Lethaia
AN INTERNATIONAL JOURNAL OF PALAEONTOLOGY AND STRATIGRAPHY

Challenges in using modern pollen analogues for Cenozoic palaeoecology: examples from the European Neogene

VALENTÍ RULL

LETHAIA

The use of modern pollen analogues in palaeoecology is well established in Quaternary studies; however, the reliability of this approach decreases with increasing geological age due to evolutionary changes. Establishing a definitive chronological boundary beyond which modern pollen analogues remain reliable is currently problematic. This limitation affects not only palaeoenvironmental reconstructions based on the niche conservatism hypothesis for individual extant species, but also community- and biome-level reconstructions that assume compositional and environmental constancy over time. This paper discusses four case studies from the European Neogene—focusing on individual species, communities, and biomes—where the use of modern pollen analogues under the untested assumption of niche conservatism is common. These studies include: (1) quantitative palaeoclimatic estimates using the climatic envelope of extant species; (2) comparisons between Middle Miocene European mangroves and present-day Middle-East mangrove communities; (3) the use of *Artemisia* pollen as an indicator of dry steppe biomes; and (4) the occurrence of taxodiaceous coastal marsh forests in Europe after the Miocene Climatic Optimum. The main conclusion is that assuming species' niche conservatism and extrapolating this assumption to communities and biomes is unwarranted and may lead to unsupported conclusions. Therefore, empirical testing of species' niche conservatism across the relevant time spans is essential. Alternative and complementary methods—such as the fossil community approach and the use of pollen-independent proxies (e.g. stable isotopes, biomarkers)—are strongly recommended. ☐ *Modern analogues, niche conservatism, palaeoclimatology, communities, biomes, Europe, Neogene*

Valentí Rull ✉ [vrull@csic.es], Spanish National Research Council (CSIC), Botanic Institute of Barcelona, Pg. del Migdia s/n, 08038 Barcelona, Spain and Institut Català de Paleontologia Miquel Crusafont (ICP-CERCA), Universitat Autònoma de Barcelona, c/Columnes s/n, 08193 Cerdanyola del Vallès, Barcelona, Spain; *manuscript received on 05/05/2025; manuscript accepted on 25/09/2025; manuscript published on 23/12/2025 in Lethaia 59*(1).

The use of modern pollen analogues is common in Quaternary palaeoecology and palaeoclimatology, based on the assumption that the ecological and environmental requirements of extant species have remained constant over the last ~2.6 million years (e.g. Birks & Birks 1980; Delcourt & Delcourt 1991; Cronin 2009; Bradley 2015; Rull 2020). This assumption has led to detailed quantitative estimates of climatic and other environmental parameters using transfer functions, which apply the environmental envelope of extant species to fossil pollen taxa (Birks *et al.* 2012). However, this assumed niche constancy—also known as niche conservatism (Wiens *et al.* 2010)—declines over time due to evolutionary processes, progressively reducing the likelihood of finding reliable modern analogues for fossil pollen taxa. Therefore, niche-conservatism uncertainty (NCU) increases with time, and a chronological boundary for the reliability of modern analogues beyond the Quaternary has not yet been established (Fauquette 2017; Matthaeus *et al.* 2023).

In spite of this, the use of modern analogue approaches in Cenozoic palaeoecology and palaeoclimatology remains common. These methods range from detailed palaeoclimatic estimates to reconstructions of past community and biome dynamics, based on the additional assumption that extant communities and biomes have also remained compositionally and environmentally stable over time. The concept of compositional stability also emerged from Quaternary studies (Prentice *et al.* 1996; Ni *et al.* 2010) and was later adopted for the Neogene (e.g. Mahler *et al.* 2022; Altoaguirre *et al.* 2023). Some macroecological surveys support this perspective. For example, phylogenetic niche conservatism—the tendency of lineages to retain niche-related traits through speciation events (Crisp & Cook 2012), or the retention of ecological traits over time among related species (Wiens *et al.* 2010)—has been considered a major factor structuring vegetation types and biomes globally (Crisp *et al.* 2009). Similar results

https://doi.org/10.18261/let.59.1.8

have been reported for the European Cenozoic (Lososová *et al.* 2020).

