



On the use of extant Middle-East mangroves as modern analogues for Miocene Mediterranean-Paratethyan mangroves

Valentí Rull^{1,2} · Alba Vicente² · Johannes M. Bouchal^{3,4} · Isaac Casanovas-Vilar²

Received: 9 April 2025 / Revised: 23 September 2025 / Accepted: 24 November 2025 / Published online: 4 February 2026
© The Author(s) 2026

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-Paratethyan (M-P) coasts (~45° N). These *Avicennia*-only mangroves have been considered impoverished mangroves controlled by the general latitudinal temperature gradient. They have also been compared with the extant Middle East (ME) mangroves around the Arabian Peninsula, characterised 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 palaeoenvironments for MCO M-P mangroves indicate mild rainy climates. Currently, *Avicennia* (represented by *A. marina*) is mainly tropical and its latitudinal boundaries are characterised by warm-temperate, humid climates with frost-free mild winters. We conclude that current ME mangroves cannot be considered modern analogues for the MCO M-P mangroves. Finding such modern analogues is challenging, and further studies are recommended to uncover their ecological and biogeographical patterns.

Keywords Miocene · Mangroves · Mediterranean · Paratethys · Middle East · Modern analogues · *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-Paratethyan (M-P) coasts (now central and southern Europe), reaching up to approximately 45° N latitude (Fig. 1). The MCO M-P mangroves were dominated by *Avicennia*, while *Rhizophora* and other significant mangrove taxa were absent (Plaziat et al. 2001; Popescu et al. 2021).

Based on the dominance of *Avicennia* and other salt-marsh taxa, the MCO M-P 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 and Suc 2007; Suc et al. 2018; 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

✉ Alba Vicente
alba.vicente@icp.cat; avicenro@gmail.com

¹ Botanic Institute of Barcelona, Spanish National Research Council (CSIC), Barcelona, Spain

² Institut Català de Paleontologia Miquel Crusafont (ICP-CERCA), Universitat Autònoma de Barcelona, Cerdanyola del Vallès, Barcelona, Spain

³ Department of Botany and Biodiversity Research, University of Vienna, Vienna, Austria

