Middle Miocene Mediterranean mangroves and potential modern analogs

Valentí Rull[1,2], Alba Vicente[2], Isaac Casanovas-Vilar[2]

[1]*Botanic Institute of Barcelona, Spanish National Research Council (CSIC), Pg. del Migdia s/n, 08038 Barcelona, Spain.*
[2]*Institut Català de Paleontologia Miquel Crusafont (ICP-CERCA), Universitat Autònoma de Barcelona, c/Columnes s/n, 08193 Cerdanyola del Vallès, Barcelona, Spain.*

Abstract. During the Miocene Climatic Optimum (MCO; 17–15 Ma), the northern boundary of mangroves – now situated at ~30° N – extended along the northern Mediterranean coasts (~45° N). These *Avicennia*-only mangroves have been considered impoverished mangroves controlled by the general latitudinal temperature gradient. The MCO Mediterranean mangroves have been compared with the extant Middle East (ME) mangroves around the Arabian Peninsula, characterized by the dominance of *Avicennia* and their low diversity. However, these extant communities are not a latitudinal feature but rather an anomaly shaped by extreme environmental conditions (aridity, hypersalinity, sediment supply) that only a few mangrove species can tolerate. In contrast, reconstructed environments for MCO Mediterranean mangroves indicate mild, rainy climates. We conclude that current ME mangroves cannot be considered modern analogs for the MCO Mediterranean mangroves. Finding such modern analogs is challenging, and further studies are recommended to uncover their ecological and biogeographical patterns.

Keywords: Miocene, mangroves, Mediterranean, Middle East, modern analogs, *Avicennia*

Introduction

Currently, the Mediterranean coasts above 30° N latitude are devoid of mangroves, as these ecosystems are restricted to tropical and subtropical latitudes (Spalding et al., 2010). The primary mangrove-forming trees belong to the pantropical genera *Avicennia* and *Rhizophora*, which dominate mangrove ecosystems worldwide (Tomlinson, 2016) (Fig. 1). The distribution of *Rhizophora* and *Avicennia* is largely similar, including their latitudinal boundaries, with two exceptions: the Middle East (ME) in the Northern Hemisphere and New Zealand in the Southern Hemisphere (Fig. 1). *Rhizophora* is rare in the ME and absent in New Zealand/SE Australia, with *Avicennia* dominating the mangroves in both regions.

During the Miocene, particularly during the Miocene Climatic Optimum (MCO; ~17–15 Ma), when global temperatures were 4–8°C higher than today (Westerhold et al., 2020), the northern limit of mangrove distribution extended to the northern Mediterranean coasts (now southern Europe), reaching up to approximately 45° N latitude (Fig. 1). MCO Mediterranean mangroves were dominated by *Avicennia*, while *Rhizophora* and other significant mangrove taxa were absent (Popescu et al., 2021).

Based on the dominance of *Avicennia* and other salt-marsh taxa, the MCO Mediterranean mangroves and the associated coastal vegetation have been regarded as comparable to those growing on the present-day arid or semiarid Middle East (ME), particularly along the coasts surrounding the Arabian Peninsula (Jiménez-Moreno & Suc, 2007; Suc et al., 2021; Popescu et al., 2021). These areas mark the northernmost boundary of mangroves today (Fig. 1). If this comparison is accurate, the extant ME mangroves could serve as modern analogs for the MCO Mediterranean mangroves, which could have significant ecological and evolutionary implications. Nevertheless, this topic has not been thoroughly analyzed from biogeographical and paleoenvironmental perspectives.

