Historical biogeography of Middle-East mangroves: paleobotanical evidence

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Abstract

This paper reconstructs the origin, diversification, and decline of Middle East (ME) mangroves from the Late Cretaceous to the present using the MESMA database, a comprehensive compilation of fossil pollen and macrofossil records integrated with paleogeographic, tectonic, climatic and sea-level evidence. To date, global paleobiogeographical and evolutionary syntheses of mangroves have emphasized the role of the ME region as either a dispersal corridor or a biogeographical barrier, rather than as a research focus in its own right. The earliest reliable ME mangrove records correspond to *Nypa* from the Late Cretaceous, when the present-day Arabian Peninsula formed part of the Nubian Plate along the southern Tethyan margin. A potential Albian precursor suggests that the ME may have played a role in the early evolution of the *Nypa* lineage, which, if confirmed, would represent the earliest mangrove record worldwide. Mangrove diversification began in the Eocene with the arrival of *Avicennia* and *Acrostichum*, followed by *Rhizophora* in the Oligocene, leading to the highest diversity levels recorded in the region. This diversification is remarkable because it occurred during the Eocene/Oligocene transition, a phase associated with mangrove decline in most other parts of the world. A major biodiversity crisis took place during the Middle Miocene, when regional desertification associated with the Middle Miocene Climatic Transition, likely linked to the Arabia–Eurasia collision and the resulting closure of the Tethys Sea, caused the disappearance of most mangrove elements, leaving only *Avicennia* and *Rhizophora* as surviving mangrove-forming taxa. This event established the low-diversity pattern that characterizes present-day ME mangroves. Quaternary records are scarce, but Holocene sequences from southern Arabia document a pronounced reduction of *Rhizophora* between approximately 6.5 and 4.5 ka BP, coinciding with the termination of the Holocene Humid Period, after which the genus survived only in a few relict areas, whereas the more stress-tolerant *Avicennia* persisted and became dominant. In contrast to previous studies, this synthesis identifies the ME as a significant region for mangrove evolution per se, rather than merely in relation to other biogeographical regions. The study also highlights substantial gaps in the fossil record and several unresolved questions that provide promising avenues for future research.

Keywords

Mangroves, Middle East, biogeography, evolution, paleogeography, paleoclimates, plant fossils

1. Introduction

Mangroves are land–sea transitional forested wetland ecosystems that occupy the outer margin of all continents, extending to the limit of normal tidal influence along tropical and subtropical coasts, roughly between 30° N and 30° S worldwide (Spalding et al., 2010) (Fig. 1). They play an important role in coastal protection and in sustaining both continental and marine biodiversity and ecosystem processes (Nagelkerken et al., 2008). In addition, mangroves are significant contributors to global biogeochemical cycles—particularly the carbon cycle—as a major blue carbon ecosystem that helps mitigate global warming (Fest et al., 2022).

Mangrove forests are organized around a number of dominant mangrove-forming tree species – known as major true-mangrove elements and exclusive to these communities – that define the physical structure of the community, and without which mangrove ecosystems cannot persist (Table 1). These mangrove-forming taxa exhibit specialized morphological and physiological adaptations that allow them to tolerate intertidal conditions with soft, anoxic sediments and fluctuating water levels and salinity (Tomlinson, 2016). These adaptations occurred at various evolutionary times across different unrelated lineages, constituting one of the most striking cases of evolutionary convergence in the plant kingdom (Xu et al., 2017; He et al., 2020). Minor true-mangrove elements are also exclusive to mangroves and exhibit similar adaptations; however, they rarely form pure stands and typically occupy a marginal position within the community.

Among mangrove-forming taxa, only *Rhizophora* (Rhizophoraceae) and *Avicennia* (Acanthaceae) have a global distribution, although their species are disjunctly distributed across two major biogeographical regions: the Atlantic–East Pacific (AEP) and the Indo–West Pacific (IWP), which are separated by the African continental barrier (Tomlinson, 2016; Duke, 2017) (Fig. 1). The remaining mangrove genera are confined either to the AEP or the IWP, with the exception of the fern genus *Acrostichum* (Pteridaceae), which also has a cosmopolitan distribution. The IWP region, with 17 true-mangrove genera and 54 species, is far more diverse than the AEP, which has only 6 genera and 11 species (Table 1).

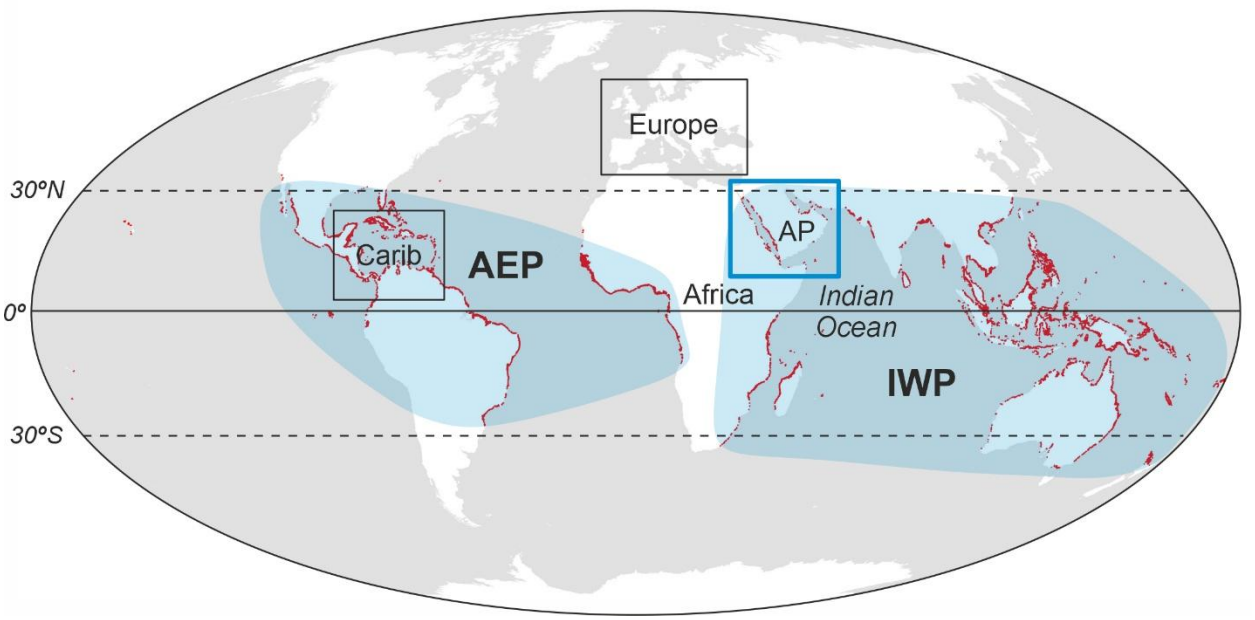

Figure 1. Worldwide mangrove distribution (red fringes) highlighting the Atlantic-East Pacific (AEP) and Indo-West Pacific (IWP) biogeographical regions (blue shading). The study area is indicated by a blue box, while regions previously studied using the same methodology (Europe and the Caribbean) are denoted by black boxes. AP, Arabian Peninsula. Base map from Rull (2022), downloaded from https://data.unep-wcmc.org/datasets/5 (last accessed April 15, 2026).

Table 1. Extant mangrove-forming tree genera distributed across global mangrove biogeographical regions, indicating the number of species present in each region (Tomlinson, 2016; Duke, 2017). Note the greater diversity in the IWP region (17 genera, 54 species) compared to the EAP region (6 genera, 11 species). The genera included in this review, together with their corresponding fossil representatives, are marked with an asterisk. Note that only three of the major mangrove elements and two (or one, if *Pelliciera* is excluded) of the minor mangrove elements are represented. The fossil pollen *Proxapertites* (notably *P. operculatus* and *P. cursus*) has sometimes been linked to *Nypa*, but is now considered to belong to the Araceae (Zetter et al., 2001; Hesse & Zetter, 2007).

Type	True-mangrove extant genera	AEP	IWP	Fossil pollen/spore/macrofossil (P/S/M) representatives in the ME record
Major	*Rhizophora* (Rhizophoraceae)*	4	8	*Zonocostites ramonae* (P)
	Avicennia (Acanthaceae)*	3	5	*Avicennia* (P/M)
	Laguncularia (Combretaceae)	1		
	Nypa (Arecaceae)*		1	*Spinizonocolpites baculatus* (P)*, S. prominatus* (= *S. echinatus*) (P)*, Nypa* (M), *Nipadites* (M)*, Rubiaceocarpum markgrafi* (M)*, Apeibopsis gigantea* (M)
	Lumnitzera (Combretaceae)		3	
	Bruguiera (Rhizophoraceae)		7	
	Ceriops (Rhizophoraceae)		5	
	Kandelia (Rhizophoraceae)		2	
	Sonneratia (Sonneratiaceae)		9	
Minor	*Acrostichum* (Pteridaceae)*	1	2	*Deltoidospora adriennis* (S)
	Conocarpus (Combretaceae)	1		
	Pelliciera (Tetrameristaceae)*[1]	1		*Psilatricolporites crassus* (= *Lanagiopollis crassa*) (P)
	Excoecaria (Euphorbiaceae)		1	
	Pemphis (Lythraceae)		1	
	Camptostemon (Malvaceae)		2	
	Xylocarpus (Meliaceae)		2	
	Osbornia (Myrtaceae)		1	
	Aegialitis (Plumbaginaceae)		2	
	Aegiceras (Primulaceae)		2	
	Scyphiphora (Rubiaceae)		1	

[1]Questioned in this work due to identification issues (Rull, 2025, 2026).

The origin of these global biogeographical patterns has been explained by either dispersalist or vicariant processes. Dispersalist hypotheses propose that ancestral lineages originated in the more species-rich IWP region and later dispersed to the AEP region (Van Steenis, 1962), whereas vicariant models suggest that mangroves evolved during the Late Cretaceous along the margins of the tropical Tethys Sea and subsequently diversified following its closure due to the formation of the African barrier (McCoy and Heck, 1976; Ellison et al., 1999). Estimates for the timing of the IWP–AEP divergence differ widely among studies, ranging from the Late Cretaceous to the Oligocene (Ellison et al., 1999; Plaziat et al., 2001; Duke, 2017; Srivastava & Prasad, 2019). More recent molecular phylogeographical evidence suggests that both vicariance and long-distance dispersal are required to explain the present distribution of *Rhizophora* (Lo et al., 2014; Takayama et al., 2021), although the timing of speciation remains unresolved, with estimates spanning from the Eocene to the Miocene. While allopatric diversification associated with the closure of the Tethys Sea remains a widely accepted explanation across many plant

and animal groups (e.g., Celâl Şengör & Saniye, 2009; Zhao et al., 2022), the role of long-distance dispersal is often underestimated (Van der Stocken et al., 2019).

The region commonly referred to as the Middle East, encompassing the Arabian Peninsula and adjacent areas, occupies an intermediate geographical position between the EAP and the IWP (Fig. 1), but biogeographicly it belongs to the IWP. Both the Middle East and its mangroves are noteworthy for some exceptional present and past biogeographical peculiarities. Extant mangroves from this region are considered a biogeographical anomaly relative to those at similar latitudes elsewhere, owing to their limited extent and low biodiversity resulting from extreme environmental conditions—primarily high temperatures, aridity and hypersalinity (Osland et al., 2017; Meraj et al., 2025; Waleed et al., 2025). ME mangroves have sometimes been considered potential modern analogs for mangroves inhabiting Europe during the Middle Miocene Climatic Optimum (MMCO); however, their anomalous latitudinal nature does not support such an assessment (Rull et al., 2026).

The region has also been identified as a key biogeographical corridor that served as the principal pathway for the westward migration of IWP mangrove taxa during the Cenozoic, a process that was fundamental in shaping European mangroves prior to the Oligocene closure of the passage between Africa and Asia by the Arabian Peninsula (Rull, 2026). This peninsula was part of the African Plate prior to the Africa–Asia collision (Macgregor & Reeves, 2025) and thus carried floristic elements of African origin. Consequently, the closure of the Tethys seaway would have marked not only the loss of a dispersal pathway for marine and coastal organisms but also the convergence of elements from three different regions: IWP, Africa and western Asia.

Despite these singularities and their global significance, ME mangroves and their ancestors have received little attention compared with other more extensive and diverse mangrove regions, notably the Caribbean and Southeast Asia (Ward et al., 2016). This is especially true in fields such as evolutionary biology, physiology and molecular biology (Friis & Burt, 2020). These authors identified the evolutionary history of Middle East mangroves and their biogeographical relationships with other mangrove-bearing regions—the main focus of this review—as an important knowledge gap that deserves further investigation. To date, global mangrove paleobiogeographical and evolutionary syntheses have emphasized the role of the Middle East region as either a dispersal pathway or a biogeographical barrier for mangroves, rather than as a research target in its own right (e.g., Ellison et al., 1999; Morley, 2000; Plaziat et al., 2001; Duke, 2017; Srivastava & Prasad, 2019). As a result, a spatiotemporal integrative understanding of ME mangroves in terms of their origin, evolution and the acquisition of their current taxonomic composition and biogeographical patterns is still lacking.

Recently, an initiative has been launched to investigate mangrove origin and development from the Cretaceous to the present using palaeobotanical evidence as the primary proxy for mangrove communities structured around mangrove-forming tree species. This effort focuses on biogeographically significant mangrove-bearing regions worldwide. To date, comprehensive reviews are available for the Caribbean region and Europe (Rull, 2024, 2026). This paper is the third in the series to apply the same methodology, contributing toward a future integrated synthesis of mangrove origin and evolution at the global scale. Indeed, the combination of CARMA (CAribbean MAngroves; Rull, 2024), EURMA (EUropean MAngroves; Rull, 2026), and MESMA (Middle East MAngroves; this paper), together with other similar datasets that may be developed in the future (for example WAFMA from Western Africa, which is in progress, will provide a robust and comprehensive body of evidence for addressing global patterns of mangrove evolution and biogeography without losing fine-grained detail, as these datasets are based on primary, site-by-site fossil evidence.

2. Study area

2.1. Geographical and geological setting

The area considered in this review extends approximately from 10° to 40° N latitude and 25° to 65° E longitude (Fig. 2) and includes 21 countries: 6 in northeastern Africa (Djibouti, Ethiopia, Eritrea, Egypt, Somalia and Sudan) and 14 in southwestern Asia (Bahrain, Iran, Iraq, Israel, Jordan, Kuwait, Lebanon, Oman, Palestine, Qatar, Saudi Arabia, Syria, the United Arab Emirates and Yemen). Tectonically, this area

is defined by the complex interactions among the Arabian, African (Nubian and Somali), Eurasian, Indian and Anatolian plates.

Countries located in the northernmost part currently lack mangrove communities, but they are included in the study because they form part of the Arabian Plate, whose long-term dynamics are fundamental to understanding mangrove evolution in the region. Turkey was already included in the analysis of Cenozoic European mangroves, but the localities in its central and southern regions are also considered here because of their proximity to the junction of the Anatolian with the Arabian and Nubian plates.