⁴ AZ Pollen Research (AZPR), Stockerau, Austria

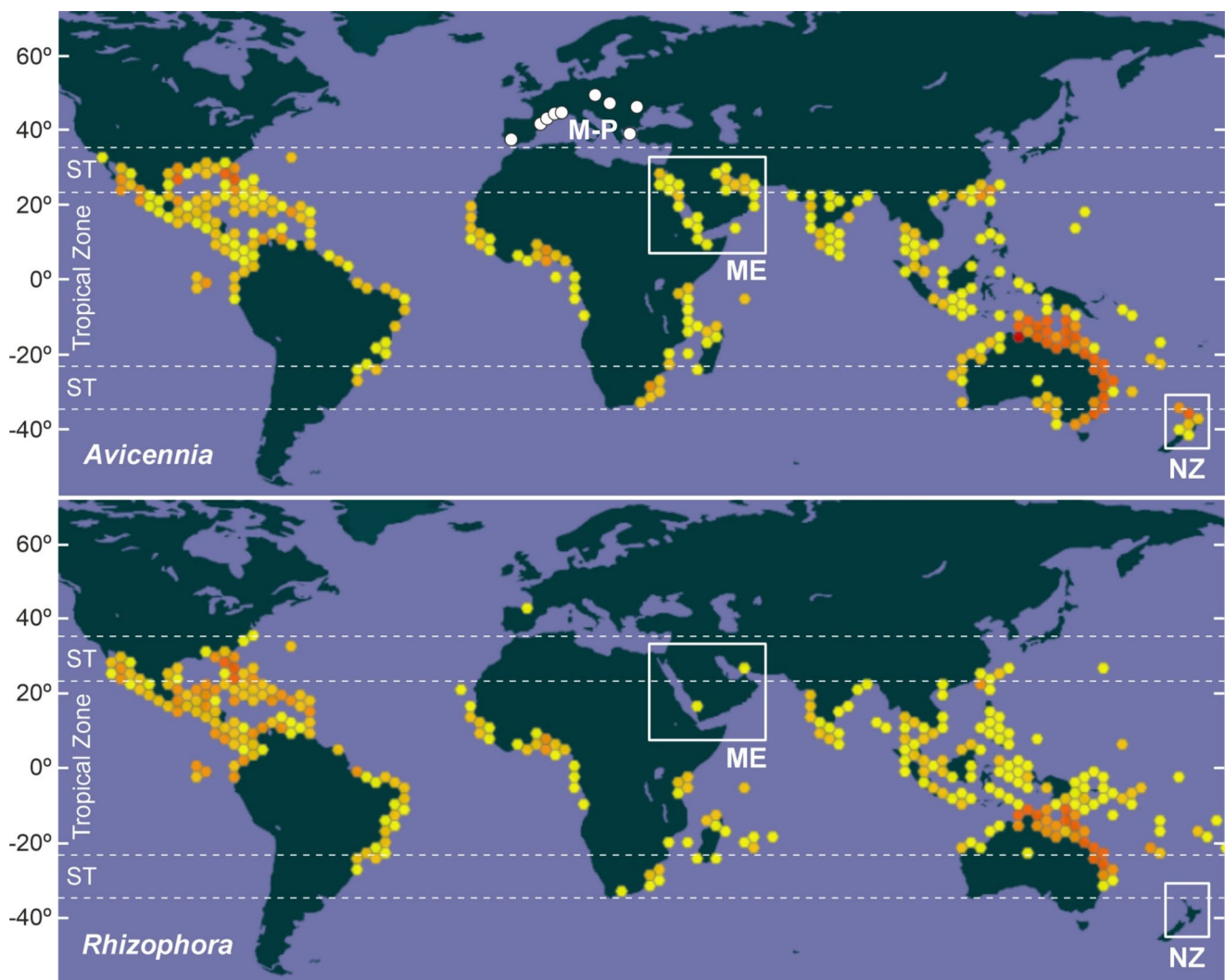


Fig. 1 Current worldwide distribution of the main mangrove-forming trees *Avicennia* and *Rhizophora*, represented by red (higher occurrence density) to yellow (lower occurrence density) polygons. Retrieved from the Global Biodiversity Information Facility (GBIF; 5 October 2024), filtered by “human observations”, 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 ($>40^{\circ}$ 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-Paratethyan (M-P) 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

serve as modern-analogue communities, in terms of latitudinal distribution and environmental requirements, for the MCO M-P mangroves, which could have significant ecological and evolutionary implications. Nevertheless, this topic has not been thoroughly analysed from biogeographical and palaeoenvironmental perspectives.

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 analogues of the Miocene M-P mangroves. To support this, we briefly describe the (palaeo)environmental features of both mangrove communities and compare these patterns within a global biogeographical perspective.

Finally, we explore alternative modern analogues and suggest some further research directions for a more comprehensive assessment.

The MCO Mediterranean-Paratethyan 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 $\sim 35^{\circ}$ 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 characterised 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 northern M-P 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 M-P mangrove areas (Popescu et al. 2021). MCO mangroves in the Iberian Peninsula could have grown under drier climates (see also Postigo-Mijarra et al. 2009 and Barrón et al. 2010) 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 the same climatic niche to that of their modern counterparts (niche conservancy), which remains untested. Consequently, this method may introduce bias and lead to circular reasoning if used to infer past mangrove distribution and palaeoecology (review in 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 of 11–17 °C for MAT and up to 20 °C for sea surface temperature or SST (You et al. 2009; Goldner et al. 2014). 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).

A recent review by Waleed et al. (2025) 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; Supplementary Information 1.1), and high evaporation rates, typically ten times greater than precipitation. These extremely hot and arid conditions are generally unfavourable 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. 2025). MAT are highly variable geographically, ranging from 20 °C in the NW to 30 °C in the SE Arabian Peninsula (Patlakas et al. 2019).

