. Study area

This study focuses on the southeastern African coasts (SEAF), south of the Equator, from southern Somalia to South Africa, and the islands of the western Indian Ocean (Fig. 2). This region is also referred to in the

literature as the Western Indian Ocean (WIO) region (e.g., Bosire et al., 2015), but the former term is preferred here, as the mangroves of the northwestern Indian Ocean were already analyzed in the MESMA dataset, which forms a different and coherent biogeographical unit (Rull, 2026b). However, the name WIO, along with EIO for Eastern Indian Ocean, will be used when citing original references that use these terms (Fig. 1).

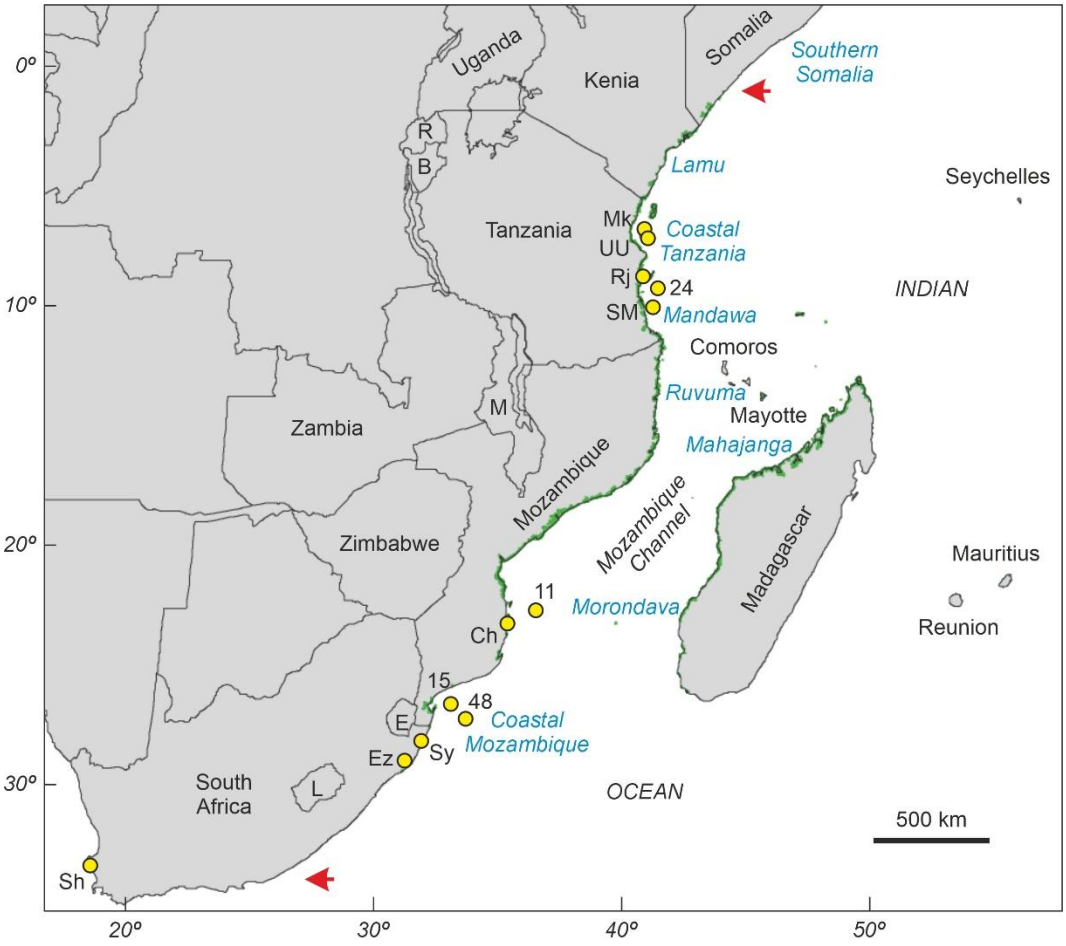

Figure 2. Map of southeastern African mangroves (green patches) after Bunting et al. (2022). Red arrows mark the latitudinal boundaries of mangrove communities in the study area (Carbone & Accordi, 2000; Naidoo, 2016; Adams & Rajkaran, 2021). Coastal sedimentary basins with Late Cretaceous-Cenozoic sediments are indicated in blue letters. B, Burundi; E, Eswatini; L, Lesotho; M, Malawi; R, Rwanda.