Given the cultural (Eurocentric) connotations of the term "Middle East," a more descriptive and neutral biogeographical designation for the study area—such as the northern sector of the Western Indo-Pacific coastal realm (Spalding et al., 2007), abbreviated as NWIP—may be preferable. An alternative is the purely geographical term "northwestern Indian Ocean (NWIO) coasts." The traditional term "Middle East" (thereafter ME) is retained here to maintain consistency with existing literature and facilitate comparisons, although it may be revised in the future.

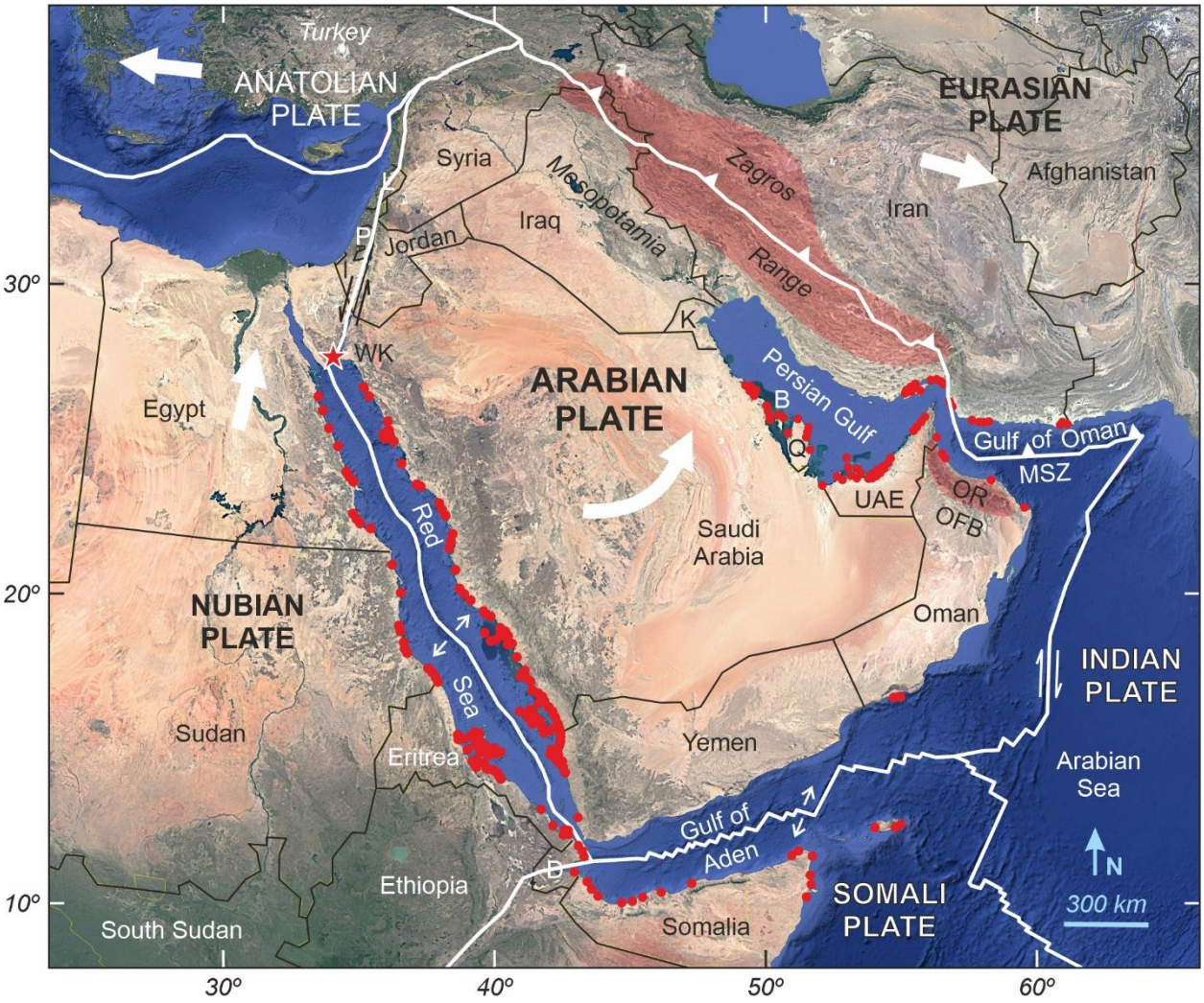

Figure 2. Detailed Google Earth map of the study area. Extant mangroves are represented as red dots/areas, redrawn from Meraj et al. (2025). Somalia occurrences according to Mohamed (2026). The northernmost mangrove (WK, Wadi Kid) is indicated by a star. Tectonic plates have been drawn with Google Earth using the corresponding layer from the US Geological Survey (downloaded from https://www.usgs.gov/programs/earthquake-hazards/google-earthtmkml-files; last accessed March 18, 2026). Details and plate motion vectors (white arrows) from Peña et al. (2022). Countries: B, Bahrain; D, Djibouti; I, Israel; K, Kuwait; L, Lebanon; P, Palestine; Q, Qatar; UAE, United Arab Emirates. Tectonic units (Oman): MSZ, Makran subduction zone; OFB, Oman foreland basin; OR, Oman Range.

The geology of the Middle East is dominated by a broad contrast between the stable Arabian Platform and the tectonically active mountain belts that border it to the north and northeast. Precambrian crystalline rocks of the Arabian–Nubian Shield are extensively exposed along the Red Sea margins and across western Saudi Arabia, forming the oldest geological foundation of the region (Fig. 3). These rocks are overlain eastward by widespread Paleozoic, Mesozoic and Cenozoic sedimentary successions that cover much of the Arabian Peninsula.

The Mesopotamian Foredeep extends from southeastern Turkey through Iraq toward the Persian Gulf, forming a major sedimentary basin filled with thick Cenozoic deposits. This basin developed in response to the collision between the Arabian and Eurasian plates, which also produced the highly deformed Zagros Fold-and-Thrust Belt along the northeastern margin of the Arabian Plate. Similar tectonic deformation characterizes the Bitlis Suture Zone in southeastern Turkey. To the west, the Dead Sea Fault System marks a major transform boundary extending from the Gulf of Aqaba northward through the Levant. Further south, the Red Sea and Gulf of Aden represent young rift systems associated with the separation of Arabia from Africa. These regions are characterized by extensive Cenozoic volcanic rocks and active faulting. The East African Rift continues southward from the Gulf of Aden, linking Middle Eastern tectonics with those of eastern Africa. Overall, the region records the interaction of ancient continental crust, extensive sedimentary basins, active rifting, transform faulting, and continental collision (Sembroni et al., 2024).

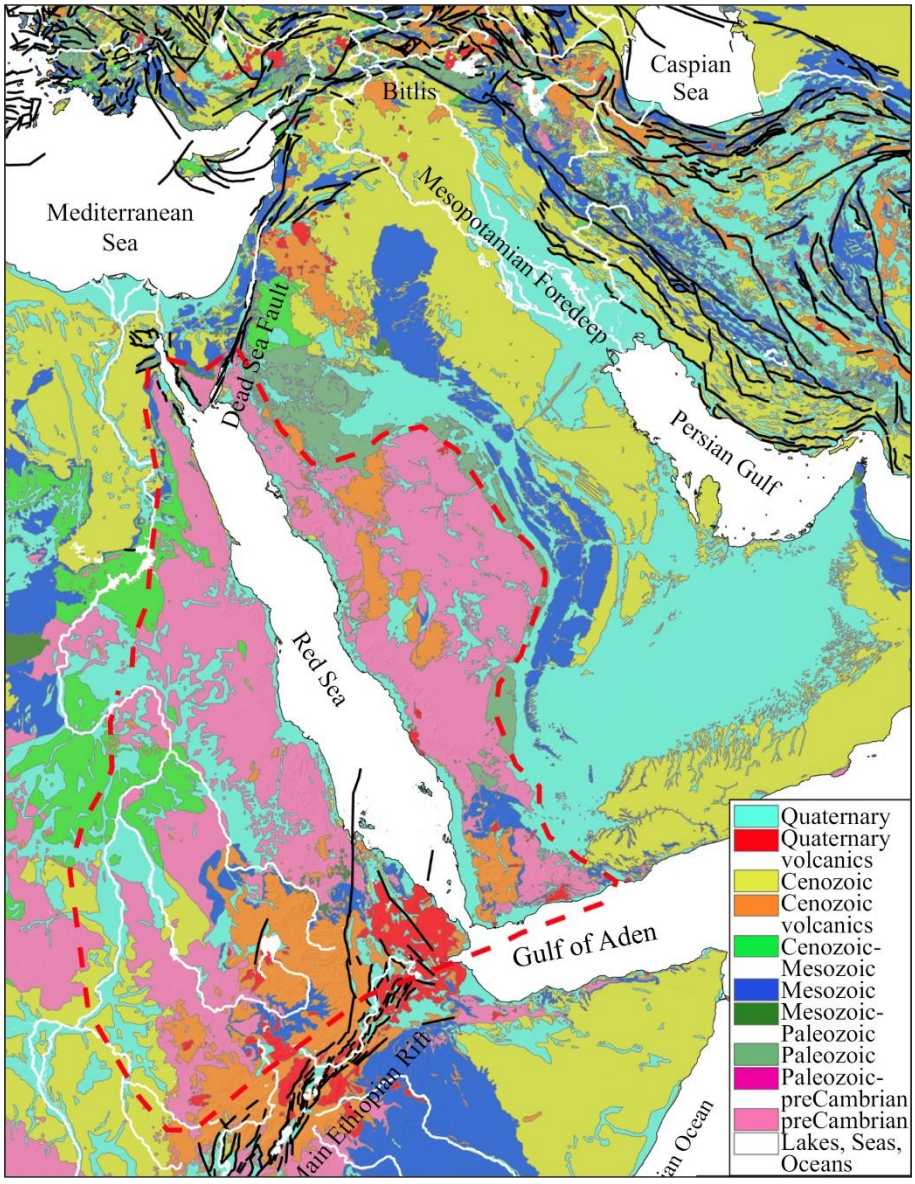

Figure 3. Geological map of the study area. Modified from Sembroni et al. (2024). The Arabian-Nubian Precambrian Shield is highlighted by a dashed red line.

2.3. Paleogeographical and tectonic evolution

The dynamics of the Arabian Plate and its precursor over time have been crucial for mangrove biogeography, not only in the study area but also on a global scale, particularly with respect to the westward biotic interchange between the IWP region and present-day Europe (Rull, 2026).

During the Late Cretaceous (ca. 70 Ma), the area now occupied by the Arabian Plate was part of the African Plate complex, specifically the Nubian Plate, which migrated northeastward and was separated from the Eurasian Plate by the Tethys Sea (Fig. 4). At that time, the Indian Plate, in its northward migration, had not yet reached low latitudes, and a continuous Tethyan corridor facilitated east–west dispersal and migration of tropical biota. The Arabian Plate had not yet separated from the Nubian Plate (Fig. 2) and formed part of its northeastern margin, a typical Mesozoic configuration (Giraud & Bosworth, 1999). In the Early Eocene (50 Ma), the Tethyan connection still existed, but the Indian Plate had reached the Eurasian Plate, and the available marine pathway for IWP biota to disperse westward had to adopt a more southerly route to bypass the Indian wedge. A similar configuration persisted during the Late Eocene (35 Ma), although the marine connection had become considerably shallower due to the progressive convergence of the African and Eurasian plates.

The closure of the Tethys seaway occurred during the Oligo–Miocene transition, with estimates ranging from 27 to 21 Ma (Pirouz et al., 2017; Torfstein & Steinberg, 2020). This event broadly coincided with the break-up of the Arabian Plate from the Nubian Plate, which began in the Late Oligocene (~25 Ma) (Stern & Johnson, 2010). Further independent rifting of the Arabian Plate as an isolated plate led to the opening of the Red Sea through separation from the Nubian Plate at approximately 25 Ma (Bosworth et al., 2005; Bosworth, 2015), and of the Gulf of Aden through separation from the Somali Plate at approximately 20 Ma (Fournier et al., 2010). Present-like configuration was established by the Middle Miocene (~15 Ma), except for the continued opening of the Red Sea and the Gulf of Aden, as well as ongoing shortening and deepening of the Arabian Gulf, whose modern shoreline was attained only very recently following the last glaciation (Lambeck, 1996).

The collision of the Arabian and Eurasian plates produced the Zagros Range as a major collisional fold–thrust belt (Sembroni et al., 2024) (Fig. 2). According to Alavi (2007), continued convergence shortened and thickened the former Arabian passive margin through a combination of basement-involved thrusting and detachment folding within the sedimentary cover, generating the elongated anticlines and thrust systems that characterize the Zagros today. The growing orogenic load simultaneously flexed the Arabian lithosphere downward, creating the Mesopotamian–Persian Gulf foreland basin, also known as the Zagros foreland basin. This subsiding basin acted as a major depocenter for sediments eroded from the uplifting Zagros range, linking tectonic deformation, mountain building, and foreland sedimentation within a coupled tectono-sedimentary system.

In the easternmost sector of the Arabian Plate, presently northeastern Oman, oceanic lithosphere of the Arabian Sea began to subduct northward beneath the Eurasian margin following the Tethys closure, forming the Makran subduction zone and the Oman foreland basin, behind the Oman Range. This process generated an active accretionary prism and forearc basin system along the margin of the Gulf of Oman, characterized by sediment accretion, thrust imbrication, and progressive outward growth of the submarine wedge (Kopp et al., 2000).