However, these studies rely on phylogenetic inference and modelling, rather than empirical palaeontological evidence, and do not resolve the NCU conundrum, neither for species' niche traits nor for community or biome composition. Therefore, assuming niche conservatism across taxonomic, geographical, and temporal scales is unwarranted and may lead to questionable past ecological and biogeographical reconstructions. As a consequence, modern analogue approaches that uncritically adopt niche conservatism as a premise should be approached with caution.

Among the many examples in the literature that rely on these assumptions, we have selected four from the European Mediterranean Neogene including inferences involving individual species, communities and biomes. The first case relies on the assumption of climatic niche conservatism of extant species to quantitatively estimate Neogene climates, particularly palaeotemperature and palaeoprecipitation, which has been widely used in Europe (Utescher *et al.* 2014; Suc *et al.* 2018). The second example is the use of modern mangrove communities from the Middle East as modern analogues for those that existed along the northern Mediterranean coasts during the Middle Miocene Climatic Optimum (MMCO) (Plaziat *et al.* 2001; Popescu *et al.* 2021). This case was chosen in light of a recent study that provides a detailed description of Middle East mangroves and their environmental context (Waleed 2024). The third example concerns the widespread use of *Artemisia* fossil pollen as a straightforward indicator of temperate, mostly cold and arid, steppe biomes (Zagwijn 1960; Suc 1984). This case is revisited in response to a recent thorough study on *Artemisia* pollen morphology and the broad range of biomes inhabited by species of this genus (Lu *et al.* 2022). Finally, Bouchal & Denk (2020) recently questioned the reliability of distinguishing *Taxodium/Glyptostrobus* (Cupressaceae) pollen and, consequently, the inference of taxodiaceous coastal marsh forests in Europe after the MMCO.

The main aim of this discussion is to highlight the need to avoid using unsupported general modern-analogue assumptions as premises for interpreting past ecosystems and their environmental features. The intention is not to dismiss the use of modern-analogue approaches, but rather to improve their reliability by taking into account the specific characteristics of each taxon and community under study. A comprehensive review of the subject is beyond the scope of this paper, which focuses on specific case studies from the currently defined European continent.

Species level: palaeoclimatic estimates

Pollen-based Cenozoic palaeoclimatic estimates using modern analogue approaches—such as the widely used Coexistence Approach (Mosbrugger & Utescher 1997) or the Climate Amplitude Method (Fauquette *et al.* 1998), among others—assume climatic niche conservatism in individual species and community constancy over evolutionary timescales. In this framework, precise quantitative estimates of past climatic variables are obtained from fossil taxa that share pollen morphology with extant species—known as nearest living relatives (NLRs)—by transferring the climatic envelope of these NLRs to their assumed fossil representatives. These methods have been challenged from both theoretical and practical perspectives.

Theoretically, the assumptions of niche conservatism and community constancy have been considered unrealistic, as they remain empirically untested in most reconstructions. Testing climatic niche conservatism requires independent palaeoclimatic and palynological evidence. Non-empirical methods—such as molecular phylogenetic inference and species distribution modelling—suggest that the presence or absence of niche conservatism in plants throughout the Cenozoic depends on both the geological timescale and the taxa under study, with no general rule being universally applicable (e.g. Svenning 2003; Abbink *et al.* 2004; Byrstriakova *et al.* 2011; Loera *et al.* 2012; Martín-Hernanz *et al.* 2014; Weeks *et al.* 2014; Benítez-Benítez *et al.* 2017; Zhang *et al.* 2021; Vieira *et al.* 2023; Qian *et al.* 2024; Quirk *et al.* 2024; Fernández-Mazuecos & Glover 2025; Liu *et al.* 2025). Therefore, niche conservatism in the target taxa over the time interval of interest cannot be assumed a priori.