The total mangrove extent within the study area is approximately 7532 km², roughly one third of that in tropical West Africa (>21,000 km²) and more than 20 times that of the Middle East (320 km²). Other mangrove regions beyond Africa, such as the Caribbean and Southeast Asia, support substantially larger mangrove extents, with nearly 15,000 km² and >38,000 km², respectively (Bunting et al., 2022). Within the study area, the largest mangrove extents occur in Mozambique (3027 km²), Madagascar (2776 km²), and Tanzania (1108 km²), whereas at the latitudinal extremes—Somalia (35 km²) and South Africa (26 km²)—mangroves are restricted to scattered marginal occurrences in protected sites. The northernmost Somali localities occur near the Equator (Carbone & Accordi, 2000), whereas the southernmost South African sites, which are among the southernmost mangroves in the world, occur at approximately 33°S (Naidoo, 2016; Adams & Rajkaran, 2021) (Fig. 2). On the smaller islands and archipelagos, including the Comoros, Mayotte, the Seychelles and Mauritius, mangrove extent ranges from 1 to 7 km², whereas Reunion lacks mangroves (Bunting et al., 2022).

The SEAF mangrove flora consists of 11 genera with 13 species, all from the IWP region except the cosmopolitan *Acrostichum aureum*, including seven mangrove-forming tree species, four minor true-mangrove species and two mangrove associates (Table 1). *Sonneratia alba*, alone or together with *Avicennia marina*, usually dominates the seaward fringe, where salinity is similar to that of seawater and

mangroves are exposed to wave action. In South Africa, where *S. alba* does not occur, *A. marina* is the dominant on the exposed seaward fringe. The intertidal zone is characterized by *Rhizophora mucronata* in its lower part and *Ceriops tagal* and *Bruguiera gymnorhiza* in its upper part, where wave energy is lower. Along the landward margin, *Xylocarpus granatum*, *Lumnitzera racemosa* and *Heritiera littoralis* occur depending on local substrate, flooding regime and disturbance patterns. Owing to its broad tolerance of salinity and substrate conditions, *A. marina* may also occur at different positions along the sea–land gradient, especially in disturbed sites (Diop et al., 2002; Taylor et al., 2003; Bosire et al., 2015). Detailed examples of a variety of mangrove zonation patterns can also be found in Punwong et al. (2013a, b, c, 2018), Sefton & Woodrofe (2021) and Englong et al. (2023, 2024).

Table 1. Genera of major and minor true-mangrove elements, and mangrove associates (*sensu* Tomlinson, 2016), from Southeast Africa, compiled from Diop et al. (2002), Taylor et al. (2003), Bosire et al. (2015) and Naidoo (2023). Fossil representatives according to Germeraad et al. (1968) and Muller (1981). NR, not recorded as fossils.

Type	Genera (family)	Species	Fossil representatives
Major	*Rhizophora* (Rhizophoraceae)[1]	*R. mucronata*	*Zonocostites ramonae*
	Avicennia (Acanthaceae)[1]	*A. marina, A. officinalis*	*Avicennia*
	Lumnitzera (Combretaceae)	*L. racemosa*	*Lumnitzera*
	Bruguiera (Rhizophoraceae)	*B. gymnorrhiza*	*Bruguiera*
	Ceriops (Rhizophoraceae)	*C. tagal (=C. somalensis)*	*Ceriops*
	Sonneratia (Sonneratiaceae)	*S. alba*	*Florschuetzia meridionalis*
	Nypa (Arecaceae)[2]	*N. fruticans*	*Spinizonocolpites baculatus, S. echinatus*
Minor	*Pemphis* (Lythraceae)	*P. acidula*	NR
	Xylocarpus (Meliaceae)	*X. granatum, X. moluccensis*	NR
	Acrostichum (Pteridaceae)	*A. aureum*[1]	*Deltoidospora adriennis*
Associates	*Heritiera* (Malvaceae)	*H. liroralis*	NR
	Barringtonia (Lecythidaceae)	*B. racemosa*	*Marginipollis*

[1]Cosmopolitan
[2]Only in the Seychelles (Sefton & Woodrofe, 2021)

In the Seychelles, Sefton & Woodrofe (2021) documented the presence of small populations of *Nypa fruticans* near the transition to terrestrial forests in some mangrove communities. *Nypa* is a monospecific palm genus naturally restricted to the IWP region, extending from India to Taiwan and Australia. It was introduced by humans into West Africa in the 19th century and has become naturalized in the Neotropics, possibly having reached the region from Africa via ocean currents (Dransfield et al., 2008). Rahman et al. (2024) also reported its occurrence in Madagascar, although the source of this record remains unclear. Neither the Seychellian nor the Malagasy records are corroborated by other sources, including the Global Biodiversity Information Facility (GBIF; www.gbif.org; last accessed 20 July 2026). If confirmed, these occurrences most likely represent human introductions.

The IUCN Red List of Mangrove Ecosystems (https://iucn.org/node/33749/red-list-mangrove-ecosystems; last accessed 13 July 2026) classifies the East African mangroves as of Least Concern, except those from South Africa, which are placed in the Endangered category. The main threats to SEAF mangroves are urban expansion, aquaculture, salt production, rice cultivation, firewood and timber extraction, domestic and industrial pollution, oil pollution, inappropriate fishing and agricultural practices, and reduced freshwater input and sediment supply (Naidoo, 2023).