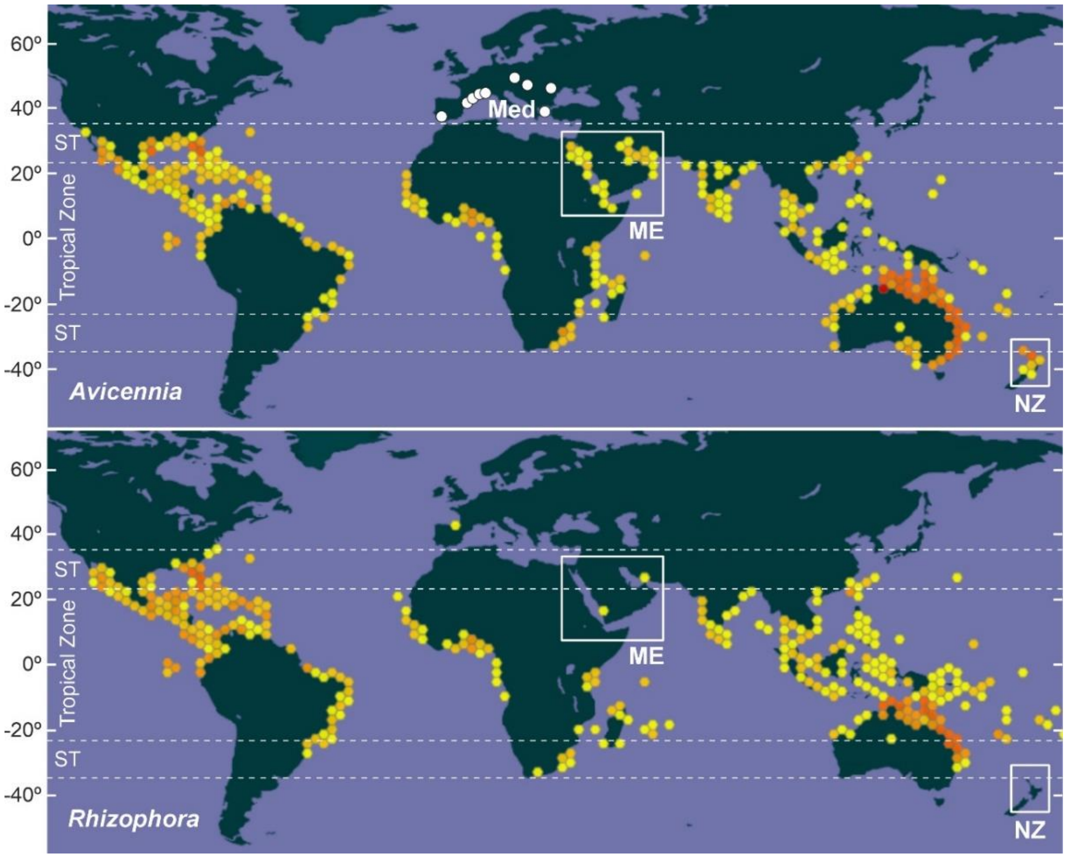

Figure 1. Current worldwide distribution of the main mangrove-forming trees *Avicennia* and *Rhizophora*, represented by red (higher occurrence density) to yellow (lower occurrence density) polygons. Retrieved from the Global Biodiversity Information Facility (GBIF; 5 October 2024), filtered by "human observations", which excludes fossils, botanical gardens, herbaria and other records not based on natural occurrences of living mangroves. The occurrence of *Rhizophora* at the north of the Iberian Peninsula (>40° N) corresponds to a misidentification, as checked in the GBIF database. White dots represent the localities with MCO (Miocene Climatic Optimum; 17-15 Ma) Mediterranean (Med) mangroves, according to Popescu et al. (2021). White boxes indicate the regions where *Avicennia* is the main or the only mangrove-forming tree (ME, Middle East; NZ, New Zealand). ST, Subtropical zones.

This paper aims to show that, despite the dominance of *Avicennia* and their position on the northern edge of mangrove distribution, the extant ME mangroves are unlikely to represent modern analogs of the Miocene Mediterranean mangroves. To support this, we briefly describe the (paleo)environmental features of both mangrove communities and compare these patterns within a global biogeographical perspective. Finally, we explore alternative modern analogs and suggest some further research directions for a more comprehensive assessment.

The MCO Mediterranean mangroves

These *Avicennia*-only mangroves Have been considered impoverished communities located at the northernmost edge of mangrove distribution, following a hypothetical global gradient: from diverse, well-developed mangroves (up to ~35° N) to *Avicennia*-only mangroves (extending to ~70–80° N), with an intermediate zone of diverse yet "scrawny" mangroves between approximately 35° N and 70° N (Popescu et al., 2021). This gradient likely characterized the hothouse Earth conditions (averaging 12–16°C above present-day temperatures) of the Early Eocene Climatic Optimum (EECO; 54–49 Ma), a period when Earth's climate was more equable than today (Sago et al., 2013; Westerhold et al., 2020). During the general Oligocene cooling (icehouse Earth) these mangrove belts could have been more compressed around the Equator.