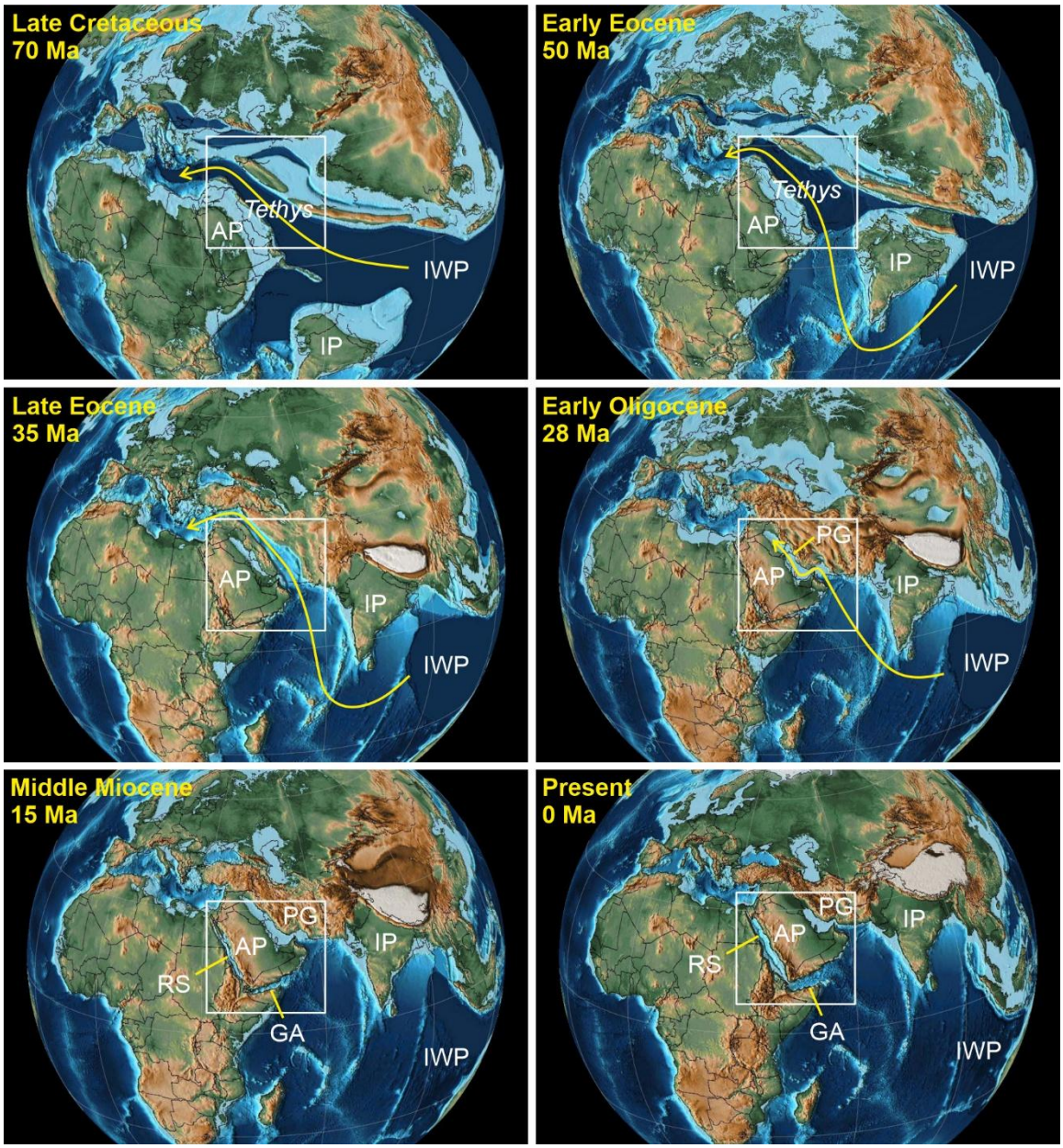

Figure 4. Late Cretaceous to present global paleogeographical trends taking the present Middle East position as the reference (white box). Time slices were selected according to the main paleogeographical shifts potentially significant for mangrove dynamics in the study area and its eventual influence on regional patterns. Maps were generated with GPlates 2.5.0 using the Scotese (2016) PALEOMAP PaleoAtlas, freely available at https://www.earthbyte.org/paleomap-paleoatlas-for-gplates/ (last accessed May 21, 2026). AP, Arabian Plate or its precursor; IP, Indian Plate; GA, Gulf of Aden; PG, Persian Gulf; RS, Red Sea.

2.4. Petroleum geology

The stratigraphic interval spanning the Late Cretaceous, Paleogene and Neogene – which is the focus of this review – constitutes the primary reservoir-seal architecture responsible for the world's largest hydrocarbon accumulations in the ME. The main oil/gas fields are concentrated along the Africa/Eurasia collision zone, in the Mesopotamian, Persian Gulf and Oman foreland basins (Fig. 5). This distribution is relevant for understanding the geographic pattern of fossil localities in the MESMA dataset, as discussed in Section 3.3. The formation of the ME petroleum system, which is largely linked to the tectonic evolution, was compiled by Alsharan & Nairn (1997), and can be summarized as follows.

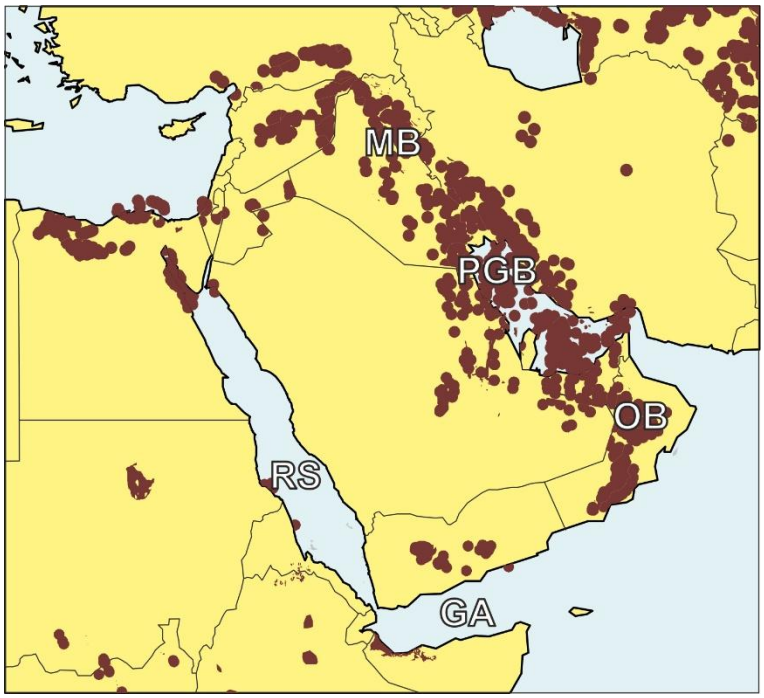

Figure 5. Oil/gas fields (brown) in the study area. Note the main concentration along the collision zone of the Mesopotamian (MB), Persian Gulf (PGB) and the Oman (OB) foreland basins, in contrast to the rifting zones of the Red Sea (RS) and the Gulf of Aden (GA) basins. Downloaded and modified from the U.S. National Energy Technology Laboratory (https://arcgis.netl.doe.gov; last accessed May 16, 2026).

During the Late Cretaceous, a prolonged period of high sea levels and stable subsidence across the Arabian Plate facilitated the development of extensive, high-productivity carbonate platforms characterized by shallow-marine limestones that exhibit excellent primary porosity and substantial lateral continuity, functioning as the region's most prolific regional reservoir rocks. This dominant carbonate regime persisted into the Paleogene within the Tethys shallow-marine domain, but subsequent tectonic compression related to the early phases of the Zagros orogeny induced widespread natural fracturing within these Cenozoic limestone successions, a structural overprint that significantly enhanced secondary permeability and transformed these otherwise dense carbonates into highly efficient, high-flow-rate reservoirs.

The entire petroleum system was finalized and structurally sealed during the Neogene due to the definitive collision between the Arabian and Eurasian plates, a major tectonic event that compressed the thick sedimentary package into high-amplitude, continuous anticlinal folds to create massive structural traps, while concurrently restricting the marine basin to induce hyper-saline conditions that deposited thick, regionally extensive evaporite sequences, primarily composed of halite and anhydrite, which now provide an absolute top seal that prevents vertical hydrocarbon migration and ensures the long-term preservation of the immense underlying Paleogene and Cretaceous oil accumulations.

2.2. Extant mangroves and climatic insights

Most extant mangroves are located along the coasts of the Red Sea and the Persian Gulf (also known as the Arabian Gulf), with fewer occurrences in the Gulfs of Aden and Oman and only scattered occurrences in the Arabian Sea. The northernmost ME mangrove (Wadi Kid; ~28°10'N) is located on the southern Sinai Peninsula (Fig. 2) and is also the northernmost mangrove in the entire IWP region (Por et al., 1977).

Mangrove extent is very limited, with a total area of ~320 km², reaching maxima in Iran (~75 km²) and in Eritrea and the United Arab Emirates (70~ km² each), and minima (<2 km²) in Egypt, Oman and Bahrain (raw data from Bunting et al., 2020). These figures are very low compared with those of other regions of similar extent, such as the Caribbean coasts, which has a total mangrove area of approximately 14,700 km², or southeast Asia, with 48,200 km² (Bunting et al., 2022; Rull, 2024). In general, climatic conditions in the ME are unfavorable for mangrove development (Quistoudt et al., 2012), with average

temperatures ranging from about 20 °C in the northwest to 30 °C in the southeastern Arabian Peninsula (and seawater temperatures reaching up to 28 °C in summer), along with very low precipitation (generally less than 100 mm per year on average, with maxima around 250 mm) (Patlakas et al., 2019; Waleed et al., 2025). In addition, the absence of large, permanent freshwater inputs significantly reduces the supply of coastal sediments and nutrients required for mangrove growth and promotes hypersaline conditions (exceeding 40 ppt) in adjacent seas, beyond the tolerance range of most mangrove species (Waleed et al., 2025).

Under these conditions, only two highly tolerant true-mangrove species—out of more than 50 recorded in the IWP region (Table 1)—are able to persist: *Avicennia marina* and *Rhizophora mucronata* (Waleed et al., 2025). Saenger et al. (2019) mention the scattered occurrence of *Bruguiera* and *Ceriops* but do not provide the original references supporting these records. A search of the Global Biodiversity Information Facility (GBIF; https://www.gbif.org/; last accessed on 13 May 2026) did not retrieve any occurrence records of these genera from the ME region. Furthermore, detailed studies of the region (e.g., Haseeba et al., 2025a, b; Waleed et al., 2025) do not report the occurrence of either genus.

A. marina occurs throughout ME mangroves and consistently dominates the canopy, whereas *R. mucronata* is rare or absent, being restricted to localized settings with some freshwater input from streams, which are uncommon in the region (Haseeba et al., 2025a, b; Waleed et al., 2025) (Fig. 6). Both species display a range of morphological, physiological, reproductive and phenological adaptations that enable them to cope with these harsh conditions. Nevertheless, stress from high temperatures, aridity, and limited sediment and nutrient availability constrains growth, resulting in dwarf forms of *A. marina* and *R. mucronata* compared with populations of the same species elsewhere in the IWP region (Waleed et al., 2025). This situation contrasts with other IWP mangroves located within the same latitudinal range but under more favorable environmental conditions, which are among the healthiest and most diverse in the pantropical belt (Tomlinson, 2016; Duke, 2017). This makes ME a biogeographically distinct mangrove province within the IWP region, differing from other provinces such as East Africa, South Asia, Southeast Asia and East Asia–Australasia (Saenger et al., 2019).

Mangrove research has experienced an exponential increase during the 21st century, particularly along the Persian Gulf and Red Sea coasts of Iran, Saudi Arabia, and Egypt, where these ecosystems are most extensively distributed (Fig. 2). The predominant research themes focus on human-related issues, including baseline ecological characterization, environmental impacts, management, and conservation. Concerns about the future of Middle Eastern mangroves under ongoing global change have become a major driver of research in the region (Friis & Burt, 2020).

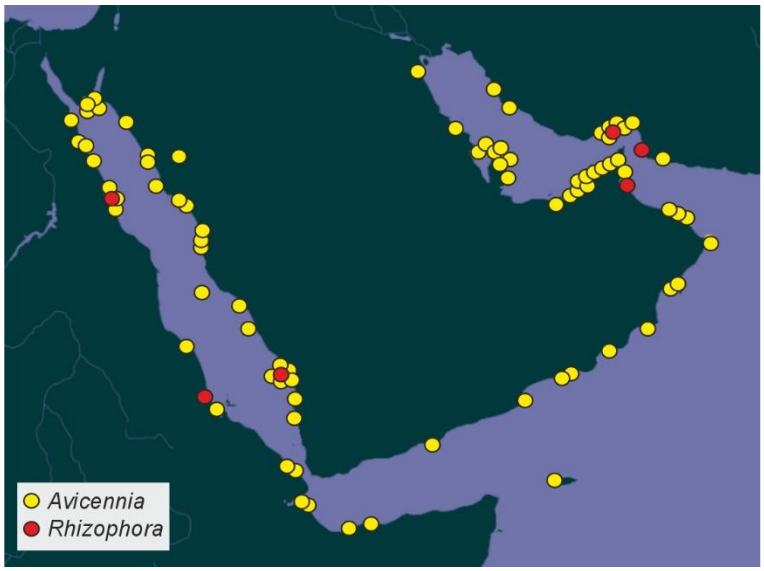

Figure 6. Comparison between *Avicennia* and *Rhizophora* occurrences in the Middle East mangroves according to the Global Biodiversity Information Facility (GBIF; https://www.gbif.org/; last accessed, 13 May 2026).

3. The MESMA dataset

3.1. Methodological hints

This synthesis is based on the MESMA (Middle East MAngroves) dataset, which gathers the published studies, preferably original sources whenever possible; review papers are not used as primary sources of evidence. In a region with as much oil activity as the ME, many studies are never made public because the information is considered confidential by the various operating companies. This means that it is difficult to determine whether an area or a time interval with little available information is genuinely understudied or simply subject to a higher level of confidentiality. Therefore, gaps in information are difficult to interpret and cannot a priori be considered evidence of absence. Since the subject of study—mangroves—are coastal ecosystems, it is expected that their fossils will be found preferentially in transitional land-sea sedimentary environments and will be scarcer or absent in more continental or marine settings. Consequently, lithology and sedimentology may provide useful information for interpreting possible information gaps.

Searches were conducted within the available global literature syntheses mentioned above, as well as in standard bibliographic databases, mainly Web of Science, Scopus, Google Scholar, OpenAlex, The Lens and BASE, along with the large and comprehensive fossil pollen database PALYNODATA (White, 2008). The search criteria consisted of combinations of geographical names (countries, seas, gulfs), chronostratigraphic units (periods, epochs, ages) and extant/fossil taxonomic terms from Table 1. Reviews and syntheses were also used to identify the original references in which the primary evidence was published, and the most recent papers were examined to locate older literature. When geographical coordinates were not provided in the original references, the locality was determined using Google Earth. In a few cases (e.g., Lake Nasser), the exact locality is not provided, and the point on the map is placed approximately at the center of the study area. The data were not reinterpreted, and the original information on age, location and taxonomy was reported.

The fossils considered include pollen and macroremains (e.g., roots, wood, leaves, fruits), or their corresponding impressions or molds, from vascular plants whose nearest living relatives (NLRs) belong to the genera listed in Table 1 as major and minor true-mangrove elements and their associated taxa. In some cases, fossils were identified in the original literature by their NLRs (e.g., *Avicennia*), whereas in others the form genus was used (e.g., *Spinizonocolpites* for *Nypa*). In this review, the NLR names are used for consistency. When available, descriptions and images provided in the original references were used to verify taxonomical identity and botanical affinities.

A conservative evidence-based approach was adopted, and only fossils reliably attributed to known mangrove taxa, as listed in Table 1, were used. Mangroves are regarded as ecosystems, rather than as sedimentary environments. Indeed, they are not merely coastal or intertidal ecosystems adapted to flooding and salinity, but rather well-defined and characteristic taxonomic, physiognomic, structural, biogeographical and ecological communities (Chapman, 1976; Saenger, 2003; Tomlinson, 2016). Other coastal communities—e.g., beach forests, swamp forests, salt marshes or seagrass meadows—may also be adapted to intertidal environments and variable salinity without constituting mangroves. For this reason, inferences regarding the presence of mangrove communities based solely on sedimentological reconstructions of coastal or tidal environments, without taxonomic and ecological support, were not considered.