Concerns have also been raised about the establishment of reliable botanical affinities, which largely depends on the taxonomic resolution achievable in the fossil pollen record—typically at the genus or family level—compared to NLRs. This is especially critical in genera and families with homogeneous pollen morphology. Another drawback is that modern-analogue-based methods implicitly overlook the possibility that extinct species, as well as species originated after the time interval under study, with the same pollen morphology that extant taxa may be present in fossil assemblages. Additionally, the potential for modern-analogue approaches to result in circular reasoning when studying vegetation responses to climate shifts has been highlighted. Reviews and discussions addressing these issues can be found in Grimm & Potts (2016), Lu *et al.* (2022); Matthaeus *et al.* (2023), Quirk *et al.* (2024) and Rull *et al.* (2024).

Another untested assumption is that pollen morphology and ecophysiological traits linked to climatic requirements evolve in a similar manner. However, Krassilov (2000) showed that 'sporophytic and pollen characters show only weak correlation over their evolutionary history.' According to the author, in some cases, pollen morphology is a conservative trait compared to other plant characteristics, while in other cases, the opposite is true. There is no general rule that can be universally applied; each case requires specific analysis.

The uncertainty associated to niche conservatism would also apply to community composition over time. In this case, empirical palynological data show that the taxonomic composition of many communities has actually varied over time, even during the most recent Quaternary period, largely due to range shifts of extant species (Jackson & Williams 2004; Williams & Jackson 2007; Rull 2020). These compositional changes have been even more pronounced throughout the Palaeogene and the Neogene, due to evolutionary factors such as speciation and extinction, in addition to large-scale dispersal (e.g. Rull 2024). Therefore, extant communities cannot be assumed a priori to be modern analogues for past Cenozoic communities.

From a practical standpoint, pollen-based palaeoclimatic estimates derived from modern-analogue methods have consistently shown significant discrepancies when compared with pollen-independent and modelling approaches (e.g. Kvaček 2007; You *et al.* 2009; Herold *et al.* 2011; Goldner *et al.* 2014; Zhang *et al.* 2019; Salocchi *et al.* 2021; Botsyun *et al.* 2022; Gilson *et al.* 2022). According to Popescu *et al.* (2021), this could be due to the excessive weight that pollen-based methods assign to megathermal plants, particularly those from mangroves, in pollen-based palaeoclimatic reconstructions.

In summary, given the current state of knowledge, pollen-based palaeoclimatic reconstructions using modern-analogue approaches should be interpreted with caution and await further developments that may improve their reliability, with emphasis on empirical palaeoecological testing of previous assumptions. The use of pollen-independent methods of palaeoclimatic estimation, especially those based on isotopic and biomarker proxies, is highly recommended (Rull *et al.* 2024).

Communitiy level: Mediterranean mangroves

Mangroves are intertidal forest communities currently restricted to tropical and subtropical coasts between approximately 30°N and 30°S (Spalding *et al.* 2010). However, during the Miocene—particularly the Middle Miocene Climate Optimum (MMCO; 17–15 Ma), when global temperatures were 4–8 °C higher than today (Westerhold *et al.* 2020)—pollen records indicate that the northern limit of mangrove distribution extended to the northern Mediterranean-Paratehyan coasts, reaching up to approximately 45°N (Plaziat *et al.* 2001; Popescu *et al.* 2021). These MMCO mangroves have been referred as *Avicennia*-only mangroves, as they were dominated by *Avicennia* (Acanthaceae) – one of the two globally distributed genera of mangrove-forming trees (Tomlinson 2016; Duke 2017) – whereas *Rhizophora* (Rhizophoraceae), the other conspicuous mangrove genus, along with other mangrove-forming tree genera, was absent (Popescu *et al.* 2021).