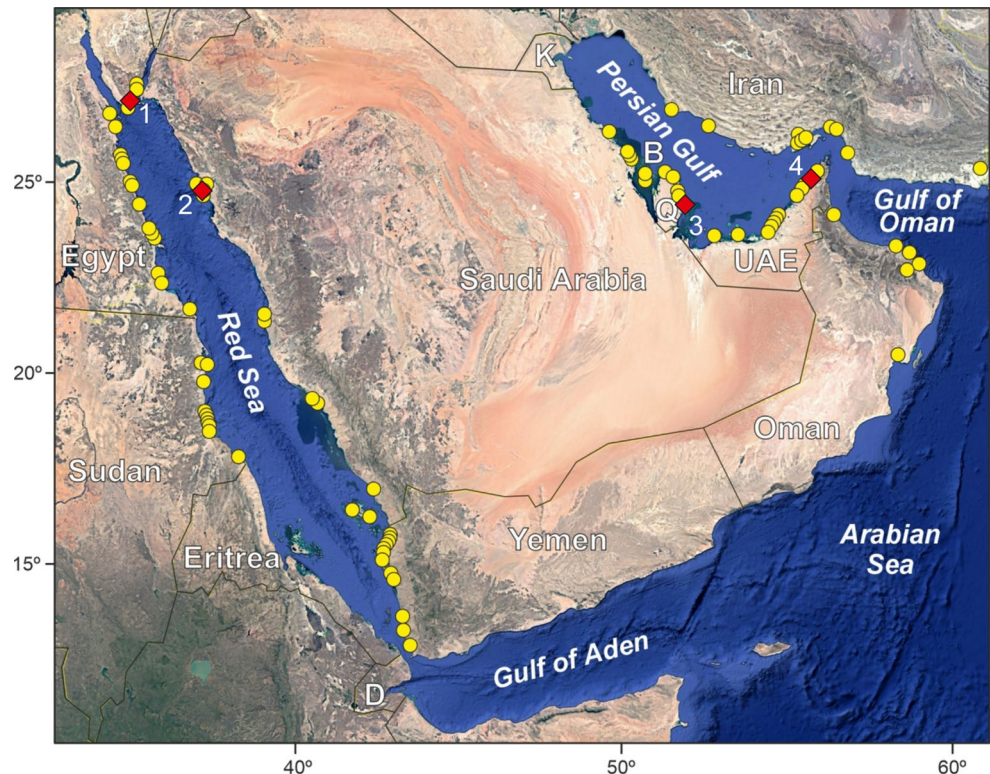
Under these conditions, only two highly tolerant mangrove species, out of the more than 50 species known in the Indo-West Pacific (IWP) region (Duke 2017), are able to survive: *Avicennia marina* and *Rhizophora mucronata*. The first is found in all ME mangroves and consistently dominates the canopy, 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. 2025). 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. 2025).

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 favourable environmental conditions are among the healthiest and most diverse in the pantropical belt (Duke 2017; Tomlinson 2016).

Climatic niche of extant *Avicennia marina*

The current geographical and climatic ranges of *Avicennia* can shed light on the climatic factors that limit its occurrence and define its latitudinal boundaries. The widest latitudinal distribution corresponds to *A. marina*, which is the dominant

Fig. 2 Distribution of mangrove areas (yellow) included in the review by Waleed et al. (2025). 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. Countries: B Bahrain; D Djibouti; K Kuwait; Q Qatar; UAE United Arab Emirates. Base map from Google Earth. Meteorological stations (red diamonds; see Supplementary Information 1.1): 1 Sharm el Sheikh; 2 Hanak; 3 Doha; 4 Um al-Qaiwain



in the ME mangroves and one of the species (along with *A. officinalis*) suggested to have inhabited the M-P MCO mangroves, as noted above. The geographical distribution and climatic variables used in this study for *A. marina* were retrieved from the GBIF and WorldClim databases (see Supplementary Information 1.3 for methods and Supplementary Information 2 for data). According to these data, the latitudinal boundaries of the species are 29.32° N (Kuwait) and 41.25° S (New Zealand), and the main climatic parameters characterising its distribution are shown in Table 1.