From a paleogeographic perspective, it is noteworthy that the SEAF coasts developed following the breakup of Gondwana (Fig. 2). Madagascar began to separate from Africa approximately 120–116 Ma ago but remained attached to India until about 90–85 Ma (Ali & Aitchison, 2008). This has important implications for organism dispersal and biotic interchange, which are discussed in greater detail in the historical biogeography section.

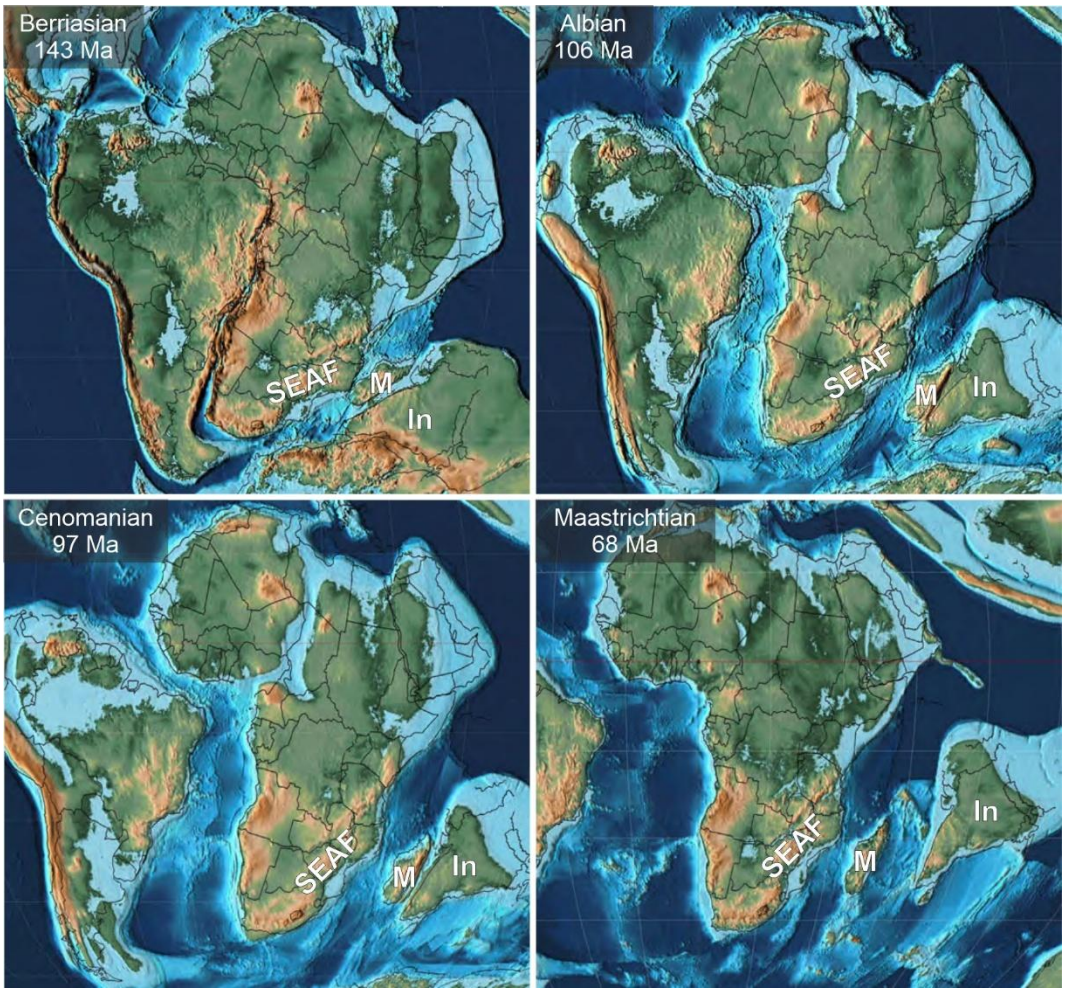

Figure 3. Cretaceous breakup of Gondwana. SEAF, southeastern African coasts; M, Madagascar; In, India. Paleogeographic maps modified from Scotese (2014).

3. Methods

Compilation of the SEAMA dataset followed the protocol established for the CARMA, EURMA, MESMA and WAFMA datasets (Rull, 2024, 2026a, b, c). The dataset adopts an ecosystem-based perspective in which the taxonomic composition of mangrove communities is the primary focus rather than the characteristics of the associated coastal sediments. Consequently, only extant mangrove taxa together with their recognized fossil equivalents (Table 2) were accepted. Taxa regarded as mangrove elements exclusively on the basis of unsupported botanical affinities or morphological interpretations of fossil remains were not incorporated. Similarly, reports of presumed "mangrove muds" lacking independent taxonomic verification (e.g., Zinke et al., 2017) were not included. It should be emphasized that this and previous fossil datasets are exclusively paleobotanical, and that other fossils commonly regarded as indicators of mangroves, such as mollusks, foraminifers and other zoological remains, are not considered.