The use of fossil taxa with unclear botanical affinities that are associated in the literature with “mangrove” or “mangrove-like” vegetation/environments for non-biological reasons was also avoided. This includes, for example, fossil remains of extinct plants whose mangrove affinity is inferred rather than demonstrated, as in the case of the fern fossil *Weichselia* (Smith et al., 2001). This example is discussed in more detail in the paleobiogeography section (4.1). Unidentified remains or ichnofossils attributed to mangrove vegetation were likewise excluded from the analysis—although they are mentioned in the location list for completeness (Table 2)—to avoid ambiguous interpretations. For example, fossil rod-like structures interpreted as mangrove roots (pneumatophores) are seldom preserved, although some have later been reinterpreted as trace fossils (burrows) produced by marine invertebrates, or as composites of pneumatophores and burrows produced by unknown organisms (Gee et al., 2019; Abdel-Fattah &

Gingras, 2020). A paper reporting particulate organic matter presumed to be of mangrove origin (Hamzeh et al., 2025) is also listed for completeness but not used in the biogeographical analysis. The same applies to features such as “mangrove peat” or “mangrove (paleo)soil” (e.g., Kenig et al., 1989).

Faunal fossils and remains linked to mangrove ecosystems through modern analogs, such as mollusks and foraminifera (e.g., Ghandour et al., 2021; Hamzeh et al., 2025), are not included in the analysis. This is not intended to dismiss such relationships, which are ecologically consistent in modern settings, but rather reflects the fact that this review is limited to plant fossils as representatives of the fundamental taxonomic and structural basis of these ecosystems. In any case, studies of mangrove-related fossil fauna constitute only a small portion of the retrieved ME literature.

These criteria favor evidence-based evolutionary and biogeographical reconstructions and reduce reliance on speculative interpretations. They also minimize the risk of circular reasoning and the propagation of misinterpretations in the literature. It is both easier and more scientifically sound to add a new mangrove component to the database once its affinity with this ecosystem has been demonstrated than to correct the database—and the associated misinterpretations—if the taxon is later shown not to belong to mangrove ecosystems.

The chronostrtigraphical framework of this study was provided by latest version of the International Chronostrigraphic Chart (Cohen et al., 2013; v. 2024-12). Epochs and age boundaries are indicated using a slash (e.g., Paleocene/Eocene), whereas age ranges are expressed with a dash (e.g., Middle-Late Miocene). Global paleotermperature and paleoeustatic trends were taken from Westerhold et al. (2020) and Miller et al. (2020), respectively.

3.2. General observations

The MESMA dataset is presented in Table 2 and Fig. 7. It includes 78 localities distributed across 12 countries, with Egypt being the most represented (20%), followed by Turkey (18%), Sudan (15%) and Oman (13%). The least represented countries (1% or less) are Iran, Iraq, Ethiopia and Qatar. Saudi Arabia, Somalia, UAE and Yemen occupy intermediate positions (3-8%). No records were found for Bahrain, Djibouti, Eritrea, Israel, Jordan, Kuwait, Lebanon, Palestine or Syria.

Geologically, 31% of the records are Cretaceous, 29% Paleogene, 17% Neogene, and 22% Quaternary. Cretaceous records are concentrated mainly in northeastern Africa, whereas Paleogene and Neogene sites are predominantly located in Egypt and Turkey, and Quaternary localities are more frequent on the southeastern Arabian Peninsula. Taxonomically, only five of the 20 known true mangrove genera (Table 1) are represented. Three of these genera (*Avicennia*, *Nypa* and *Rhizophora*) are mangrove-forming trees, whereas the other two (*Acrostichum* and *Pelliciera*) are minor mangrove components. Three genera (*Acrostichum*, *Avicennia* and *Rhizophora*) are globally distributed in modern mangroves, whereas the other two are restricted either to the Indo-West Pacific (IWP) region (*Nypa*) or the Atlantic-East Pacific (AEP) region (*Pelliciera*). The case of *Pelliciera* is particularly noteworthy because it is considered a genuine AEP element, and its occurrence in Cenozoic records from Europe and the Middle East has been questioned following detailed morphological analyses of fossil pollen (Rull, 2025). As in the European dataset (EURMA), *Pelliciera* records are included in this analysis to preserve the original evidence, although their reliability is considered in the interpretations (Rull, 2026).

3.3. Geographical patterns

Some regions are more extensively represented than others in the MESMA dataset (Fig. 7). The areas with the highest number of mangrove records are the Anatolian Peninsula, northeastern Africa, especially Egypt, and the southeastern Arabian Peninsula, notably Oman and the UAE. Less represented areas include the interior Arabian Peninsula, the Levant, and southwestern Asia, especially Iran and Iraq. Based on the available evidence, it remains difficult to determine to what extent this pattern reflects chronostratigraphical or paleoenvironmental constraints, differential preservation, research bias, confidentiality practices of oil companies or cultural differences.

Geological constraints occur in areas where exposed rocks are older than the Late Cretaceous—when the first mangrove records appeared globally—or where sedimentary environments were

unsuitable for mangrove growth and/or preservation, notably in inland and open/deep-marine settings. In the study area, the absence of prospective rocks for chronostratigraphic reasons is largely restricted to the Precambrian Arabian–Nubian Shield, whereas Late Cretaceous and Cenozoic sediments are widely distributed across the remaining regions (Fig. 3). The lack of suitable sedimentary environments occurs mainly in the Red Sea (RS) and Gulf of Aden (GA) basins, which are largely devoid of Cenozoic terrestrial fossils in general.

Indeed, as rifting basins, the RS and GA sediments consist mainly of marine and marginal-marine siliciclastics, evaporites, and carbonates, reflecting progressively increasing water depths that culminated in foram-rich marls and deep-water limestones by the Early Miocene (Hughes & Johnson, 2005). Between the Early and early Middle Miocene, coinciding with the Arabia–Eurasia collision, sedimentation shifted to marine mudstones and submarine evaporites, although deep-water environments persisted. The development of extensive carbonate platforms was typical of this interval (Koeshidayatullah et al., 2015). The Middle Miocene was characterized by continued oceanic spreading and the deposition of thick evaporites, followed in the Late Miocene by shales and anhydrites. Finally, during the Pliocene and Pleistocene, sedimentation became predominantly alluvial, with coarse sands and gravels prevailing. In summary, marine and deep-marine environments—rather than the coastal intertidal settings required for mangrove development—dominated throughout the time interval considered in this study.

Some pollen occurrences are reported in review and summary papers about RS and GA regions, although the localities and ages are not specified with the precision required for this study. For example, Filatoff & Hughes (1996) noted the occurrence of pre-rifting (Late Cretaceous–Early Paleogene) palm and fern floras typical of tropical humid climates, followed by syn-rift assemblages dominated by savanna-type grass vegetation and Neogene halophytic plants characteristic of arid sabkha environments. The only mention of mangroves concerns Cretaceous–Paleocene *Nypa*, previously reported by Srivastava & Binda (1991), as well as sporadic occurrences of Miocene *Avicennia*-type pollen, although no further details are provided. The same authors also noted that other mangrove elements common in tropical regions elsewhere, such as *Rhizophora* or *Sonneratia*, are rare in the fossil record. Hughes & Johnson (2005) likewise mentioned some pollen occurrences but without reference to mangroves. A few more detailed Paleogene–Neogene studies are available and are included in this synthesis (Table 2; Fig. 7), with the exception of Moltzer & Binda (1981, 1984), which did not report mangrove pollen.

The situation in the RS–GA region contrasts with that of the Mesopotamian–Persian Gulf and Oman basins, where Cenozoic rocks are abundant and have been fundamental to the development of petroleum systems, as noted above. Therefore, neither geological constraints nor a lack of economic interest can be invoked to explain the scarcity of mangrove records in the MESMA dataset. In this case, confidentiality issues are likely involved. As a former exploration biostratigrapher at a major Caribbean oil company (Rull, 2002), the author is aware of the large volume of biostratigraphic information contained in internal company reports, or not reported at all, that remains unavailable for reviews and syntheses such as the present study. Based on the available evidence, it is not possible to assess the significance of this situation for the ME region. Interestingly, however, most records from the Persian Gulf and the Gulf of Oman correspond to the Holocene, which is of less interest to the oil industry. The lack of mangrove records across extensive continental areas of southwestern Asia—including Syria, Iran, Iraq, and the Levant—is striking and, based on the available evidence, remains difficult to explain.

Cultural differences among countries, reflected in variable research effort and publication intensity, may also contribute to the observed geographical patterns in evidence availability. For example, Egypt has a more established tradition of publishing palynostratigraphic data than other countries in the region with comparable levels of oil-industry activity. A similar situation exists in Turkey, where biostratigraphic research has been closely linked to the coal industry, as the country ranks among the world's major lignite producers (Yilmaz, 2006). Despite their strategic importance as energy producers, both countries have a long tradition of stratigraphic research and fossil documentation, including records of terrestrial vegetation and mangrove ecosystems.

505 **Table 2.** The MESMA dataset. Fossil localities compiled in this review and their main features (see Fig. 7 for location). Fossil types: CH, charcoal; FS, fruits/seeds; LF, leave molds/impressions; PO,
506 particulate organic matter; PS, pollen/spores; PT, peat; RT, roots casts/molds/rhizoliths; RZ, rhizomes; SL, soils/paleosols: TS, trunks/twigs/stems; WF, wood fragments.
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Map	Site	Country	Latitude	Longitude	Period	Epoch	Age	Mangrove taxa	Fossil type	References
Qm	Qeshm	Iran	26°51'08"N	55°39'49"E	Quaternary	Holocene	L Holocene	Unidentified	PO	Hamzeh et al. (2020)
Fi	Filim	Oman	20°36'36"N	58°10'12"E	Quaternary	Holocene	M-L Holocene	*Rhizophora* *Avicennia*	PS	Lézine et al. (2017)
KJ	Kwar-al-Jaramah	Oman	22°29'24"N	59°45'36"E	Quaternary	Holocene	M-L Holocene	*Rhizophora* *Avicennia*	PS	Lézine (2009) Lézine et al. (2017)
Sy	Suwayh	Oman	22°05'35"N	59°40'01"E	Quaternary	Holocene	M-L Holocene	*Rhizophora* *Avicennia*	PS CH	Lézine et al. (2002, 2010) Berger et al. (2013)
AD	Abu Dhabi	Oman	24°27'00"N	54°26'24"E	Quaternary	Holocene	M-L Holocene	Unidentified	RT	Khanna et al. (2021)
RR	Ras ar Ru'ays	Oman	22°10'54"N	59°45'47"E	Quaternary	Holocene	M Holocene	*Avicennia?*	RT	Decker et al. (2020)
Al	Alashkara	Oman			Quaternary	Holocene	M Holocene	*Avicennia*	WF RT	Berger et al. (2013)
Qy	Quriyat	Oman	23°15'47"N	58°54'57"E	Quaternary	Holocene	M Holocene	*Avicennia?*	RT	Decker et al. (2020)
Sw	Sawadi	Oman	23°35'16"N	58°22'58"E	Quaternary	Holocene	M Holocene	*Avicennia?*	RT	Decker et al. (2020)
AD	Abu Dhabi	UAE	24°17'47"N	54°20'35"E	Quaternary	Holocene	Holocene	Unidentified	PT/SL/RT/TS	Kenig et al. (1989)
Mi	Sabkha Matti	UAE	23°50'36"N	52°01'50"E	Quaternary	Pleistocene Holocene	Pleistocene Holocene	Unidentified	RT	Kirkham (1998)
92	MD92-1002	Yemen	12°01'32"N	44°19'02"E	Quaternary	Holocene	E-M Holocene	*Rhizophora* *Avicennia*	PS	Fersi et al. (2016)
76	MD 76 135	Yemen	14°26'06"N	50°31'03"E	Quaternary	Pleistocene Holocene	L Pleistocene Holocene	*Avicennia* *Rhizophora*	PS	Van Campo et al. (1982)
Z1	Zeugen 1	UAE	24°05'47"N	53°42'48"E	Quaternary	Pleistocene	L Pleistocene	Unidentified	RT	Wood et al. (2012)
Z4	Zeugen 3-4	UAE	24°19'15"N	54°15'07"E	Quaternary	Pleistocene	L Pleistocene	Unidentified	RT	Wood et al. (2012)
Z5	Zeugen 5	UAE	25°11'49"N	55°19'04"E	Quaternary	Pleistocene	L Pleistocene	Unidentified	RT	Wood et al. (2012)
23	DSDP 231	Somalia	11°53'24"N	48°15'00"E	Neogene Quaternary	Miocene Pleistocene	Tortonian M Pleistocene	*Rhizophora*	PS	Bonnefille (2010)
GH	GH 404-2A	Egypt	27°46'36"N	33°46'21"E	Neogene	Miocene	Burdigalian Langhian	*Rhizophora*	PS	El Atfy et al. (2017)
Kt	Kultak	Turkey	37°04'42"N	27°56'24"E	Neogene	Miocene	L Burdigalian Langhian	*Avicennia* *Acrostichum*	PS	Kayseri-Özer (2014)
Dm	Dawmat	Saudi Arabia	27°33'37"N	48°37'53"E	Neogene	Miocene	E-M Miocene	*Avicennia?*	RT	Whybrow & McClure (1980/81)
Br	Barakah	UAE	24°04'14"N	52°26'17"E	Neogene	Miocene	E-M Miocene	*Avicennia?*	RT	Whybrow & McClure (1980/81)
EM	El Mellaha	Egypt	27°13'17"N	33°47'36"E	Neogene	Miocene	Aquitanian Burdigalian	*Nypa*[1]	PS	El Diasty et al. (2020)
Dz	Denizli	Turkey	37°46'59"N	29°05'47"E	Neogene	Miocene	Aquitanian	*Acrostichum*	PS	Kayseri-Özer (2014)
Ke	Kale	Turkey	37°27'05"N	28°48'47"E	Neogene	Miocene	Aquitanian	*Acrostichum*	PS	Kayseri-Özer (2014)