The MMCO *Avicennia*-only Mediterranean-Paratethyan mangroves have been considered taxonomically and ecologically comparable to those currently found in the arid and semi-arid regions of the Middle East, particularly along the coasts surrounding the Arabian Peninsula (Jiménez-Moreno & Suc 2007; Suc *et al.* 2018; Popescu *et al.* 2021). These regions represent the northernmost boundary of modern mangrove distribution, where *Avicennia* is the dominant mangrove-forming tree. If this comparison holds, modern Middle-East mangroves could serve as modern analogueues for reconstructing the ecological characteristics of MMCO Mediterranean-Paratethyan mangroves. However, this comparison has yet to be fully explored from biogeographical and palaeoenvironmental perspectives (Rull *et al.* 2025).

The Miocene *Avicennia*-only Mediterranean-Paratethyan mangroves, located at the northernmost edge of mangrove distribution, were considered impoverished compared to the taxonomically rich mangroves of lower latitudes. According to Popescu *et al.* (2021), this was the result of a temperature-driven latitudinal pattern. These authors estimated a mean annual temperature (MAT) of 18–20 °C and mean annual precipitation (MAP) exceeding 1000 mm/year, except in some localities of the Iberian Peninsula—particularly in the southwestern sector—where climates were drier (see also Postigo-Mijarra *et al.* 2009; Barrón *et al.* 2010). As mentioned above, these pollen-based estimates were higher than others based on pollen-independent proxies and palaeoclimate modeling, which yielded MAT values of 11–17 °C and sea surface temperatures (SST) of around 20 °C (You *et al.* 2009; Goldner *et al.* 2011).

Regarding current Middle East mangroves, a recent review covering most African and Asian coasts surrounding the Arabian Peninsula has revealed highly diverse environmental conditions (Waleed

2025). MAT vary significantly across the region, ranging from 20 °C in the NE to 30 °C in the SE. SST can reach up to 28 °C in summer, while MAP is generally below 100 mm/year, with evaporation rates typically ten times higher. Additionally, the absence of large permanent freshwater sources limits sediment and nutrient supply essential for mangrove growth and results in hypersaline coastal conditions exceeding 40 ppt. These extremely hot, arid and hypersaline environments are generally unfavorable for mangrove development (Quisthoudt *et al.* 2012).

Only two mangrove-forming tree species—*Avicennia marina* and *Rhizophora mucronata*—are capable of surviving the harsh environmental conditions of the Middle East. *Avicennia marina* typically dominates the mangrove canopy, whereas *Rhizophora mucronata* is rare or entirely absent, found only in a few locations with some freshwater input (Waleed 2025). Due to the intense environmental stress, both species exhibit stunted, dwarf growth forms when compared to populations thriving in more favorable climates. Overall, the sparse, low-stature, and species-poor *Avicennia*-dominated mangroves of the Middle East reflect a unique regional adaptation to aridity and related environmental pressures (Osland *et al.* 2017), rather than a pattern driven by latitude-dependent temperature gradients. In contrast, other Asian mangroves occurring at similar latitudes (approximately 10°–30° N), but under more favorable environmental regimes, rank among the most diverse and healthy mangrove ecosystems in the pantropical zone (Tomlinson 2016; Duke 2017).

These observations suggest that the present-day Middle East mangroves represent a latitudinal anomaly within the northern tropical–subtropical mangrove belt, driven by regional aridity and hypersalinity rather than by the latitudinal temperature gradient. Consequently, these extant mangroves are unlikely to serve as appropriate modern analogues for the Miocene Mediterranean mangroves, considered as a temperature-driven latitudinal feature. This view is further supported by the contrasting climatic conditions estimated for Miocene mangroves, particularly the absence of extreme heat and aridity. Additionally, some studies from the NE Iberian Peninsula do not support the presence of hypersaline conditions (Bitzer 2004). Combined with the absence of a present-day northern latitudinal zone dominated solely by *Avicennia* mangroves, the above observations make it difficult to identify suitable modern analogues for the MMCO Mediterranean mangroves. In the Southern Hemisphere, *Avicennia* mangroves occur in the Mediterranean antipodes (New Zealand and southeastern Australia), where minimum temperatures—a latitude-dependent factor—are the primary drivers of mangrove distribution and diversity (Osland *et al.* 2017). Further comparisons with these systems could offer valuable insights.