Some evidence exists for a southward retreat in Europe but the topic is still under study (Popescu et al., 2021). During the MCO, these marginal *Avicennia* mangroves could have expanded poleward again reaching the past northern Mediterranean coasts, spanning a latitudinal range of approximately 15° (30–45° N) (Fig. 1), and based on pollen evidence, may have been dominated by *A. marina* and *A. officinalis* (Popescu et al., 2021).

It was estimated that mean annual temperatures (MAT) at that time were ~18–20°C and that mean annual precipitation (MAP) exceeded 1000 mm in most MCO Mediterranean mangrove areas (Popescu et al., 2021). MCO mangroves in the Iberian Peninsula could have grown under drier climates, with values slightly (in the NE sector) or significantly below (in the SW sector) 1000 mm. It should be noted that these estimates were derived from fossil pollen records (including *Avicennia*) as proxies, assuming a similar climatic niche to that of their modern counterparts. Consequently, this method may introduce bias and lead to circular reasoning if used to infer past mangrove distribution and paleoecology (Rull et al., 2024). Popescu et al. (2021) acknowledge that MCO climatic values derived from pollen may be overestimated, as climate modeling and biomarker data suggest lower values – 11-17°C for MAT and up to 20°C for sea surface temperature or SST (You et al., 2009; Goldner et al., 2011). Similar discrepancies have been observed throughout much of the Cenozoic (Salocchi et al., 2021).

The extant Middle East mangroves

The mangrove extent in the ME is limited, with only one country (Iran) having over 100 km², three (Eritrea, Saudi Arabia, and UAE) exceeding 70 km², and one (Yemen) with approximately 15 km². The remaining countries have less than 10 km², with two (Bahrain and Kuwait) below 1 km² (Bunting et al., 2022). This totals roughly 380 km², representing a mere 0.25% of the global mangrove extent—a comparatively small area alongside other regions of similar size, such as Southeast Asia (~48,200 km²; 33%) or the Caribbean (~14,700 km²; 10%) (Bunting et al., 2022; Rull, 2024).