Tv	Tavas	Turkey	37°34’23”N	29°04’17”E	Neogene	Miocene	Aquitanian	*Acrostichum*	PS	Kayseri-Özer (2014)
Bd	Burdur	Turkey	37°43’06”N	30°16’56”E	Neogene	Miocene	Aquitanian	*Acrostichum*	PS	Kayseri-Özer (2014)
A2	Melut AY2	Sudan	10°34'37"N	33°05'56"E	Neogene	Miocene	E Miocene	*Rhizophora*	PS	Eisawi (2007)
A3	Melut AY3	Sudan	09°45'33"N	33°11'44"E	Neogene	Miocene	E Miocene	*Rhizophora*	PS	Eisawi (2007)
AG	Abu Gharadig	Egypt	29°43’45”N	28°32’18”E	Neogene	Miocene	E Miocene	*Acrostichum*	PS	Ibrahim et al. (2024)
HS	Hilal-Shoab Ali	Egypt	27°46’36”N	33°46’21”E	Neogene Paleogene	Oligocene Miocene	Chattian Aquitanian	*Rhizophora*	PS	El Atfy et al. (2013)
Aa	Amana-1X	Egypt	29°33’24”N	29°25’24”E	Paleogene	Oligocene	Oligocene E Miocene	*Rhizophora* *Pelliciera*[2]	PS	El Atfy et al. (2022)
Cg Mr	Chilga Margargaria	Ethiopia	12°30'35"N 12°30’31”N	36°52'05"E 37°06’57”E	Paleogene	Oligocene	L Oligocene	*Acrostichum*	LF	Jacobs et al. (2005) García Massini et al. (2006, 2010) Pan et al. (2006)
Ma	Mugla	Turkey	37°12’55”N	28°21’48”E	Paleogene	Oligocene	Rupelian	*Acrostichum* *Avicennia* *Pelliciera*[2]	PS	Kayseri-Özer (2014)
Ms	Milas	Turkey	37°18’42”N	27°46’51”E	Paleogene	Oligocene	Rupelian	*Acrostichum* *Avicennia* *Pelliciera*[2]	PS	Kayseri-Özer (2014)
Me	Mersin	Turkey	36°38’43”N	34°38’29”E	Paleogene	Oligocene	Rupelian	*Nypa*	PS	Kayseri-Özer (2014)
Mu	Mut	Turkey	36°38’43”N	33°26’13”E	Paleogene	Oligocene	Rupelian	*Nypa*	PS	Kayseri-Özer (2014)
Qt	Qattara	Egypt	29°40’53”N	27°07’09”E	Paleogene	Eocene Oligocene	L Eocene E Oligocene	*Pelliciera*[2]	PS	El Atfy et al. (2021)
Dk	Duhok	Iraq	36°52’00”N	43°03’40”E	Paleogene	Eocene	M-L Eocene	*Nypa* *Pelliciera*[2]	PS	Al-Atrushe & Al-Hasson (2025)
Ht	Wadi Al-Hitan	Egypt	29°16’15”N	30°01’26”E	Paleogene	Eocene	Bartonian Priabonian	*Nypa?* *Avicennia?* *Rhizophora?*	RZ/RT	El-Saadawi (2005) El-Saadawi et al. (2018)
AK	Al-Khor	Qatar	25°40'49.47"N	51°29'48.66"E	Paleogene	Eocene	Lutetian Bartonian	Unidentified	TS?	Sadooni & Al-Saad (2012)
Mk	Mokattam	Egypt	30°01’18”N	31°18’12”E	Paleogene	Eocene	Lutetian	*Nypa*	FS	Fraas (1867) Bonnet (1904) Kräusel & Stromer (1924) Kraüsel (1939) Chandler (1954)
Kw	Al Khawd	Oman	23°33’57”N	58°07’25”E	Paleogene	Eocene	Lutetian	*Nypa*	PS	Racey et al. (2025)
Sv	Sivrihisar	Turkey	39°27’05”N	31°32’16”E	Paleogene	Eocene	Ypresian Lutetian	*Nypa*	PS	Akkiraz et al. (2022)
Yg	Yozgat	Turkey	39°49’16”N	34°48’31”E	Paleogene	Eocene	M-L Eocene	*Avicennia* *Pelliciera*[2] *Nypa*	PS	Akkiraz et al. (2008)
Sg	Sorgun	Turkey	39°48’46”N	35°11’25”E	Paleogene	Eocene	M-L Eocene	*Avicennia*	PS	Akkiraz et al. (2008)

								Pelliciera[2] *Nypa*		
Jd	Jeddah	Saudi Arabia	21°31'45"N	39°09'40"E	Paleogene	Eocene	Ypresian	*Nypa*	PS	Srivastava & Binda (1991)
As	Aswan	Egypt	23°39′08″N	32°11′27″E	Paleogene	Eocene	E Eocene	*Nypa*	FS	El-Noamani & Ziada (2025)
Kw	Al Khawd	Oman	23°33′57″N	58°07′25″E	Paleogene	Eocene	E Eocene	*Nypa* *Avicennia*	PS	El Beialy (1998)
Dz	Denizli	Turkey	37°46′59″N	29°05′47″E	Paleogene	Eocene	Eocene	*Acrostichum* *Pelliciera*[2] *Nypa*	PS	Kayseri-Özer (2014)
Am	Armutalani	Turkey	37°53′47″N	29°36′13″E	Paleogene	Eocene	Eocene	*Acrostichum* *Pelliciera*[2] *Nypa*	PS	Kayseri-Özer (2014)
Qs	Quseer/Kosseir	Egypt	26°05′05″N	34°16′49″E	Paleogene	Paleocene	Danian	*Nypa*	FS	Chandler (1954)
Ns	Lake Nasser	Egypt	22°42′22″N*	32°11′50″E*	Paleogene	Paleocene	ND	*Nypa*	FS	Lejal-Nicol (1987)
Mq	Abu Minqar	Egypt	26°31′05″N	27°39′43″E	Cretaceous Paleogene	Cretaceous Paleocene	Maastrichtian Danian	*Nypa*[3]	FS PS	Gregor & Hagn (1982) Tantawy et al. (2001) El-Soughier et al. (2011) El Soughier (2020) Abu El-Kheir et al. (2021) El-Hedeny et al. (2021)
Kk	Kaikang	Sudan	09°21'00"N	29°07'37"E	Cretaceous	L Cretaceous	L Maastrichtian	*Nypa*	PS	Cole et al. (2017)
Ko	Kosti	Sudan	13°07'59"N	32°38'28"E	Cretaceous	L Cretaceous	Maastrichtian	*Nypa*[4]	PS	Awad (1994)
A1/2	Melut AY1/2	Sudan	10°34'37"N	33°05'56"E	Cretaceous	L Cretaceous	Maastrichtian	*Nypa*	PS	Eisawi (2007)
A3	Melut AY3	Sudan	09°45'33"N	33°11'44"E	Cretaceous	L Cretaceous	Maastrichtian	*Nypa*	PS	Eisawi (2007)
A4	Melut AY4	Sudan	08°34'00"N	33°45'36"E	Cretaceous	L Cretaceous	Maastrichtian	*Nypa*	PS	Eisawi (2007)
Gf	Gedaref	Sudan	14°01′28″N	35°22′07″E	Cretaceous	L Cretaceous	Maastrichtian	*Nypa*	PS	Eisawi & Schrank (2009)
HH	Hed Hed	Somalia	09°32'00"N	44°47'00"E	Cretaceous	L Cretaceous	Maastrichtian	*Nypa*	PS	Schrank (1990, 1994)
Fr	Foram 1	Egypt	27°38′42″N	25°12′21″E	Cretaceous	L Cretaceous	Maastrichtian	*Nypa*	PS	Schrank (1991)
Kg	Kharga	Egypt	25°26′21″N	30°33′31″E	Cretaceous	L Cretaceous	Maastrichtian	*Nypa*	PS	Schrank (1991, 1992)
Ab	Abu Gabra	Sudan	10°52'55"N	27°18'59"E	Cretaceous	L Cretaceous	Maastrichtian	*Nypa*	PS	Babikir (1997)
Md	Muglad	Sudan	11°02'05"N	27°44'57"E	Cretaceous	L Cretaceous	Maastrichtian	*Nypa*	PS	Eisawi et al. (2012) Kaska (1989)
Mt	Melut	Sudan	10°26′25″N	32°12′06″E	Cretaceous	L Cretaceous	Campanian Maastrichtian	*Nypa*	PS	Eisawi & Schrank (2008) Kaska (1989)
As	Aswan	Egypt	23°39′08″N	32°11′27″E	Cretaceous	L Cretaceous	Campanian Maastrichtian	*Nypa*	PS	Schrank (1992)
Kh	Kahraman	Egypt	30°52′42″N	26°36′53″E	Cretaceous	L Cretaceous	Campanian Maastrichtian	*Nypa*	PS	Schrank & Ibrahim (1995) Abdel-Kireem et al. (1996)
Mm	El Mahamid	Egypt	25°24'02"N	32°35'51"E	Cretaceous	L Cretaceous	Campanian Maastrichtian	*Nypa*	PS	Schrank (1992)

Ki	Bir Kiseiba	Egypt	22°40'17"N	29°54'31"E	Cretaceous	L Cretaceous	Campanian Maastrichtian	*Nypa*	PS	Schrank (1992)
Qs	Quseer/Kosseir	Egypt	26°05’05”N	34°16’49”E	Cretaceous	L Cretaceous	Campanian Maastrichtian	*Nypa*	PS	Schrank (1992)
Ff	Farafra	Egypt	27° 3'24"N	27°58'13"E	Cretaceous	L Cretaceous	Campanian Maastrichtian	*Nypa*	PS	Schrank (1991)
AG	Abu-Gharadig	Egypt	29°43’45”N	28°32’18”E	Cretaceous	L Cretaceous	Campanian Maastrichtian	*Nypa*	PS	Abdel-Kireem et al. (1996)
Sn	Shendi	Sudan	16°41'25"N	33°25'51"E	Cretaceous	L Cretaceous	Campanian Maastrichtian	*Nypa*	PS	Eisawi (2018)
At	Al-Fatk	Yemen	16°17'40"N	52°32'11"E	Cretaceous	L Cretaceous	Santonian Campanian	*Nypa*	PS	Alaug et al. (2013)
No	El-Noor	Egypt	31°19’35”N	26°04’19”E	Cretaceous	L Cretaceous	Turonian Coniacian	*Nypa*[5]	PS	El-Soughier (2013)
Bh	Bahariya	Egypt	28°23’06”N	28°54’31”E	Cretaceous	L Cretaceous	Cenomanian	*Avicennia?*[6]	LF	Darwish & Attia (2007)
Sf	Safaniya	Saudi Arabia	27°56'16"N	48°39'39"E	Cretaceous	E Cretaceous	Albian	*Nypa?*	PS	Srivastava (2000)

[1]Identification doubtful (D.T. Pocknall, pers. comm.)
[2]Identification doubtful (Rull, 2025).
[3]Oldest macrofossil records worldwide (Wu et al., 2024).
[4]Identification doubtful (Pocknall et al., 2023).
[5]Wrong identification; the illustration provided corresponds to *Verrucatosporites*, a monolete spore.
[6]Identification considered as “highly speculative” (El Atfy et al., 2023a).

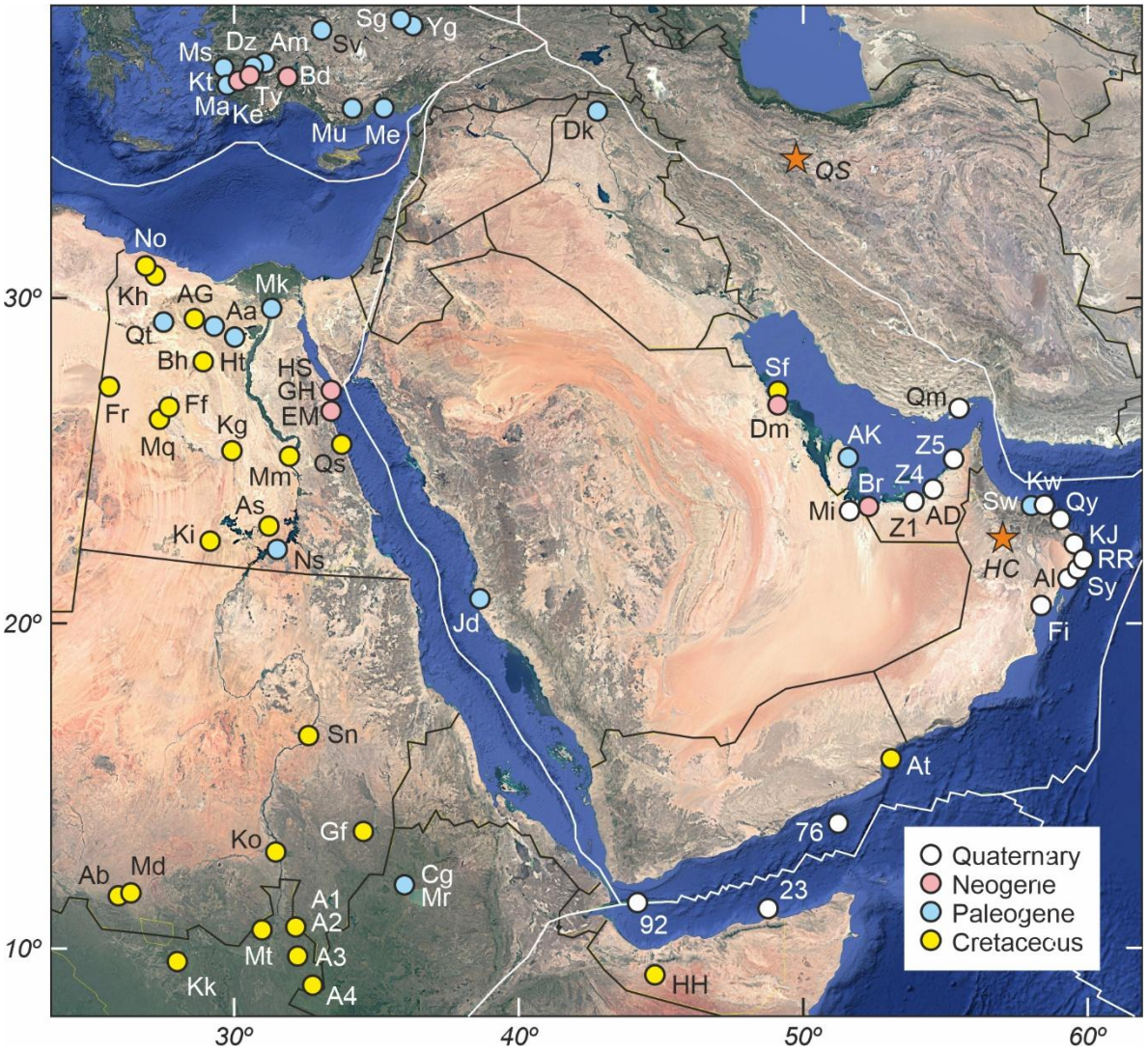

Figure 7. Localities with fossil records used in this review (see Table 2 for more details) using the same base map of Fig. 2. Orange stars represent the sites with paleoclimatic records discussed in the text (HC, Hoti Cave; QS, Qom section).

The presence of significant gaps in the palynostratigraphic record prompted the author to expand the search beyond conventional bibliographic and taxonomic resources by incorporating Google Search and AI tools such as ChatGPT and Gemini. As this expanded search failed to identify additional records, the resulting spatiotemporal gaps are more likely to reflect genuine absences of mangroves than deficiencies in information retrieval, although lack of research or unpublished records may contribute to the pattern in some areas.

4. Paleobiogeographical trends

This section uses the MESMA dataset to analyze biogeographical trends through time, which form the core of the review. It combines the fossil record with paleogeographical shifts derived from plate tectonics, along with independent paleoclimatic and paleoeustatic records, to investigate biogeographical shifts in terms of habitat suitability and the waxing and waning of dispersal pathways and barriers.