Today, *Avicennia*-only mangroves occur sporadically, either as pioneering communities on recently formed mudflats or in hypersaline areas within broader mangrove ecosystems across tropical and subtropical regions (Thatoi *et al.* 2016). It is plausible that MMCO mangroves developed under similar conditions, though on a much broader regional scale. However, further research is needed to determine whether meaningful parallels exist between ancient and modern *Avicennia* stands. If no clear analogues can be identified, MMCO Mediterranean mangroves may represent an extinct mangrove type—a phenomenon not uncommon in mangrove history, particularly throughout the Cenozoic (Rull 2024). In palaeoecology, communities with no modern counterparts are relatively frequent, even during the Quaternary, when the species involved were already extant (Jackson & Williams 2004; Williams & Jackson 2007).

Biome level

Artemisia dry steppes

The presence of significant amounts of *Artemisia* (Asteraceae) pollen in fossil records has traditionally been considered an indicator of arid and semi-arid biomes, particularly steppes, in temperate regions (Wang 2004). This interpretation applies to pre-Holocene records, as *Artemisia* species are common weeds and ruderal plants associated with human activities such as grazing and other intensive or extensive agricultural practices, which began to play a significant role during the Early Holocene Neolithization (Roberts 2014). In the Neogene, steppes dominated by *Artemisia*, with *Ephedra* present, began to be important at the end of the Miocene (6.2-5.6 Ma) in the eastern Mediterranean area (Anatolia), coinciding with the Antarctic glaciation and the desiccation of the Mediterranean Sea. At the beginning of the Pliocene, these steppes expanded across the entire Mediterranean region, reaching the westernmost part during the Middle Pleistocene (Suc *et al.* 2018).

According to the most widely accepted view, the European Pleistocene was characterized by the alternation of cold steppes—dominated by *Artemisia*, *Ephedra*, and other Asteraceae—during glacial phases, and deciduous forests with thermophilous elements during interglacials (Zagwijn 1960; Suc 1984). However, Subally *et al.* (1999) noted that this pattern was disrupted, or even reversed, in some Mediterranean regions, with *Artemisia* reaching its highest values during interglacials, as indicated by independent isotopic proxies. The same authors analysed the ecological niches of Mediterranean *Artemisia* species and found that, although steppe representatives were dominant, other species were distributed along environmental gradients of elevation—and thus temperature—and hydroclimatic conditions. Subally & Quézel (2002) suggested that *Artemisia* peaks during glacial and interglacial periods may correspond to different species, and recommended identifying *Artemisia* pollen at the species level and incorporating independent palaeoclimatic proxies.

The main limitation is that *Artemisia* pollen is highly homogeneous, making identification at the species level challenging—particularly under light microscopy (LM), which is the standard method used in pollen analysis. Although several attempts have been made, they have primarily focused on resolving phylogenetic questions rather than supporting environmental reconstruction. (e.g. Jiang *et al.* 2005; Ghahraman *et al.* 2007; Hayat *et al.* 2010; Hussain *et al.* 2019). Suc *et al.* (2004) were the first to attempt linking *Artemisia* pollen morphology with environmental preferences. Using scanning electron microscopy (SEM), they found that the key distinguishing feature was the morphology and size of spinules, and they preliminarily associated these traits with various Mediterranean species differing in thermal and edaphic requirements. Unfortunately, this classification was not further developed.