The temperature and precipitation ranges for *A. marina* are remarkably broad, with mean annual temperatures (MAT) spanning ~10–31 °C and total annual precipitation (TAP) ranging from ~3–4550 mm. These values highlight the species' high climatic tolerance. In contrast to the hot

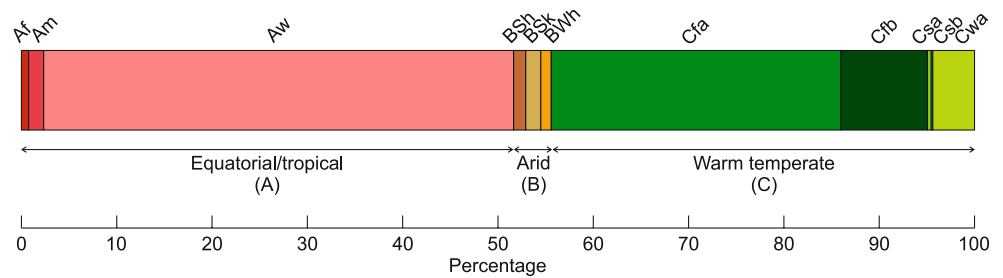
and arid ME climates described above, the southernmost distribution limits occur in temperate, wetter regions with mild winters (see Supplementary Information 1.2). Notably, the minimum temperature of the coldest month (mTCM) reaches 1 °C, suggesting that seasonal frost acts as a limiting factor for *A. marina* (Osland et al. 2017). With respect to precipitation, this species can persist under near-zero rainfall, as observed in ME mangroves. According to the Köppen–Geiger climatic classification (Supplementary Information 1.4), *A. marina* occurs across equatorial/tropical (A), arid (B) and warm temperate (C) climates (Fig. 3).

The climates with the highest number of *A. marina* occurrences are equatorial/tropical (A), accounting for ~52% of cases, and warm temperate (subtropical/temperate), with ~44%. The former (Af, Am, Aw) correspond to the tropical core of the species' distribution, whereas the latter are more characteristic of subtropical (Cfa, Csa, Cwa) and temperate (Cfb, Csb) latitudes, including the distribution boundaries. Arid climates (BSh, BSk, BWh), with only ~4% of total occurrences, are exceptional within the species' geographical range. Its persistence under such conditions is likely attributable to the broad hydroclimatic tolerance of *A. marina* compared with other mangrove species (Quisthoudt et al. 2012). The absence of climate types with seasonal or permanent frost—i.e. temperate (Cfc, Csc, Cwc), snow (D), and polar (E) climates—further reinforces the limiting role of this factor in the distribution of *A. marina*.

Table 1. Main temperature and precipitation parameters for the climatic niche of *Avicennia marina*. MAT, mean annual temperature; mTCM, minimum temperature of the coldest month; TAP, total annual precipitation; PDQ, precipitation of the driest quarter (the three-month season with lowest precipitation). Raw data in the Supplementary Information.

	MAT (°C)	mTCM (°C)	TAP (mm)	PDQ (mm)
Minimum	10.07	1.00	3	0
Average	23.28	13.43	1234	32
Maximum	30.86	24.80	4553	215

Fig. 3 Köppen–Geiger climatic types suitable for *Avicennia marina* growth expressed as percentage occurrences. *Af* rainforest (fully humid); *Am* monsoonal (seasonal); *Aw* savannah (dry winter); *BSh* steppe (hot and arid); *BSk* steppe (cold and arid); *BWh* desert (hot and arid); *Cfa* fully humid (hot summer); *Cfb* fully humid (warm summer); *Csa* hot and dry summer; *Csb* warm and dry summer (Mediterranean); *Cwa* hot summer and dry winter



In summary, *A. marina* thrives across a wide range of climatic conditions, both within its core distribution and at its latitudinal boundaries. Its core range is tropical, whereas the northern and southern limits are predominantly subtropical/temperate rainy and frost-free, with only a very small proportion occurring in locally arid climates. This pattern supports the view that the peculiarities of ME mangroves represent a latitudinal anomaly.

Discussion

The available information disclosed above suggests that the existing ME mangroves are unlikely to serve as modern analogues 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, palaeoclimatic 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 M-P 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 analogues for MCO M-P 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 (realised 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 M-P mangroves.

In summary, based on the available evidence, potential modern analogues for MCO *Avicennia*-only mangroves would have grown in mild and rainy climates. 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 M-P mangroves may lack modern analogues, which is not unusual among mangrove communities that have varied over time, particularly during the Cenozoic (Rull 2024). In palaeoecology, past communities with no modern analogues are not uncommon, even during the Quaternary, when extant species were already present (Jackson and Williams 2004; Williams and Jackson 2007).

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 palaeoenvironmental 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 M-P 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.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s12549-025-00693-y>.