A previous comment on dispersal is pertinent. The colonization of new areas by a given taxon is usually referred to as dispersal *sensu lato*; however, in biogeography, it is useful to distinguish between long-distance dispersal (LDD) and migration. Here, the definitions proposed by Pielou (1979) are adopted. Long-distance dispersal, or jump dispersal, is the movement of organisms across great distances in short periods of time, usually shorter than the lifespan of an individual, and across inhospitable terrains. In

contrast, migration is a slower colonization process that occurs across hospitable terrains and lasts for generations (diffusion) or for sufficiently long periods to accommodate evolutionary change (secular migration). In the case of mangroves, long-distance dispersal involves intercontinental movement across oceans, with ocean currents acting as the main agents, whereas secular migration proceeds through the lateral expansion of populations via the progressive colonization of nearby habitats promoted by coastal currents (Van der Stocken et al., 2019).

4.1. Earliest potential Middle-East mangroves

Using the criteria established in this review—that is, the record of known mangrove taxa as presented in Table 1—the earliest consistent mangrove records correspond to the Late Cretaceous, specifically the Campanian–Maastrichtian (Table 2). However, some occasional earlier potential occurrences have been suggested and merit mention, one in the Albian and another in the Cenomanian.

The first reported potential mangrove element in the ME is monosulcate palm pollen of *Nypa* affinity from Albian sediments in the Persian Gulf (Srivastava, 2000). Pocknall et al. (2023) interpret this pollen as a potential *Nypa* ancestor and consider it the earliest known global record of this lineage. The significant spatial and temporal isolation of this finding—i.e., more than 1400 km from the nearest other Cretaceous mangrove occurrence (Fig. 7) and approximately 20–30 million years older than the Campanian–Maastrichtian—precludes any reliable assessment of the geographical patterns and temporal continuity of these potential mangrove occurrences in the region and globally. To date, the most parsimonious interpretation is to consider it a spatiotemporal outlier pending further research. If it is confirmed that this pollen represents a precursor of *Nypa*, the lineage would have evolved locally in the ME region.

The purported Cenomanian mangroves inferred from the fossil assemblage of the Bahariya Oasis in northern Egypt became iconic following the discovery of the giant sauropod dinosaur *Paralititan* (Smith et al., 2001). The site is now known as the mangrove-dinosaur site (Coiffard et al., 2025), and *Paralititan*—so named because of both its large size and its paralic habitat—is considered a unique dinosaur associated with mangrove environments. Mangrove conditions were inferred from the presence of the salt-tolerant tree-fern represented by *Weichselia reticulata* macroremains and from the sedimentological interpretation of low-energy littoral environments (Smith et al., 2001; Lacovara et al., 2003). Further investigations at the mangrove-dinosaur site also reported fossil leaves attributed to the well-known mangrove element *Avicennia* (Darwish & Attia, 2007; El-Saadawi et al., 2016). The Cenomanian Bahariya record is particularly significant because, if the paleoenvironmental interpretation is correct, it could represent the earliest mangrove community in the ME region. However, subsequent reassessments of the Bahariya record have challenged this interpretation.

Indeed, the mangrove affinity of *Weichselia* is not generally accepted, and the autecology of this extinct fern remains highly debated (Blanco-Moreno et al., 2018, 2020). Consequently, inferring mangrove ecosystems from its occurrence has been regarded as still speculative by El Atfy et al. (2023a). The same authors also questioned the identification of the fossil leaves attributed to *Avicennia*, considering this interpretation likewise highly speculative. *Avicennia* is not recorded in any other ME Cretaceous sediments, and its first appearances correspond to the Early Eocene (Table 2), close to the earliest global record, which dates to the Paleocene/Eocene boundary (Popescu et al., 2021).

More recent analyses of new samples (El Atfy et al., 2023b), together with reexaminations of previously collected fossil material (Coiffard et al., 2025), have adopted a more conservative approach to taxonomic assignment. Rather than assigning precise affinities, these studies use morphotypes to characterize the fossil assemblages and identify significant lateral and vertical variations that reflect complex spatiotemporal vegetation patterns, ranging from floodplain to coastal tropical humid environments within the Bahariya Formation. Therefore, based on the currently available evidence, interpreting the Cenomanian Bahariya Formation as a mangrove environment, and considering the giant *Paralititan* as a mangrove-dwelling dinosaur, appears premature. Unfortunately, this idea risks becoming established in the ME literature through repetition. *Weichselia* has also been reported from other ME localities (El-Khayal, 1985; Blanco-Moreno et al., 2018; El Atfy et al., 2023b), although no inferences regarding mangrove environments were made.

4.2. Late Cretaceous-Paleocene

During the Late Cretaceous, well before the collision between the Arabian and Eurasian plates, southwestern Eurasia, extending from present-day Turkey to Iran, was covered by the Tethys Sea (Ali et al., 2013; Moghadam et al., 2020), and land–sea transitional environments suitable for mangrove development were absent from the region (Fig. 8). The present-day Arabian Peninsula, then still part of the Nubian Plate, was emergent in its southwestern sector, corresponding to the Precambrian Arabian Shield, whereas its northeastern sector was characterized by open to deep-marine environments, with shallow-marine carbonate platforms bordering both Tethys coastal margins (Ziegler, 2001). Extensive carbonate platforms are generally unfavorable for widespread mangrove development because they are sediment-starved systems lacking a regular supply of terrigenous mud and stable fine-grained substrates (Woodroffe et al., 2016; Breithaupt et al., 2017). Consequently, Late Cretaceous mangrove records are restricted to the southwestern sector of the study area, primarily in northwestern Africa.

Nypa was the only mangrove component, and a large proportion of its records are from continental areas. Extant *Nypa* requires a salinity range of 0‰ to 10‰ for optimal development, as salinities exceeding 10‰ inhibit germination (Zhang et al., 2024). Therefore, it can be inferred that Late Cretaceous ME *Nypa* grew preferentially in inland, and occasionally coastal, freshwater to brackish-water environments. Interestingly, all *Nypa* localities are situated on the forefront of the Nubian–Arabian Plate, whereas none occurs on the Eurasian side of the Tethys. The oldest purported *Nypa* record in the MESMA dataset, identified as *Spinizonocolpites* in the original reference, comes from the Turonian–Coniacian of Egypt (El-Soughier, 2013). However, the illustrated specimen assigned to *Spinizonocolpites* is actually a monolete spore belonging to the form-genus *Verrucatosporites*, which has affinities with the Polypodiaceae (Tryon & Lugardon, 1990). Therefore, the earliest confirmed *Nypa* record is from the Turonian–Coniacian of Yemen (Alaug et al., 2013); all other records are Campanian–Maastrichtian in age (Table 2).

According to Muller (1981), *Nypa* appeared more or less simultaneously in South America, Africa and Southeast Asia during the Late Cretaceous as a result of rapid invasion by seaborne dispersal across the tropics. However, its geographical origin remains unknown. The Turonian–Coniacian record from Yemen is currently the oldest documented Late-Cretaceous record worldwide. This, together with the Albian record from Saudi Arabia discussed above, makes the ME region a strong candidate for the origin of the *Nypa* lineage. This hypothesis is consistent with recent molecular phylogeographic studies (Wu et al., 2024).

It is interesting to note that, although the Tethyan seaway remained open for dispersal through either LDD, coastal migration, or both, Europe was devoid of mangroves during the Late Cretaceous and the Paleocene (Rull, 2026). Therefore, the ME region emerges as a key area for the origin of mangroves worldwide, whereas its role as a corridor for the dispersal of mangrove taxa from the IWP to Europe and other regions developed later.

4.3. Eocene

A diversification of mangrove taxa occurred during the Eocene, with the establishment of *Avicennia*, *Acrostichum*, and *Pelliciera*, although the occurrence of the latter has been questioned (Rull, 2025). These taxa were recorded mainly in Turkey, with a single *Avicennia* record from Oman; the remaining records correspond to *Nypa*, which remained dominant in the Nubian–Arabian Plate (Fig. 8). Most of the new records were from the Tethyan coasts, suggesting that coastal migration from the IWP core was active by this time. This diversification began during the Early Eocene Climatic Optimum (EECO) and the associated sea-level rise, and continued throughout the Eocene (Fig. 9).

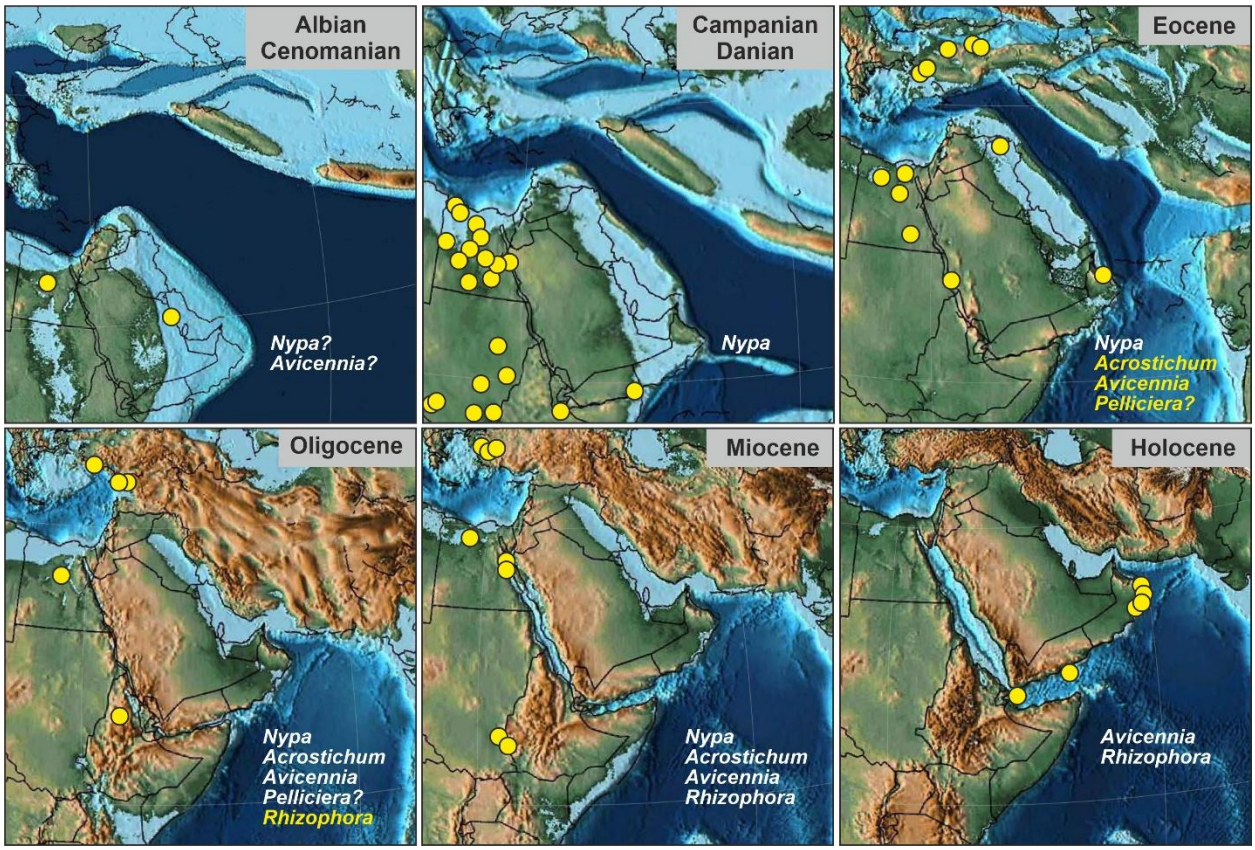

Figure 8. Paleobiogeographical trends of mangrove taxa from the Cretaceous to the Quaternary. Maps were generated with GPlates 2.5.0 using the Scotese (2016) PALEOMAP PaleoAtlas, freely available at https://www.earthbyte.org/paleomap-paleoatlas-for-gplates/ (last accessed May 21, 2026).

Notably, other mangrove taxa, such as *Aegialitis*, *Aegiceras*, *Excoecaria*, Rhizophoraceae, Sonneratiaceae and *Xylocarpus*, were already present in Europe by the Early-Middle Eocene (Rull, 2026), suggesting that the ME region could have acted as a corridor for these taxa from the IWP core since the Paleocene/Eocene boundary (P/E). The absence of these taxa in the ME region during the Eocene could be due to local extirpation, although the lack of records discussed above may also have played a role. In any case, the low diversity of mangrove taxa, compared with other IWP biogeographical provinces as observed today (Saenger et al., 2019), seems to have originated long ago, at least by the early Paleogene. This situation persisted throughout the Paleocene and Eocene, when a variety of global paleoclimatic and paleoeustatic changes took place (Fig. 9), and, based on the available evidence, cannot be linked to any of these paleoenvironmental changes.

The possibility that LDD predominated over coastal migration would be consistent with this pattern, at least in theory. However, the progressive shallowing of the Tethyan seaway and the resulting expansion of coastal environments, together with the more or less continuous presence of *Acrostichum*, *Avicennia* and *Nypa* along the Anatolian coasts (the proto-Mediterranean gateway to the European domain), challenge this interpretation. The hypothesis of an early Paleogene colonization of the present-day European continent by mangroves from the core IWP region via the ME Tethyan corridor is fully consistent with the available paleobiogeographical evidence. However, the lack of fossil evidence documenting such a process along the Tethyan coasts of both Europe and the ME represents a significant knowledge gap that should be addressed by future research.