The literature survey was conducted using several major bibliographic resources, including Web of Science (WoS), Scopus, Google Scholar, OpenAlex, The Lens, BASE and the fossil pollen database PALYNODATA (White, 2008). Search strategies combined geographic descriptors, chronostratigraphic terms and the modern and fossil taxa listed in Table 2. Review articles and global syntheses served only to identify the original publications documenting the fossil evidence, whereas recent papers were screened to recover additional later references. Consequently, the database was constructed exclusively from original sources, with reviews and syntheses used solely as guides to the primary literature (although, in this case, they proved to be of little help owing to the virtual absence of SEAF fossil records).

Owing to the scarcity of paleobotanical records, the search was expanded beyond conventional bibliographic and taxonomic resources to include Google Search and AI tools such as ChatGPT and Gemini.

As this expanded search yielded no additional records, the resulting spatiotemporal gaps are more likely to reflect genuine absences of mangroves than deficiencies in information retrieval.

4. The SEAMA dataset

The SEAMA dataset consists of 10 pollen and one charcoal sites, all of them Quaternary in age. Seven are restricted to the Holocene, whereas four extend into the Middle–Late Pleistocene, reaching ages of up to 350 ka (Table 3). Five of these sites are located in Tanzania, four in Mozambique and two in South Africa. Most extant mangrove genera (Table 1) are represented, except *Heritiera* and *Pemphis*. In some cases, the pollen of *Bruguiera* and *Ceriops* could not be distinguished. The absence of pre-Quaternary records is striking.

Table 3. The SEAMA dataset composed almost exclusively of Quaternary pollen records.

Map	Site	Country	Latitude	Longitude	Age	Mangrove taxa	References
Ch	Chibuene	Mozambique	22°02'51"S	35°19'24"E	900-1200 CE	*Bruguiera*[1]	Ekblom et al. (2014)
SM	Songa Mnara	Tanzania	09°02'57"S	39°34'34"E	4.5-0 ka	*Rhizophora* *Avicennia* *Bruguiera/Ceriops* *Sonneratia* *Acrostichum* *Lumnitzera*	Englong et al. (2024)
UU	Unguja Ukuu	Tanzania	06°17'55"S	39°21'30"E	5-0 ka	*Rhizophora* *Avicennia* *Bruguiera/Ceriops* *Sonneratia* *Acrostichum* *Lumnitzera*	Punwong et al. (2013c, 2018), Englong et al. (2023)
Rj	Rufiji Delta	Tanzania	07°51'25"S	39°20'26"E	6-0 ka	*Rhizophora* *Avicennia* *Bruguiera* *Sonneratia* *Xylocarpus* *Acrostichum* *Nypa*[1]	Punwong et al. (2013b, 2018)
Sy	Lake Sibaya	South Africa	27°20'54"S	32°41'03"E	7-0 ka	*Bruguiera*	Neumann et al. (2008)
Mk	Makova Bay	Tanzania	05°57'23"S	39°11'37"E	8-0 ka	*Avicennia* *Bruguiera/Ceriops* *Rhizophora* *Sonneratia* *Xylocarpus* *Acrostichum*	Punwong et al. (2013a, 2018), Woodrofe et al. (2015)
Ez	Lake Eteza	South Africa	28°29'07"S	32°09'37"E	10-0 ka	*Bruguiera* *Avicennia* *Barringtonia*	Neumann et al. (2010)
15	GeoB20615	Mozambique	25°33'04"S	33°12'11"E	17-0 ka	*Rhizophora* *Bruguiera*	Neumann et al. (2025)
24	GeoB12624	Tanzania	08°14'03"S	39°45'10"E	20-0 ka	*Rhizophora*	Bouimetarhan et al. (2015)
11	GeoB9311	Mozambique	21°33'00"S	36°25'00"E	200-0 ka	*Rhizophora* *Avicennia*	Dupont & Kuhlmann (2017)
48	MD96-2048	Mozambique	26°10'00"S	34°01'00"E	350-0 ka	*Rhizophora*	Dupont et al. (2011)

[1]Charcoal remains

[2]Interpreted by the authors as the result of long-distance transport, possibly from West Africa, where it was introduced in the 20th century.