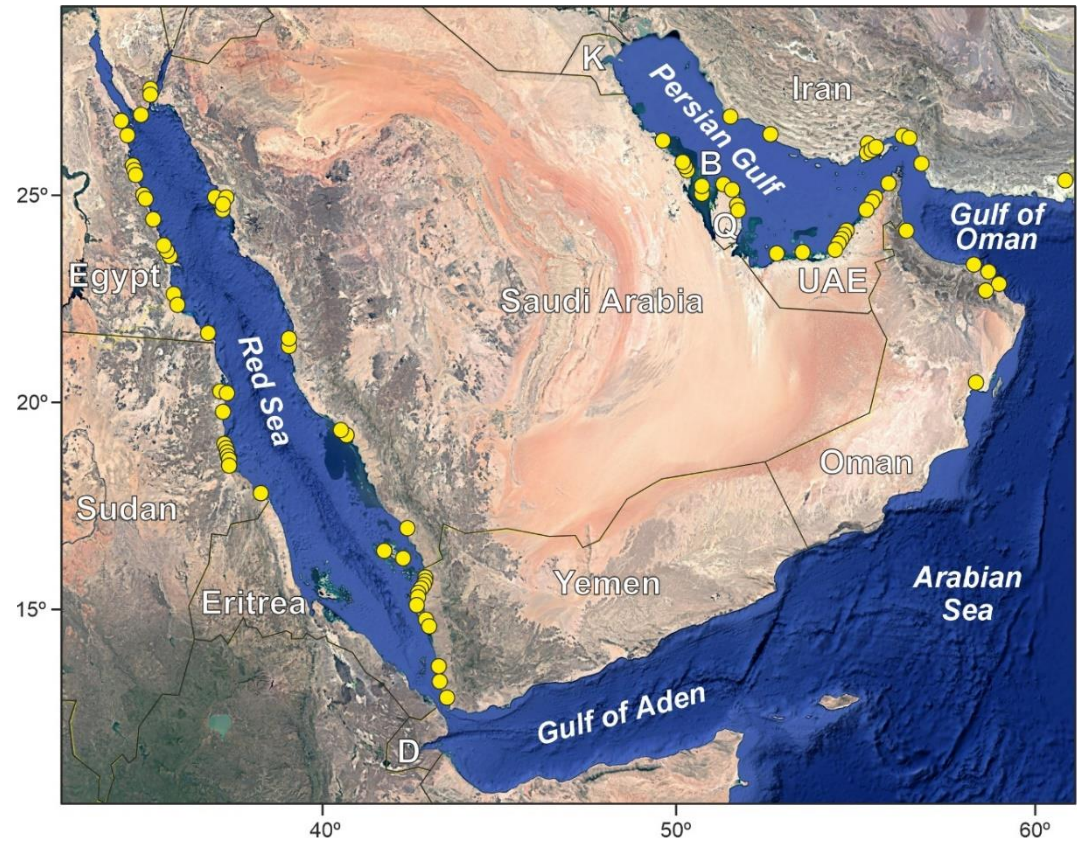

Figure 2. Distribution of mangrove areas (yellow) included in the review by Waleed et al. (2024). The coasts of Eritrea, Djibouti and Kuwait were not included in that study but mangroves follow the same environmental, botanical, and ecological patterns as in the rest of the region (Jawad, 2021). Note the absence of mangroves along the southern coasts of the Arabian Peninsula corresponding to the Gulf of Aden and the Arabian Sea. B, Bahrain; D, Djibouti; K, Kuwait; Q, Qatar; UAE, United Arab Emirates. Base map from Google Earth.

A recent review by Waleed et al. (2024) includes mangroves from most ME countries and can be considered representative of the region (Fig. 2). The most notable environmental conditions in the ME areas are high seawater temperatures (reaching up to 28°C in summer), very low precipitation (less than 100 mm per year, with maximum values around 250 mm), and high evaporation rates, typically ten times greater than precipitation. These extremely hot and arid conditions are generally unfavorable for mangroves (Quisthoudt et al., 2012). Additionally, the lack of large, permanent freshwater flows significantly reduces coastal sediment and nutrient supplies necessary for mangrove growth and creates hypersaline conditions (exceeding 40 ppt) in nearby seas, beyond the tolerance range of most mangrove species (Waleed et al., 2024). MAT are high variable across space, ranging from 20°C in the NW to 30°C in the SE Arabian Peninsula (Patlakas et al., 2019).

Under these conditions, only two highly tolerant mangrove species, out of the more than 50 species known in the Indo-West Pacific (IWP) region (Duke, 2017), are able to survive: *Avicennia marina* and *Rhizophora mucronata*. The first is found in all ME mangroves and consistently dominates the canopy, whereas the second is scarce or absent, occurring only in specific environments with some freshwater input from local streams, which are rare in the region (Waleed et al., 2024). Both *A. marina* and *R. mucronata* exhibit a range of morphological, physiological, reproductive, and phenological adaptations to withstand the challenging environmental conditions of the ME. However, stress from high temperatures, aridity, and limited sediment/nutrient supply restricts tree growth, resulting in dwarf forms of *A. marina* and *R. mucronata* in ME mangroves compared to counterparts of the same species in other IWP regions (Waleed et al., 2024).

In summary, the sparse, dwarf, and low-diversity *Avicennia*-dominated mangroves in the ME are a regional peculiarity driven by aridity and associated environmental constraints (Osland et al., 2017), rather than a feature linked to the global temperature gradient by latitude. Indeed, IWP mangroves located within the same latitudinal range (approximately 10°–30° N) but under more favorable environmental conditions are among the healthiest and most diverse in the pantropical belt (Duke, 2017; Tomlinson, 2016).