Acknowledgements The reviewers contributed to the improvement of the manuscript.

Funding Open Access funding provided thanks to the CRUE-CSIC agreement with Springer Nature. Generalitat de Catalunya/CERCA Programme, AGAUR (2021 SGR 00620), Leonardo 2024 Fundación BBVA grant, and project PID2020/117289GB-I00/AEI/10.13039/501100011033, funded by the Agencia Estatal de Investigación of the Ministerio de Ciencia e Innovación (Spain) to I.C.-V. and AGAUR Beatriz de Pinós contract to A.V. (2022 BP 00179).

Data availability Data are available in the Supplementary Information 2.

Declarations

Conflict of interest The authors declare no conflicts of interest.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Barrón, E., Rivas-Carvalho, R., Postigo-Mijarra, J. M., Alcalde-Olivares, C., Vieira, M., Castro, L., Pais, J., & Valle-Hernández, M. (2010). The Cenozoic vegetation of the Iberian Peninsula: A synthesis. *Review of Palaeobotany and Palynology*, 162, 382–402.
- 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., Worthington, T. A., Spalding, M., Murray, N. J., & Robelo, L.-M. (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 discontinuities, and common evolutionary processes. In V. H. Rivera-Monroy, S. Y. Lee, E. Kristensen, & R. R. Twilley (Eds.), *Mangrove ecosystems: A global biogeographic perspective* (pp. 17–53). Cham: Springer.
- 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.
- Jackson, S. T., & Williams, J. W. (2004). Modern analogs in Quaternary paleoecology: here today, gone yesterday, gone tomorrow? *Annual Reviews of Earth and Planetary Sciences*, 32, 496–537.
- Jawad, L. A. (2021). *The Arabian Seas: Biodiversity, environmental challenges and conservation measures*. Cham: Springer Nature.
- Jiménez-Moreno, G., & Suc, J.-P. (2007). Middle Miocene latitudinal climatic gradient in Western Europe: evidence from pollen records. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 253, 208–225.
- Osland, M. J., Feher, L. C., Griffith, K. T., Cavanaugh, K. C., Enwright, N. M., Day, R. H., Stagg, C. L., Krauss, K. W., Howard, R. J., Grace, J. B., & Rogers, K. (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.
- Plaziat, J.-C., Cavagnetto, C., Koeninger, J.-C., & Baltzer, F. (2001). History and biogeography of the mangrove ecosystem, based on a critical reassessment of the paleontological record. *Wetlands Ecology and Management*, 9, 161–179.
- Popescu, S.-M., Suc, J.-P., Fauquette, S., Bessedik, M., Jiménez-Moreno, G., Robin, C., & Labrousse, L. (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.
- Postigo-Mijarra, J. M., Barrón, E., Gómez Manzanique, F., & Morla, C. (2009). Floristic changes in the Iberian Peninsula and Balearic Islands (south-west Europe) during the Cenozoic. *Journal of Biogeography*, 36, 2025–2043.
- 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.
- 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 future 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., & Picotti, V. (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.
- Suc, J.-P., Popescu, S.-M., Fauquette, S., Bessedik, M., Jiménez-Moreno, G., Bachiri Taoufiq, N., Zheng, Z., Médail, F., & Klotz, S. (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.
- Waleed, W. A., Abdel-Maksoud, Y. K., Kanwar, R. S., & Sewilam, H. (2025). Mangroves in Egypt and the Middle east: current status, threats, and opprotunities. *International Journal of Environmental Science and Technology*, 22, 1225–1262.
- Westerhold, T., Marwan, N. Drury, A. J., Liebrand, D., Agnini, G., Anagostou, E., Barnet, J. S. K., Bohaty, S. M., De Vleeschouwer, D., Florindo, F., Frederichs, T., Hodell, D. A., Holbourn, A. E., Kroon, D., Lauretand, V., Littler, K., Lourens, L. J., Lyle, M., Pälike, H., Röhl, U., Tian, J., Wilkens, R. H., Wilson, P. A., & Zachos, J. C. (2020). An astronomically dated record of Earth's climate and its predictability over the last 66 million years. *Science*, 369, 1383–1387.
- Williams, J. W., & Jackson, S. T. (2007). Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment*, 5, 475–482.
- 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.

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.