The records in the SEAMA dataset were originally used for a variety of purposes, notably the study of vegetation dynamics in relation to climatic and eustatic changes, as well as human activities. The oldest Pleistocene records (up to 200–350 ka) document the alternation of open scrub during glacials with

deciduous and evergreen forests during interglacials, including mangrove woodlands in coastal settings. Lateglacial records (from 20–17 ka onward) have allowed the reconstruction of significant deglacial vegetation shifts, with arid conditions prevailing during cold stadials, followed by Early Holocene woodland expansion fostered by wetter and warmer climates. Coastal mangroves were also favored by increased moisture availability, enhanced river discharge and sea-level rise at the onset of the Holocene. Holocene records (from 10 ka onward) show phases of mangrove expansion coinciding with high sea levels and increased rainfall, whereas mangrove retreat is linked to declining sea level and reduced moisture availability. Human disturbance is especially evident during the last few millennia, when charcoal, used as a fire proxy, increases and mangroves decline mainly owing to cereal cultivation and fuelwood extraction. The anthropogenic introduction of exotic plants is particularly evident during the last centuries.

5. Comparisons with analogous regional datasets

While the absence of Late Cretaceous, Paleogene and Neogene records from SEAF mentioned above is already remarkable in itself, it proves exceptional when viewed in the context of the other mangrove-bearing regions analyzed to date. In these regions, all analyzed using the same methodology and therefore directly comparable, the number of localities ranges from approximately 80 to 140, for a total of more than 450, with pre-Quaternary records accounting for nearly three quarters of the total (Table 4). Paleogene records account for nearly 40%, Neogene records for about 25%, and Late Cretaceous records for around 10%. It could be asked whether the absence of pre-Quaternary records is due to the actual absence of mangroves before this period or to a lack of suitable rock archives or studies.

Table 4. Number of fossil sites for the datasets composed and analyzed using the same methodology utilized in this work.

	Cretaceous	Paleogene	Neogene	Quaternary	Total	References
Caribbean (CARMA)	5	35	43	60	143	Rull (2024)
Europe (EURMA)	0	77	37	0	114	Rull (2026a)
Middle East (MESMA)	24	23	14	17	78	Rull (2026b)
West Africa (WAFMA)[1]	17	38	19	33	107	Rull (2026c)
Southeast Africa (SEAMA)	0	0	0	11	11	This work
Total	**46**	**173**	**113**	**121**	**453**	

[1]This dataset was significantly (~40%) larger but it was reduced after journal filtering for reliability purposes.

Regarding the rocks, the SEAF margin comprises a series of coastal sedimentary basins extending from Somalia to South Africa and western Madagascar, including the Southern Somalia, Lamu, Coastal Tanzania, Mandawa, Rovuma, Coastal Mozambique, Morondava and Mahajanga basins, among others (Fig. 2). These basins preserve extensive Mesozoic and Cenozoic sedimentary successions, including Late Cretaceous, Paleogene and Neogene, marginal-marine and coastal deposits, demonstrating that sedimentary archives of the appropriate age and environment for mangrove occurrence are widespread throughout the region (Mbede, 1991; Nyaga, 1995; Salman & Abdula, 1995; Mbede & Dualeh, 1997; Boote & Matchette-Downs, 2009; Said et al., 2015; Cruciani & Barchi, 2016; Tuck-Martin et al., 2018). Therefore, the lack of mangrove records cannot be attributed to the lack of rocks of suitable ages. However, whether these rocks were deposited in the sedimentary environments favorable for mangrove occurrence and fossil preservation remains unknown.

In general, studies and reviews of Cenozoic East African biogeography focus on inland continental settings, whereas coastal environments conducive to mangrove development are barely considered or not considered at all (e.g., Morley, 2000; Jacobs & Herendeen, 2004; Kiage & Liu, 2006; Pan et al., 2006; Jacobs et al., 2010; Linder, 2017). Grímsson et al. (2024) mention the occurrence of coastal mangroves in the Eocene of Kenya but do not present any fossil evidence supporting this interpretation. Instead, they cite an earlier study by the same team (Vieira et al., 2023), which reports the occurrence of *Nypa* pollen based solely on a personal communication from one of its co-authors, without providing the corresponding fossil evidence. Based on the global distribution of *Sonneratia* and its fossil representatives (*Florschuetzia*), Mao & Fong (2013) suggest that this genus would have migrated from its assumed Eocene center of origin in Southeast Asia to China, Japan, Australia and East Africa. However, they provided no fossil records from East Africa.

Mangrove fossils of Cretaceous and Paleogene age have been reported from regions surrounding SEAF and are relevant to the present discussion. The oldest of these records is from the Maastrichtian of India, when the Indian Plate was still located close to Madagascar during its northward migration across the Indian Ocean (Fig. 3). The presence of *Nypa* in India at that time (Venkatachala & Sharma, 1974) raises the possibility that it could have dispersed to Madagascar and/or the SEAF coasts, although no fossil evidence currently supports this scenario. The other record is from Saldanha Bay (Sh; Fig. 2), on the Atlantic coast of South Africa at approximately 33°S, near the southern AEP/IWP boundary, and contains the earliest evidence of *Rhizophora* from the southern tip of Africa, dating to the Oligocene–Early Miocene (Roberts et al., 2017). This record may be relevant to the westward dispersal of *Rhizophora* from the IWP to the AEP via the southern African route. However, the lack of similar records in the SEAF area makes this assessment problematic.