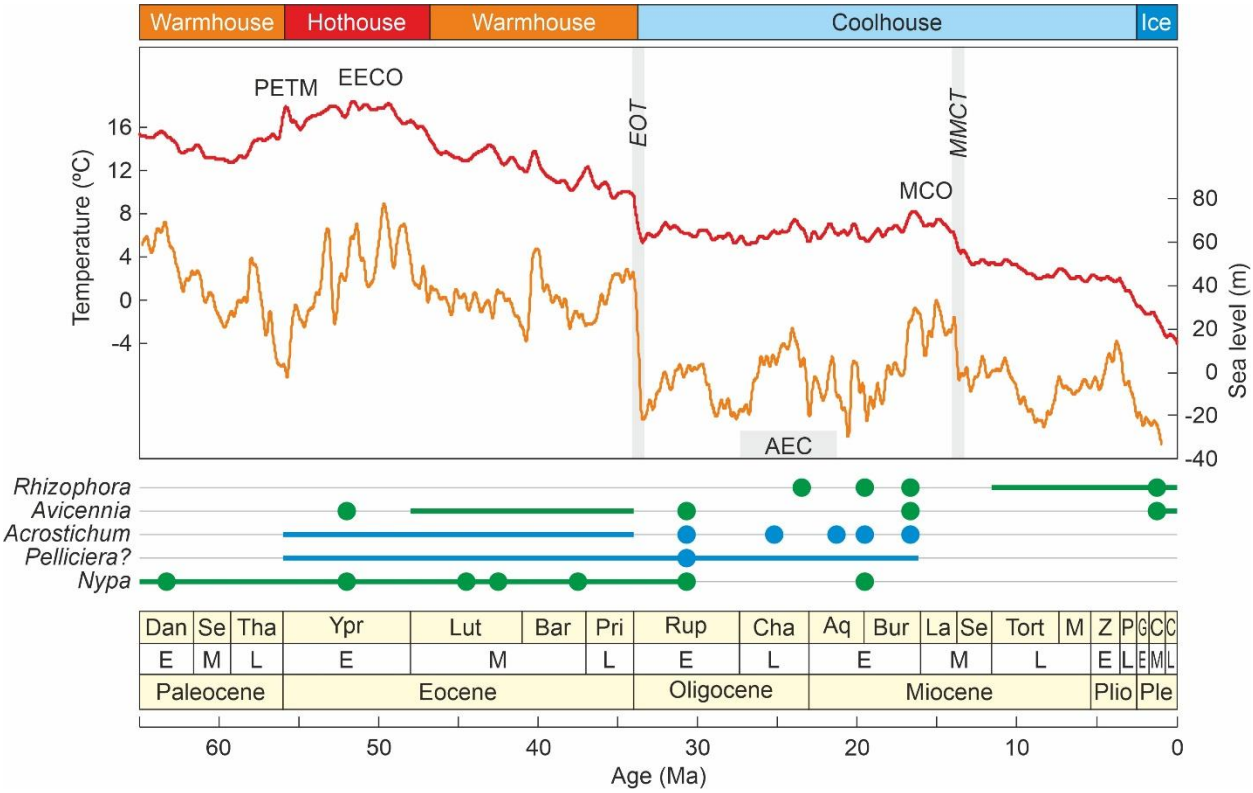

Figure 9. Chronostratigraphical ranges of mangrove taxa in the Middle East in relation to global paleoenvironmental reconstructions. Dots are records in particular time intervals and lines are records reported as ranges in the original literature. Major true-mangrove genera are in green and minor elements in blue. Global paleotemperature trends (red line) according to Wessterhold et al. (2021) and paleoeustatic trends (orange line) according to Miller et al. (2020). AEC, Arabia-Eurasia Collision; EECO, Early Eocene Climatic Optimum; EOT, Eocene/Oligocene Transition; MMCO, Middle Miocene Climatic Optimum; MMCT, Middle Miocene Climatic Transition; PETM, Paleocene/Eocene Thermal Maximum.

4.4. Oligocene

The maximum diversity of ME mangroves occurred during the Oligocene, with the addition of *Rhizophora* in an Egyptian locality, although the overall longitudinal extent of mangroves declined significantly (Fig. 8). The environmental shift that most strongly affected other mangrove regions—namely, the cooling and eustatic sea-level fall associated with the Eocene/Oligocene Transition (EOT) (Fig. 9), which led to substantial diversity declines in Europe and the disappearance of *Nypa* from the Neotropics (Rull, 2023, 2026)—does not appear to have affected ME mangroves in the same way. Similarly, the closure of the Tethyan seaway resulting from the Africa–Eurasia collision, which began during the Late Oligocene, was not associated with any decline in mangrove diversity or distribution. On the contrary, it coincided with the first appearance of *Rhizophora*. This suggests that *Rhizophora* had already crossed the Anatolian gateway before the closure of the Tethyan seaway, providing evidence for the progressive coastal colonization of the proto-Mediterranean region during the Paleogene. In summary, it is noteworthy that neither the EOT environmental disruption nor the closure of the Tethyan seaway—two key events in the evolution of mangroves elsewhere—were as influential for ME mangroves.

4.5. Miocene

The main biodiversity crisis of ME mangroves took place during the Miocene, which witnessed the last occurrences of all mangrove taxa except *Rhizophora* and *Avicennia*, marking the beginning of the present-day situation. The last occurrences of *Nypa*, *Acrostichum*, and *Pelliciera* date from the Early Miocene, between the closure of the Tethyan seaway and the Middle Miocene Climatic Transition (MMCT) (Fig. 9). A clarification is warranted regarding *Nypa*, whose range extension into the Early Miocene is based on a

single occurrence from Egypt, extending its regional record by more than 10 million years beyond the EOT. However, the pollen illustration provided in support of this record does not appear to be consistent with *Nypa* and is more likely attributable to Malvaceae (D. T. Pocknall, pers. comm.), thus requiring further investigation. If this record is discounted, *Nypa* disappeared from the ME around the EOT, as it did in Europe and the Neotropics (Rull, 2023, 2026).

The MMCT occurred at approximately 14 Ma (14.2-13.8 Ma) and was characterized by global cooling, which has been linked to large-scale shifts in oceanic circulation associated with the progressive closure of the Tethyan seaway (Hamon et al., 2013). These changes led to decreased precipitation over North Africa and South Asia and have been interpreted as precursors to the development of modern desert systems (Zhang et al., 2023). In the Middle East, extensive aridification has been documented by approximately 13 Ma using independent physicochemical proxies (Sun et al., 2021; Xu et al., 2023) (Fig. 10).

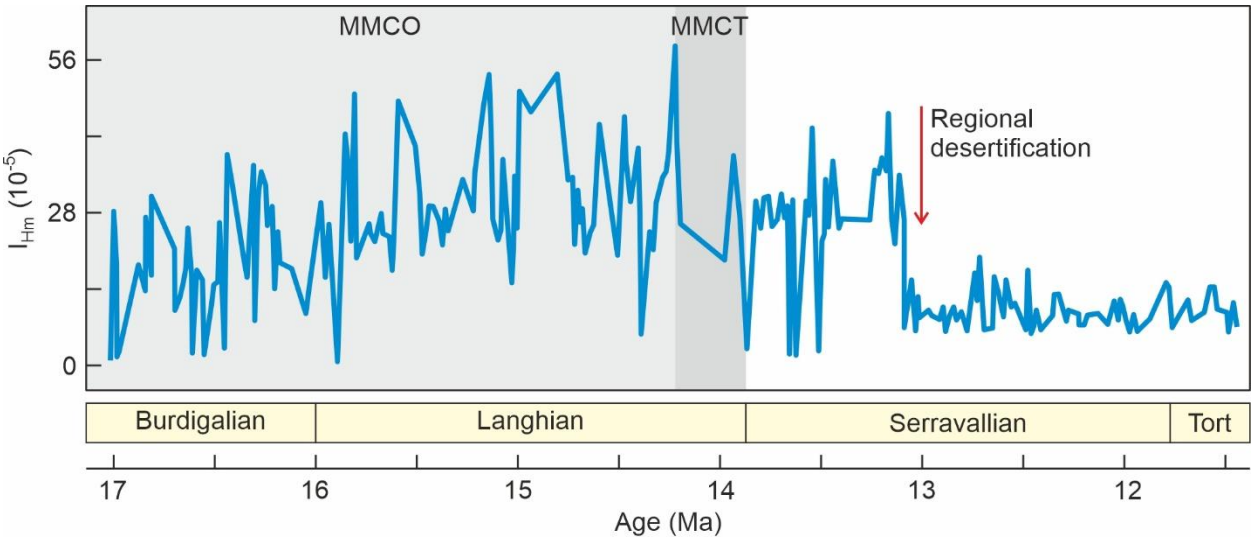

Figure 10. Middle–Late Miocene regional moisture changes reconstructed from magnetite-related sediment color properties in an outcrop of the Qom Formation (Iran) (Fig. 7). MMCO, Middle Miocene Climatic Optimum; MMCT, Middle Miocene Climatic Transition. Redrawn from Xu et al. (2023).

Therefore, the Miocene decline in mangrove diversity in the ME region, with *Avicennia* and *Rhizophora* as the only survivors, may be related to regional desertification, resulting in a situation that parallels present-day bioclimatic and biogeographical patterns. No Pliocene mangrove records were identified, and the occurrence of *Rhizophora* (Fig. 9) is based on a broadly dated Tortonian-Pleistocene record (Bonnefille, 2010).

4.6. Quaternary

The Pleistocene is also nearly absent from the ME mangrove record, and virtually all sequences are Holocene and restricted to the southern and southeastern Arabian Peninsula (Fig. 7). These records contain only *Avicennia* and *Rhizophora*, and most are quantitative pollen records that enable detailed ecosystem reconstructions and comparisons with modern analogs. A characteristic feature of these pollen diagrams is a recurrent Middle Holocene decline in mangrove cover, inferred from pollen percentages, particularly for *Rhizophora*, whereas *Avicennia* remained stable or increased slightly. Currently, *Rhizophora* is absent from most Arabian mangroves, with only two exceptions along the Red Sea and Gulf of Oman coasts (Fig. 6). However, during the Early–Mid Holocene, this mangrove tree was more widely distributed and abundant, reaching pollen percentages of up to 40% (Lézine et al., 2017). The transition to the current situation occurred between 6.5 and 4.5 ka BP, depending on the site (Lézine, 2009; Lézine et al., 2002, 2010, 2017; Fersi et al., 2016).

Some authors consider this a general mangrove collapse event that began in the southern Arabian Peninsula at approximately 6 ka BP (Decker et al., 2020). There is no evidence that this event extended to

the entire ME region, but this possibility merits further investigation. Regarding the causes of this collapse, several explanations have been proposed, including climatic change, sea-level fluctuations and anthropogenic pressure. According to Decker et al. (2020), the most likely cause was a reduction in precipitation and the resulting increase in aridity, linked to a southward shift of the Intertropical Convergence Zone (ITCZ). These authors argue that Holocene climatic variability in Arabia was comparable to that observed in northern Africa, where a poleward shift of the ITCZ led to increased precipitation in the Sahara between approximately 11 and 6 ka BP during a phase known as the African Humid Period (AHP) (deMenocal & Tierney, 2012), followed by aridification and the establishment of the present-day desert conditions.

In the ME region, especially on the Arabian Peninsula, a similar Holocene Humid Period (HHP) has been identified, beginning at approximately 15 ka BP and gradually ending between 7.5 and 4 ka BP (Fersi et al., 2016). Subsequent paleoclimatic reconstructions based on independent physico-chemical proxies dated the termination of the HHP and the establishment of the current arid climate to approximately 6.3 ka BP (Fig. 11) and supported a potential role for the southward migration of the ITCZ (Fleitmann et al., 2021). Within this generally accepted framework, local variations in the duration, intensity and underlying climatic mechanisms are possible (Enzel et al., 2015; Neugebauer et al., 2021). However, the chronological coincidence between the termination of the HHP and the Middle Holocene mangrove disruption strongly supports a potential causal connection.

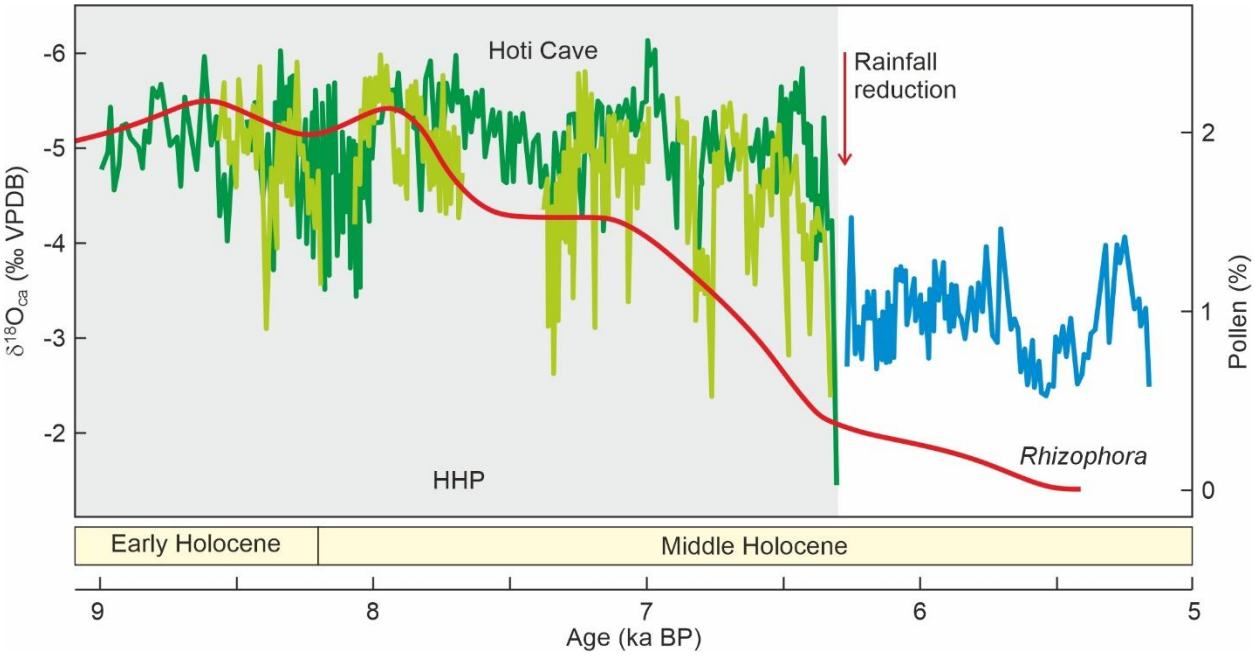

Figure 11. Early–Middle Holocene moisture trends and *Rhizophora* pollen from the Arabian Peninsula. Moisture trends (blue-green tones) reconstructed from oxygen-isotope records in stalagmite calcite from Hoti Cave (Oman) (Fig. 7). Different colors represent different stalagmites from the same cave. *Rhizophora* pollen (red line) from site 92 (Yemen) (Fig. 7). HHP, Holocene Humid Period. Redrawn from Fleitmann et al. (2021) and Fersi et al. (2016).

The potential influence of aridification on the decline of *Rhizophora* (Fig. 11) and the persistence or expansion of *Avicennia* has been analyzed in light of the climatic and environmental niches of these mangrove-forming genera. Lézine (2009) and Lézine et al. (2010, 2017) emphasize that *Rhizophora* grows best in rainy tropical climates with abundant freshwater supply, and that its growth is inhibited by aridity, cool winter temperatures, and high salinity. In contrast, *Avicennia* tolerates a wider range of moisture and salinity conditions and is particularly adapted to hypersaline and evaporitic environments. These authors argue that the disappearance of *Rhizophora* and the persistence of *Avicennia* following the termination of the HHP suggest that a hydrological threshold was reached beyond which climatic conditions and freshwater availability were insufficient for *Rhizophora* to survive.

A more detailed characterization of the climatic niche of *Avicennia* showed that this taxon is highly tolerant of a wide range of temperature and moisture conditions and is limited only by winter frost, rather

than by near-zero annual precipitation values (Quistoudt et al., 2012; Osland et al., 2017). Rull et al. (2026) considered the extant *Avicennia*-dominated mangroves of the Middle East to represent a latitudinal anomaly within the northernmost global belt of Northern Hemisphere mangroves, driven by climatic aridity and its associated ecophysiological consequences.