Recently, Lu et al. (2022) conducted a comprehensive pollen-morphological study that included species from all known *Artemisia* lineages (Sanz *et al.* 2008; Malik *et al.* 2017), along with the biomes and vegetation types in which they occur globally, accompanied by corresponding environmental characterizations. The study confirmed the high level of intra-generic pollen homogeneity and reinforced the value of spinule morphological traits as key diagnostic features. Lu *et al.* (2022) were able to distinguish only three main pollen types within a genus comprising over 500 species (World Flora Online; https://wfoplantlist.org/). These pollen types were designated as SWS (short and wide spinules), LNS (long and narrow spinules), and SG (sparse granules).

Lu *et al.* (2022) highlighted the wide range of biomes and climatic conditions in which *Artemisia* species occur—from forests to deserts, including grasslands and coastal saline environments—across various climatic zones, with a particular emphasis on temperate regions. The three defined pollen-morphological types showed little correlation with bioclimatic zones. Species with the SWS pollen type have a global distribution and occupy a wide variety of habitats, with a slight preference for humid forests and grasslands. The LNS pollen type was characteristic of generalist species found in forests, grasslands, deserts, and coastal areas, typically in regions with higher temperatures. Species with the SG pollen type were associated with low-elevation open biomes, such as dry grasslands, deserts, and saline environments. In summary, only species with the SG pollen type—and some with LNS—can be considered indicators of arid biomes; the others lack clear indicator value.

It can be concluded that *Artemisia*, when treated as a bulk pollen category, is not a reliable indicator of any specific biome or vegetation type. The difficulty in identifying pollen at the species level, along with the lack of correlation between pollen morphology and environmental preferences, complicates bioclimatic interpretation. Moreover, the need for scanning electron microscopy (SEM) to distinguish pollen types limits the applicability of the defined pollen-morphological groups in routine pollen analysis. As a result, the interpretation of *Artemisia* fossil pollen records still depends on supporting methods, such as the fossil assemblage approach or the use of independent palaeoenvironmental proxies (Rull 2025). It would be worthwhile to investigate whether recent advances—such as Fourier transform infrared spectroscopy (FTIR) (Kendel & Zimmermann 2020) and automated pollen counting using SEM (Smyth *et al.* 2015)—could offer useful support.

Taxodiaceous tropical marshes

In the Mediterranean region, it is also common to interpret the dominance of pollen from the former Taxodiaceae family as an indicator of tropical coastal forested marshes, which likely replaced the European *Avicennia*-only mangroves after the MMCO during the southward migration of the main Mediterranean biomes (Suc *et al.* 2018). This interpretation is based on identifying this pollen as *Taxodium* type, encompassing *Taxodium* and *Glyptostrobus*, two genera of trees now restricted to tropical or subtropical latitudes outside Europe. This approach not only leads to questionable biome reconstructions, as explained in this section, but has also formed the basis for debatable quantitative palaeoclimatic estimates, as discussed in above. Once again, the problem lies in pollen identification at taxonomic resolutions not supported by morphological differences.

The now-abandoned family Taxodiaceae included nine genera—*Athrotaxis*, *Cryptomeria*, *Cunninghamia*, *Glyptostrobus*, *Metasequoia*, *Sequoia*, *Sequoiadendron*, *Taiwania*, and *Taxodium*—characterized by pollen with a protuberance (papilla) at the center of the aperture (leptoma). This papillate pollen is a common Cenozoic fossil in the Mediterranean region and has traditionally been identified as *Taxodium*-type or *Taxodium/Glyptostrobus*, with corresponding bioclimatic inferences mentioned above (e.g. Bessedik 1985; Bessedik & Cabrera 1985; Fauquette *et al.* 1998a, b; Jiménez-Moreno 2005; Jiménez-Moreno & Suc 2007). With the advent of molecular phylogenetics, Taxodiaceae was dissolved as a family and reclassified as a Cupressaceae subfamily (Taxodioideae) containing three genera—*Cryptomeria*, *Glyptostrobus*, and *Taxodium*—while the remaining six genera with papillate pollen were reassigned to four other subfamilies. This reclassification did not alter traditional fossil identification practices in the region (e.g. Jiménez-Moreno *et al.* 2010; Biltekin *et al.* 2015; Fauquette 2017; Suc *et al.* 2018, 2020; Popescu *et al.* 2021).