6. Niche modelling and phylogeographic inference

Some historical biogeographic inferences about SEAF mangroves have been made for individual taxa using niche modelling based on modern analogues, as well as molecular phylogenetic and phylogeographic analyses of extant taxa. For example, Kwok et al. (2026) modelled the Cenozoic paleoecological niche of *Barringtonia* and identified potentially suitable habitats for this genus in Southeast Africa, particularly during the Eocene and Oligocene. However, neither their study nor the analysis of the SEAMA dataset presented here provides fossil evidence for the occurrence of Paleogene *Barringtonia* (including *Marginipollis*) along the SEAF coasts. Several molecular phylogeographic analyses have been conducted for relevant mangrove genera, such as *Rhizophora* and *Avicennia*, specifically for the WIO, and *Sonneratia*, *Bruguiera, Lumnitzera* and *Xylocarpus* for the entire IWP region, including some SEAF localities.

In the case of *Rhizophora mucronata*, the genetic structure allowed the differentiation of four main population groups: (i) East Africa (Kenya, Tanzania and northern Mozambique), (ii) the Mozambique Channel, (iii) the Seychelles and (iv) northern Madagascar, a pattern consistent with regional ocean circulation, the main transport mechanism for mangrove propagules (Triest et al., 2021). Considering the estimated generation time (~20 years per generation), this genetic structure would have been acquired during the Late Glacial Maximum (LGM; 22–19 ka) and the Holocene. The authors concluded that the colonization of the WIO by *R. mucronata* was more recent than that of the Eastern Indian Ocean (EIO). According to earlier phylogeographic analyses, *R. mucronata* from Kenya is nested within the Australian clade, suggesting dispersal from Australia to East Africa across the Indian Ocean (Lo et al., 2014). Phylogenetic calibration using the oldest known *Rhizophora* fossil pollen (~60 Ma) suggested that this transoceanic dispersal could have occurred during the Pleistocene.

Similar results were obtained for *Avicennia marina*. In this case, a strong genetic break was documented between the mainland African and western Madagascar coasts, and the island coasts of the Seychelles and eastern Madagascar (Triest et al., 2026). Assuming generation times of 3–5 years, the islands would have experienced multiple Late Pleistocene colonizations (110–30 ka), likely from the EIO, whereas the genetic structure of the African mainland was likely shaped by subsequent LGM–Holocene migration from these islands, favored by present-like coastal currents.

A phylogeographic study of *Sonneratia alba* encompassing most of the IWP region included a Kenyan population (Yang et al., 2017). Using a nucleotide substitution rate of ~$1.6 \cdot 10^{-9}$ substitutions per site per year (s/s/y), it was estimated that this species originated in the Miocene (<10 Ma) in the EIO region, where it split into two main lineages, the Indo-Malesian and Australian clades, during the Pliocene (~3.2 Ma). The Australian clade diverged into two populations during the Pleistocene (~1.5 Ma), and the Kenyan population showed no polymorphism with one of these Australian populations, suggesting a close origin. Therefore, the Kenyan population is most likely of Pleistocene origin. Yang et al. (2017) do not infer potential dispersal routes across the Indian Ocean, but it seems reasonable to assume that the Kenyan population also resulted from transoceanic migration from the EIO to the WIO during the Pleistocene, after 1.5 Ma. Another similar study included two *S. alba* populations from Mozambique and complemented the study by Yang et al. (2017); however, it provided no additional information on WIO clades (Wee et al., 2017).

An IWP-wide study of *Bruguiera gymnorrhiza* identified two genetic clusters, separated by the EIO Malay Peninsula, with the western cluster including two WIO populations from Madagascar (Urashi et al., 2013). Owing to the lack of *Bruguiera* fossils for calibrating molecular phylogenies, mutation rates from other plant taxa, including *Pinus* and palms (0.7×10^{-9} to 2.6×10^{-9} s/s/y), were used. These analyses indicated that *B. gymnorrhiza* lineages diverged only during the Late Pleistocene, implying that the Malagasy populations originated at that time following colonization of the WIO from the EIO. The same east-west differentiation was identified in a study of *Xylocarpus granatum* including a population from Kenya, which diverged from its EIO counterparts also in the Late Pleistocene (Guo et al., 2017).

A phylogeographic analysis of *Lumnitzera racemosa* included a Kenyan population that was found to have diverged from its closest EIO counterpart in Thailand during the Pleistocene, although no more precise timing was provided (Guo et al., 2021). In this case, the lack of *Lumnitzera* fossils hindered direct calibration, and the chronology was estimated using speciation rates for the family Combretaceae. An IWP-wide phylogeographic study of *Ceriops tagal* exists, but it does not include any representatives from SEAF (Liao et al., 2007).