A word of caution is necessary here, as using a mangrove taxon as a straightforward climatic proxy, or as a component of a climatic index based on its known niche characteristics, may ultimately lead to circular reasoning. For example, Fersi et al. (2016) used the *Rhizophora* percentage curve as a proxy for humidity, whereas Lézine et al. (2017) introduced local and regional aridity indices based on the *Avicennia*/*Rhizophora* and *Artemisia*/*Rhizophora* ratios. These parameters may be useful for comparison with independent paleoenvironmental proxies, but they are unsuitable for investigating the response of vegetation, particularly mangroves, to paleoclimatic and paleoenvironmental changes. Sometimes, circularity may emerge unintentionally, as proxy-based reconstructions can propagate through the literature and become entrenched through repeated use, while their original formulation is gradually forgotten. This is why the risk is always present and should be continuously monitored.

Archaeological evidence shows that ancient societies used and managed mangroves and their associated terrestrial and marine resources (e.g., Berger et al., 2013). However, beyond local impacts, human activities do not appear to have substantially influenced mangrove diversity and biogeography at the regional scale. More recent historical and contemporary activities, such as coastal urbanization, aquaculture and oil pollution, have had a greater impact and have prompted conservation and restoration initiatives. The reader is referred to Meraj et al. (2025) for a comprehensive review.

5. Origin, dispersal and range shifts of individual taxa

The comparison of MESMA with CARMA, EURMA and other less structured datasets can be used to infer the spatiotemporal origins and dispersal/migration patterns of mangrove-forming taxa across the world's major mangrove regions. Considering the earliest fossil appearances of each major true-mangrove component (Table 3), the following patterns can be distinguished:

- *Caribbean origin*. Excluding doubtful identifications from Europe and the ME, *Pelliciera* is an exclusive AEP component that likely originated in the Caribbean during the Eocene. The occurrence of reliable records from western Africa ranging from the Eocene to the Miocene (Rull, 2025) suggests either a potential quasi-synchronous origin or a Caribbean origin followed by rapid migration to western Africa, always within the AEP region.
- *European origin*. The present European continent was the most probable origin of *Avicennia*, whose first appearance occurred at the P/E boundary. From there, *Avicennia* would have dispersed to the ME, likely through coastal migration, during the Early Eocene, and later to the Caribbean and southeastern Asia during the Miocene. These patterns are supported by recent molecular phylogenetic studies (Li et al., 2016; Takayama et al., 2021). Other Rhizophoraceae, such as *Bruguiera* and *Ceriops*, seem to follow similar Europe-centered patterns; however, their fossil record is still too scarce to support firm conclusions.
- *Middle East origin*. *Nypa* is usually considered to have appeared almost simultaneously across the pantropical zone during the Late Cretaceous (e.g., Muller, 1981; Gee, 2001; Srivastava & Prasad, 2019). However, the discovery of a potential *Nypa* precursor in the ME, together with the suggestion of local evolution of this lineage in the study area, points to a possible ME origin followed by rapid eastward and westward dispersal worldwide. This ME–centered scenario is also supported by recent molecular phylogenetic studies (Wu et al., 2024).
- *SE Asia origin*. The earliest *Rhizophora* record dates from the Paleocene of southeastern Asia and dispersed, probably through a combination of migration and LDD, to Europe at the P/E boundary and to the Caribbean during the Middle to Late Eocene. Recent molecular phylogenetic studies also corroborate this view (Lo et al., 2014).
- *Unclear origin*. The case of *Sonneratia* is less clear, due to its almost simultaneous appearance in the Late Paleocene–Early Eocene in Europe and southeastern Asia, together with molecular phylogenetic studies indicating a Middle Eocene IWP origin (He et al., 2022).

Table 3. Earliest fossil appearances of mangrove-forming tree genera (Table 1) shared among two or more major mangrove regions worldwide at any time from the Late Cretaceous to the present. Although not a major component of extant mangroves, *Pelliciera* is included because it was the dominant tree in Eocene Caribbean mangroves (Rull, 2022); however, the possibility of misidentifications in Europe and the Middle East should be considered (Rull, 2025). Raw data are derived from comprehensive compilations, namely CARMA (Rull, 2024), EURMA (Rull, 2026) and MESMA (this work) for the Caribbean, Europe and the Middle East, respectively, and from Thanikaimoni (1978), Muller (1981) and Duke (2017) for southeastern Asia. Age assignments follow the original reports. U, unreported in the region.

Genus	Caribbean (CARMA)	Europe (EURMA)	Middle East (MESMA)	SE Asia
Avicennia	Early-Middle Miocene	Paleocene/Eocene boundary*	Early Eocene	Early Miocene
Bruguiera	U	Early Eocene*	U	Late Miocene
Ceriops	U	Early Eocene*	U	Late Miocene
Nypa	Late Cretaceous*	Paleocene/Eocene boundary	Late Cretaceous*	Late Cretaceous*
Pelliciera	Early Eocene*	Paleocene/Eocene boundary[1]	Middle-Late Eocene[1]	U
Rhizophora	Middle-Late Eocene	Paleocene/Eocene boundary	Oligocene-Early Miocene	Paleocene*
Sonneratia	U	Paleocene/Eocene boundary*	U	Early Eocene

[1]Identification doubtful
*Oldest records worldwide

These preliminary inferences should be tested with the development of new regional datasets (WAFMA and similar). For the time being, these proposals depict a spatiotemporally heterogeneous biogeographical framework, which is more complex than the classical view of a more or less homogeneous pantropical Late Cretaceous mangrove belt, subsequently differentiated by regional AEP/IWP diversification after the emergence of the African barrier (Lo et al., 2014; Duke, 2017).

The widespread geographical distribution of *Nypa* during the Late Cretaceous and the Paleogene, followed by its restriction to its present IWP range, is well known and has been attributed to environmental factors, notably EOT cooling and sea-level fall (Gee, 2001; Pocknall et al., 2023; Rull, 2024). This study provides additional data on the progression of this range contraction. Previous datasets (CARMA and EURMA) recorded the last occurrences of *Nypa* at the Eocene/Oligocene boundary in the Caribbean and in the Oligocene in Europe (Rull, 2024, 2026). In the ME, *Nypa* was also likely extirpated during the EOT, unless a single Miocene record from Egypt is confirmed.

6. Mangroves as ecosystems

As emphasized in earlier reviews, a common misconception in mangrove research using fossils is the inference of mangrove ecosystems from the occurrence of single mangrove taxa. This is the case, for example, in the Late Cretaceous of the Caribbean region, which has been analyzed in detail by the author. Until recently, the occurrence of Late Cretaceous mangroves in the Neotropics had been based solely on *Nypa* records (e.g., Ellison et al., 1999; Srivastava et al., 2019). However, as shown by modern mangrove ecology, these communities are defined by characteristic taxonomic, structural, and zonal features along environmental gradients, notably topography, flooding, and salinity. Thus, a well-defined taxonomic composition and clear zonation exist in Caribbean mangroves from the marine forefront to back-mangrove brackish and freshwater environments, characterized by the succession *Rhizophora–Avicennia–Pelliciera–Acrostichum–Mauritia*. Therefore, the identification of mangrove ecosystems in the fossil record should be based on the occurrence of characteristic taxonomic assemblages associated with environmental gradients.

Using these criteria, the first Caribbean mangroves as ecosystems were documented in the Middle Eocene (>20 million years after the Cretaceous/Paleocene boundary) and were characterized by the assemblage *Pelliciera–Nypa–Acrostichum–Mauritia* (*Rhizophora* and *Avicennia* had not yet reached the region). This assemblage was consistent with a typical mangrove composition and a flooding/salinity gradient (Rull, 2022). The earlier occurrence of *Nypa* alone since the Late Cretaceous was interpreted in terms of brackish-water conditions—characteristic of *Nypa*, which does not tolerate normal marine salinities (Zhang et al., 2024)—but it was considered insufficient to infer typical mangrove communities.

Therefore, it was proposed that the first Caribbean mangroves were not descendants of purported Late Cretaceous *Nypa* mangroves, but ecosystems that originated de novo in the Eocene (Rull, 2022).

This interpretation was made possible by the availability of quantitative pollen data—rather than presence/absence data alone, which represent another common limitation in deep-time paleontological research—which allow comparison with modern analogs. In Europe, similar quantitative studies have identified mangrove communities since the Paleocene/Eocene boundary, composed of *Nypa*, *Rhizophora*, *Sonneratia*, *Avicennia*, *Xylocarpus* and *Excoecaria*. *Nypa* has not been documented in the Cretaceous. In the ME, the situation is similar to that of the Caribbean, with numerous Late Cretaceous qualitative records of *Nypa*, but it differs in taxonomic diversity, with only two mangrove-forming taxa (*Rhizophora* and *Avicennia*) and in the scarcity of quantitative data. Therefore, the identification of mangrove ecosystems is more challenging. The first joint records of a characteristic forefront mangrove-forming taxon, *Avicennia*, and a typical back-mangrove component, *Nypa*, correspond to the Early Eocene of Oman. This could represent the first record of a true mangrove community in the region, but this should be confirmed with further research.

7. Conclusions

Based on the analysis of the MESMA dataset presented here, the following conclusions regarding the origin and development of ME mangroves can be advanced:

Origin. The earliest records of mangroves comparable to those of the present day correspond to *Nypa* and date from the Late Cretaceous. These records have been found on the northeastern Nubian Plate, along the southern shores of the Tethys Sea, well before the Arabian-Eurasian collision. A single older pollen record from the Early Cretaceous (Albian) is also available from the same region and may represent an ancestor of *Nypa*. If confirmed, this would constitute the earliest known record of the *Nypa* lineage and would suggest that the Middle East was the cradle of mangroves worldwide. Most Late Cretaceous *Nypa* records come from continental environments, consistent with the known ecological niche of extant *Nypa*, which inhabits freshwater to low-salinity brackish environments.

Diversification. ME mangroves did not diversify until the Eocene, with the arrival of *Avicennia*, probably from what is now Europe, and *Acrostichum*, whose geographical origin remains unknown. The occurrence of *Pelliciera* in the region has been called into question. This initial diversification coincided with the EECO, a phase characterized by the highest global temperatures and sea levels of the Cenozoic. Nevertheless, ME mangrove diversity remained substantially lower than in proto-Europe, which by that time harbored six additional true-mangrove elements. This is striking because the Tethyan seaway was likely the dispersal route between the IWP core area and Europe, yet no fossil evidence of this migration process has been found in the Middle East.

EOT resilience. Maximum diversity was attained during the Oligocene, at the onset of the Tethyan closure, following the addition of *Rhizophora*, likely originating from the IWP core region. This pattern contrasts with that observed in other mangrove regions, where the environmental disruption associated with the EOT led to significant reductions in mangrove distribution and biodiversity. As in Europe, *Nypa* appears to have survived across the EOT, although this inference is based on a single Miocene record of uncertain identification.

Neogene crisis. The first biodiversity crisis occurred during the Middle Miocene, when only two true mangrove components, *Avicennia* and *Rhizophora*, survived. This took place after the MMCT, a global climatic shift linked to changes in ocean circulation triggered by the closure of the Tethys Sea, whose manifestation in the Middle East was a regional desertification event that began around 13 Ma. Both the onset of regional desertification and the concomitant decline in diversity have been regarded as key precursors of the present-day situation.

Holocene crisis. A second bottleneck occurred much more recently, during the Middle Holocene, when *Rhizophora* underwent a marked decline and became restricted to a few sectors with suitable microenvironmental conditions. This paved the way for the modern ME mangrove configuration, with *Avicennia* as the dominant canopy-forming taxon. The decline of *Rhizophora* coincided with an aridification event that likely crossed a moisture threshold critical for its survival, as this genus requires humid climates and a stable freshwater supply for development. In contrast, *Avicennia* tolerates a wide range of precipitation regimes, including near-zero annual rainfall, as well as hypersaline waterlogged conditions.

Biodiversity and biogeography. Considering the entire history of mangrove occurrence in the ME, this region contrasts with other mangrove-bearing regions worldwide in its low biodiversity, as only four genera of true mangroves (excluding the doubtful *Pelliciera* record) have been identified in the fossil record. Of these, one (*Nypa*) appears to have evolved locally, whereas another (*Avicennia*) likely dispersed from Europe and a third (*Rhizophora*) from Southeast Asia. The origin of the fourth, *Acrostichum*, remains uncertain. These features made the ME region more than merely a biogeographical corridor or barrier-switching zone, as it is often regarded in many studies.

Mangrove ecosystems. Most pre-Quaternary fossil records in the MESMA dataset consist of qualitative presence/absence data, which complicates community reconstructions. If mangroves are considered well-structured ecosystems characterized by distinct taxonomic, architectural, and spatial patterns in relation to environmental gradients, the earliest mangrove communities appear to have emerged during the Early Eocene. This timing coincides with that previously documented in Europe and the Caribbean.

8. Further research

A remaining handicap for the study of ME mangroves is the presence of extensive spatiotemporal gaps in the fossil record. In some cases, these gaps have been attributed to the absence of a Late Cretaceous and Cenozoic stratigraphic record or to the unsuitability of rocks of these ages for preserving mangrove fossils due to environmental constraints. In other cases, however, suitable rocks are present, and the lack of records may reflect research biases or publication restrictions. Given the extensive development of the oil industry in the region and the importance of Cenozoic strata in petroleum systems, it is reasonable to assume that confidentiality issues may play a role.

A message to oil companies is that it is possible to contribute to scientific knowledge without compromising commercial competitiveness through agreed publication strategies. The Caribbean region, a cradle of palynostratigraphy applied to the oil industry, has provided many examples in this regard since the early development of the discipline, including publications such as Kuyl et al. (1955), Hopping (1967), Germeraad et al. (1968), Muller (1981), Lorente (1986) or Muller et al. (1987), among others – see Rull (2024) for a thorough compilation. A contribution of this kind from the Middle East would be not only very welcome but also widely recognized across all sectors, without implying any loss of competitiveness.

If the main information gaps can eventually be bridged, the following points, which have been highlighted throughout this paper, will require special attention:

- The possibility that the *Nypa* lineage evolved in the ME region, as suggested by the presence of a potential *Nypa* precursor in the Albian.
- The continental environments inhabited by Late Cretaceous–Paleocene *Nypa* populations in the northeastern Nubian Plate.
- The absence of fossil records of mangrove elements that were already present in Paleocene–Eocene Europe, despite their presumed dispersal/migration through the ME region.
- The taxonomic enrichment of ME mangroves during the EOT, a time of mangrove reduction and impoverishment in other mangrove-bearing regions worldwide.
- Whether *Nypa* persisted until the Miocene, as suggested by a single pollen record, or disappeared around the EOT, as occurred in Europe and the Caribbean.

- The reason why only *Avicennia* and *Rhizophora* survived the regional desertification that followed the MMCT.
- The occurrence of Pliocene and Pleistocene mangroves and, if present, their composition and geographical extent.
- Whether the so-called Middle Holocene mangrove collapse was restricted to the southern Arabian Peninsula or extended across the entire ME region.
- The reason why *Rhizophora* endured the intense Pleistocene glacial–interglacial cycles but ultimately succumbed to the Middle Holocene aridification event.
- In general, the reason for the low diversity of ME mangroves since their origin, compared with other mangrove regions.

Finally, it is expected that the availability of new and more comprehensive information, both temporally and spatially, will open new avenues of research that we cannot even foresee at present.

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