Discussion

The available information disclosed above suggests that the existing ME mangroves are unlikely to serve as modern analogs due to their unique, latitude-independent environmental requirements shaping their biogeography and ecology. Indeed, ME mangroves represent a latitudinal anomaly within the global northernmost belt of Northern Hemisphere mangroves. In addition, paleoclimatic reconstructions indicate markedly different environmental conditions during the MCO, when *Avicennia*-only mangroves dominated the northern Mediterranean coasts. The most significant environmental difference is that MCO Mediterranean mangroves did not grow under extremely hot and arid conditions.

Unfortunately, there are no independent records for other related ecological factors, such as hypersalinity – although some studies from the NE Iberian Peninsula do not support the occurrence of hypersaline waters (Bitzer, 2004) – or reduced sediment and nutrient supply. Likewise, pollen evidence alone cannot provide insights into the dwarf nature of mangrove trees. This, coupled with the absence of a current latitudinal belt of *Avicennia*-only mangroves, makes identifying modern analogs for MCO Mediterranean mangroves challenging. Quisthoudt et al. (2012) found that, despite the differing temperature requirements of modern *Rhizophora* and *Avicennia* species (potential niche), there is minimal difference in their northernmost latitudinal boundaries (realized niche) (Fig. 1), likely influenced by local and regional climatic factors, particularly aridity. This factor, along with water salinity and sediment/nutrient availability, is known to significantly impact mangrove distribution and composition (Osland et al., 2017), yet these parameters have not been examined for MCO Mediterranean mangroves.

In summary, based on the available evidence, potential modern analogs for MCO *Avicennia*-only mangroves would have grown in mild and rainy climates. This implies that their taxonomic composition may have differed from that of present-day ME mangroves. Presently, *Avicennia*-only mangroves are found locally on newly formed mud banks, where they serve as temporary pioneers, or in highly saline waters within mangrove ecosystems across tropical and subtropical latitudes (Thatoi et al., 2016). It is possible that MCO mangroves grew in similar conditions, albeit on a regional scale. Further research is required to identify any existing resemblances between past and present *Avicennia* mangroves. Otherwise, the MCO Mediterranean mangroves may lack modern analogs, which is not unusual among mangrove communities that have varied over time, particularly during the Cenozoic (Rull, 2024).

Further research

Based on the above information, several research directions could be proposed: 1) Testing whether the MCO Mediterranean mangroves were the European manifestation of a global phenomenon, a remnant of an assumed Eocene latitudinal gradient, or a regional peculiarity; 2) Reconciling discrepancies among different paleoenvironmental estimates by integrating various proxies (pollen, biomarkers, modeling) and identifying proxies for water salinity and other relevant parameters; 3) Seeking new localities with MCO *Avicennia* mangroves and applying a statistical community approach (Rull et al., 2024) at a regional scale to reconstruct these communities, rather than relying on the untested notion of community constancy over time. It should also be noted that most Miocene fossil pollen types are identified only to the genus or family level, overlooking the specific requirements of species and their populations, which are the actual entities that respond individually to environmental changes. It would also be highly beneficial to complement the information provided by pollen with potential insights from the fauna associated with MCO Mediterranean mangroves, both at the species and community levels, to achieve more comprehensive ecosystem and environmental reconstructions. Finally, comparisons with the *Avicennia*-only New Zealand mangroves, despite their location at the southernmost mangrove boundary on the Mediterranean antipodes, and their temperate climates, should not be disregarded. According to Osland et al. (2017) the main driver for mangrove distribution and diversity in New Zealand and SE Australia is temperature minima, which is a latitudinally-dependent feature.

References

Bitzer, K. 2004. Estimating paleogeographic, hydrological and climatic conditions in the upper Burdigalian Vallès-Penedès basin (Catalunya, Spain). Geologica Acta 2, 321-331.

Bunting, P., Rosenqvist, A., Hilarides, L., Lucas, R.M., Thomas, N.Tadono, T., et al. 2022. Global mangrove extent change 1996-2020: Global Mangrove Watch version 3.0. Remote Sensing 14, 3657.

Duke, N.C. 2017. Mangrove floristics and biogeography revisited: further deductions from biodiversity hot spots, ancestral discotinuities, and common evolutionary processes. In: Rivera-Monroy, V.H. et al. (eds.), Mangrove Ecosystems: A Global Biogeographic Perspective. Springer, Berlin, pp. 17–53.