Two points are important regarding molecular phylogenetic and phylogeographic studies. The first is that these approaches are useful for generating testable hypotheses rather than providing direct empirical evidence of biogeographical and evolutionary patterns and processes (Parenti & Ebach, 2013). The second is that reliable chronological calibration is fundamental and largely method dependent, in the sense that continued methodological improvements may lead to further revisions of phylogenetic chronologies. In both cases, the availability of well-dated fossils of the taxa included in the genetic analyses provides the most appropriate empirical evidence for hypothesis testing and chronological calibration. In the above phylogeographic studies of SEAF mangroves, reliable fossils are available only in some cases, whereas others rely on molecular clocks from related taxa, a limitation that should be addressed in future research.

7. The Malagasy Cenozoic fossil gap

The lack of pre-Quaternary mangrove fossils documented in this paper is not unique, as a similar pattern has been reported for the faunal fossil record of Madagascar. This island has been the subject of intense taxonomic, biogeographical and paleontological research owing to the diversity and endemism of its extant biota and its distinctive geological history in relation to plate tectonics (Goodman, 2022). The marked contrast between the extant and fossil faunas has hindered understanding of the origin and evolution of the modern Malagasy biota. This is particularly evident for vertebrates, despite their long history of intensive study. Their fossil record is largely restricted to three geological intervals: the Triassic–Jurassic, the Late Cretaceous and the Late Pleistocene, with the Cenozoic representing a conspicuous gap (Samonds et al., 2022). Before the breakup of Gondwana, Late Triassic to Middle Jurassic faunal assemblages displayed typical Gondwanan affinities, especially with South America (Flynn et al., 2022). By contrast, Maastrichtian assemblages, which developed after continental separation (Fig. 3), were more closely related to those of India than to their South American counterparts, probably reflecting the geographic proximity between Madagascar and India (Krause et al., 2022).

These Mesozoic faunas became largely extinct, leaving only a limited imprint on the extant biota, which has a radically different origin. Unfortunately, a major gap in the fossil record extending from the end of the Cretaceous to the Late Pleistocene (~80 ka onward) represents a serious obstacle to unraveling the origin and evolution of the modern Malagasy biota. It has been assumed that extant biotic patterns developed during the Cenozoic, but the fossil record needed to test this hypothesis is largely lacking (Samonds, 2022). This gap has been attributed, in part, to the scarcity of terrestrial Paleogene and Neogene fossil records, as most fossiliferous rocks of this age were deposited in marine environments. However, its coincidence with the absence of mangrove fossils during the same interval, as documented in this paper, suggests the possibility that it reflects a genuine paleontological feature representing an actual paleobiogeographic pattern.

Some phylogeographic studies of selected vertebrate groups have yielded divergence-time estimates within this Cenozoic gap; however, the methodological uncertainties associated with these chronological estimates preclude robust inferences, and the corresponding phylogenies are not yet fully

resolved (Samonds et al., 2022). The situation is similar for plants, where considerable work is still needed to reliably calibrate molecular clocks using suitable fossils in order to produce robust explanatory phylogenies (Wojahn et al., 2022). The available evidence suggests that the modern Malagasy biota is predominantly the result of long-distance dispersal, probably during the Cenozoic, although direct fossil evidence is still lacking. Vertebrate lineages are mainly of African origin, with some Asian elements and a few lineages interpreted as Gondwanan relicts. In contrast, the flora appears to have been strongly influenced by repeated colonization from Africa and Asia, although Australian affinities have also been proposed, with no convincing evidence of Gondwanan vicariance (Samonds et al., 2022).

Both the temporal fossil gap and the major role of long-distance dispersal, including eventual transoceanic pathways, are consistent with the results obtained here for SEAF mangroves using fossil evidence and molecular phylogeographic studies. It is especially meaningful that, after the long Cenozoic fossil silence, the floristic and faunal fossil records reappeared only during the Late Pleistocene.

8. Conclusions

The SEAMA dataset is consistent with a Pleistocene origin of SEAF mangrove communities, an inference supported by molecular phylogeographic studies, which further suggest the likely possibility of transoceanic Pleistocene dispersal from the EIO to the WIO. In most cases, such dispersal would have occurred very recently, probably during the Late Pleistocene, more specifically within the last glacial cycle. Other possibilities cannot be excluded but, given the available fossil and phylogenetic evidence, Pleistocene westward colonization from the main IWP mangrove biodiversity center in Southeast Asia is the most parsimonious conclusion. If confirmed, SEAF mangroves would be the youngest mangroves worldwide, by a margin of ~100-70 million years.