Goldner, A., Herold, N., Huber, M. 2014. The challenge of simulating the warmth of the mid-Miocene climatic optimum in CESM1. Climate of the Past, 10, 523–536.

Jawad, L.A. 2021. The Arabian Seas: Biodiversity, Environmental Challenges and Conservation Measures. Springer Nature, Cham.

Jiménez-Moreno, G., Suc, J.-P. 2007. Middle Miocene latitudinal climatic gradient in Western Europe: evidence from pollen reccords. Palaeogeography, Palaeoclimatology, Palaeoecology 253, 208–225.

Osland, M.J., Feher, L.C., Griffith, K.T., Cavanaugh, K.C., Enwright, N.M., Day, R. H., et al. 2017. Climatic controls on the global distribution, abundance, and species richness of mangrove forests. Ecological Monographs 87, 341-359.

Patlakas, P., Stathopoulos, C., Flocas, H., Kalogeri, C., Kallos, G. 2019. Regional climatic features of the Arabian Peninsula. Atmosphere 10, 220.

Popescu, S.-M., Suc, J.-P., Fauquette, S., Bessedik, M., Jiménez-Moreno, G., Robin, C., et al. 2021. Mangrove distribution and diversity during three Cenozoic thermal maxima in the Northern Hemisphere (pollen records from the Arctic-North Atlantic-Mediterranean regions). Journal of Biogeography 48, 2771–2784.

Quisthoudt, K., Schmitz, N., Randin, C.F., Dahdouh-Guebas, F., Robert, E.M.R., Koedam, N. 2012. Temperature variation among mangrove latitudinal range limits worldwide. Trees 26, 1919–1931.

Rull, V. 2024. Origin and Evolution of Caribbean Mangroves. Springer Nature, Cham.

Rull, V., Alba, D., Casanovas-Vilar, I. 2024. Middle Miocene vegetation of the Vallès-Penedès Basin (NE Iberian Peninsula), as inferred from fossil pollen records: state of the art and fututre prospects. Review of Palaeobotany and Palynology 321, 105042.

Sago, N., Valdes, P., Flecker, R., Gregoire, L.J. 2013. The early Eocene equable climate problem: can perturbations of climate model parameters identify possible solutions? Philosophical Transactions of the Royal Society A 371, 20130123.

Salocchi, A.C., Krawielicki, J., Eglinton, T.I., Fioroni, C., Fontana, D., Conti, S., et al. 2021. Biomarker constraints on Mediterranean climate and ecosystem transitions during the Early-Middle Miocene. Palaeogeography, Palaeoclimatology, Palaeoecology 562, 110092.

Spalding, M., Kainuma, M., Collins, L. 2010. World Atlas of Mangroves. Routledge, London.

Suc, J.-P., Popescu, S.-M., Fauquette, S., Bessedik, M., Jiménez-Moreno, G., Bachiri Taoufiq, N., et al. 2018. Reconstruction of Mediterranean flora, vegetation and climate for the last 23 million years based on an extensive pollen dataset. Ecologia Mediterranea 44, 53-85.

Thatoi, H., Samantaray, D., Das, S.K. 2016. The genus *Avicennia*, a pioneer group of dominant mangrove plant species with potential medicinal values: a review. Frontiers in Life Science 9, 267–291.

Tomlinson, P.B. 2016. The Botany of Mangroves. Cambridge University Press, Cambridge.

Waleed, W.A., Abdel-Maksoud, Y.K., Kanwar, R.S. Sewilam, H. 2024. Mangroves in Egypt and the Middle east: current status, threats, and opprotunities. International Journal of Environmental Science and Technology, doi 10.1007/s13762-024-05788-1.

Westerhold, T., Marwan, N. Drury, A.J., Liebrand, D., Agnini, G., Anagostou, E., et al. 2020. An astronomically dated record of Earth's climate and its predictability over the last 66 million years. Science 369, 1383–1387.

You, Y., Hubern, M., Müller, R. D., Poulsen, C. J., Ribbe, J. 2009. Simulation of the Middle Miocene climate optimum. Geophysical Research Letters, 36, L04702.