This has important implications for global mangrove biogeography and evolution. First, it strongly contrasts with other mangrove-bearing regions, such as the Caribbean, the Middle East, and Southeast Asia, where mangroves have a long history dating back to the Late Cretaceous. The case of West Africa is particularly notable. Although situated in the AEP and separated from the Neotropics by the Atlantic Ocean, its mangroves evolved *in situ* and, to some extent, in parallel with those of the Caribbean. In contrast, the mangroves of SEAF, which are also separated from the EIO biodiversity center by the Indian Ocean, appear to have emerged only within the last million years through trans-Indian Ocean dispersal of extant taxa that originated and evolved in the EIO. It is also noteworthy that the mangroves of the Middle East, although also located in the WIO, have a completely different history, beginning in the Late Cretaceous and including one of the earliest potential mangrove precursors, a possible ancestor of *Nypa*.

This interpretation is also consistent with the major Cenozoic gap in the terrestrial fossil record of Madagascar, which separates the rich Mesozoic faunas from the Late Pleistocene appearance of modern biotas. Although the causes of this gap remain uncertain, its temporal coincidence with the absence of pre-Quaternary mangrove fossils in SEAF is compatible with the hypothesis of a predominantly Pleistocene assembly of the regional biota.

From an ecological perspective, SEAF mangrove communities would have assembled during the last tens of thousands of years, probably since the LGM. Although this is not unusual for terrestrial postglacial ecosystems, the inferred colonization by transoceanic long-distance dispersal would make this case unique. This may be regarded as a large-scale natural experiment in community assembly, which has created a mangrove fringe covering more than 7,500 km² along the more than 20,000 km of coastline of the SEAF region, including Madagascar and the other WIO islands. This highlights the potential importance of Pleistocene processes in shaping the extent and taxonomic composition of modern mangrove ecosystems in other regions, regardless of whether they were newly colonized or had supported mangrove ecosystems for tens of millions of years. The fact that the newly established SEAF mangrove communities display a typical zonation pattern, similar to that of the original EIO ecosystems and based on species-specific autecological requirements, emphasizes the importance of idiosyncratic traits in the configuration and functioning of mangrove ecosystems, as a general principle potentially applicable to other regions (Rull, 2020).

Regardless of whether future discoveries eventually extend the SEAF fossil record further back in time, the present synthesis establishes a robust benchmark against which subsequent findings can be

evaluated. At present, the available evidence defines SEAF as an exceptional case among the world's mangrove regions, thereby providing a rare opportunity to formulate and test new hypotheses on the origin, assembly and evolution of coastal biotas. In this sense, the value of the SEAMA dataset lies not only in documenting the current state of knowledge but also in transforming an unexpected regional pattern into a globally relevant research question. The SEAF record challenges the widespread assumption that the world's major mangrove regions share a common deep-time history extending back to the Late Cretaceous or early Cenozoic. Instead, the available evidence indicates that regional mangrove systems may differ fundamentally in the timing and mode of their assembly.

9. Further research

Some research lines to be addressed in the future for a better understanding of the historical biogeography of SEAF mangroves in a global context have been suggested, including the most obvious one: the need for more exhaustive surveys, especially in coastal and offshore environments, to confirm or refute the absence of pre-Quaternary mangrove fossil records. It is not expected that this type of research will be prioritized over others with commercial or strategic interests, or even over climate change reconstructions or conservation-oriented surveys, which are currently experiencing a surge owing to increased public and private funding driven by environmental concerns. Researchers interested in the advancement of knowledge as a major and permanent cultural goal, regardless of its transient, immediate and fashionable political and social recognition, should not only propose basic research programs but also be aware of applied initiatives that may provide valuable raw data on the spatiotemporal patterns of fossil mangrove occurrence.

Another topic that deserves attention is molecular phylogeographic research, particularly the chronological calibration of phylogenetic trees. Such studies are usually conducted by specialists who place greater emphasis on genetic analysis and characterization than on the Earth-science context of their findings. As a result, genomic inferences, including genetic diversity, population structure and speciation patterns, are generally well supported, whereas their biogeographical and evolutionary significance is often less thoroughly addressed, especially when precise chronological frameworks are required. Calibrating phylogenies with fossils of the same taxa under study and interpreting the resulting phylogeographic results in an appropriate Earth-science context are of paramount importance for upgrading genetic findings into sound evolutionary and biogeographical inferences. Otherwise, phylogenetic data are merely population descriptors.

Finally, as newly assembled ecosystems, SEAF mangroves may benefit from studies of organisms other than true mangroves and their associates, aimed at reconstructing the ecological community as a whole, including animals, fungi and other components. In this way, more complete ecological reconstructions will provide more accurate information on the composition and ecological dynamics of mangroves as ecosystems.

Acknowledgments

No funding was received specifically for the development of this study.

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