However, a recent palynological study seriously questioned these interpretations. After a thorough and detailed morphological analysis of modern pollen, Bouchal & Denk (2020), concluded that distinguishing among the nine former Taxodiaceae genera based on pollen characteristics is 'difficult if not impossible.' They also highlighted that the extant species within these genera occupy a wide range of ecological niches, casting doubt on palaeoenvironmental interpretations that rely solely on fossil pollen and their presumed modern counterparts. Consequently, the routine assignment of papillate Cupressaceae pollen to the *Glyptostrobus–Taxodium* group—while overlooking the ecological variability of the remaining seven papillate genera—rests on weak taxonomic grounds. As such, using papillate Cupressaceae pollen alone to indicate megathermal biomes and environments, such as tropical or subtropical coastal swamps, is not justified.

Discussion

The main drawbacks of using modern pollen analogues for the European Neogene stem from uncertainties surrounding niche conservatism (NCU) and its extrapolation to community- and biome-level taxonomic composition and environmental requirements. The most common approach is to assume niche conservatism and constancy in community or biome composition a priori, often without critical evaluation—an approach that can lead to unsupported conclusions. In the case of pollen, these assumptions are especially problematic due to additional factors, including limitations in pollen morphology and taxonomic resolution, difficulties in establishing accurate botanical affinities, and the possible presence of extinct species or taxa that evolved after the period under study. As such, finding empirical evidence for niche conservatism in the taxa examined over the relevant time span is essential. Identifying reliable modern analogues and clearly defining the spatiotemporal contexts in which they are applicable should therefore be a key objective.

Alternative and complementary approaches based on direct observation of the palaeontological record—without reliance on potential modern analogues—are strongly recommended. One such method is the fossil community approach, which statistically defines fossil pollen assemblages based solely on palaeontological evidence and incorporates pollen-independent palaeoclimatic and palaeoenvironmental proxies such as stable isotopes, biomarkers, and similar indicators (Rull *et al.* 2024). This approach can be applied to individual species, communities, and biomes, and it provides empirical evidence for testing niche conservatism. As a result, it can help reduce the NCU for the taxa and time interval under study. Palaeoclimatic modeling can also contribute to testing niche conservatism, though the underlying assumptions and premises of the models must be carefully considered.

Acknowledgements. – This contribution did not receive funding specifically for its development. The CERCA Programme, Generalitat de Catalunya, provided logistic support.

References

Abbink, O.A., Van Konijnenburg-Van Cittert, J.H.A. & Visscher, H. 2004: A sporomorph ecogroup model for the Northwest European Jurassic–Lower Cretaceous: concepts and framework. *Netherlands Journal of Geosciences/Geologie en Mijnbouw 83*, 17–31.

Altoaguirre, Y., Postigo-Mijarra, J.M., Casas-Gallego, M., Moreno-Domínguez, R. & Barrón, E. 2023: Mapping the Late Miocene Pyrenean forests of the La Cerdanya Basin, Spain. *Forests 14*, 1471.

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.

Benítez-Benítez, C., Escudero, M., Rodríguez-Sánchez, F., Martín-Bravo, S. & Jiménez-Mejías, P. 2017. Pliocene-Plesitocene ecological niche evolution shapes the phylogeography of a Mediterranean plant group. *Molecular Ecology 27*, 1696-1713.

Bessedick, M. 1985: *Reconstruction des environments Miocenes des regions nord-ouest Mediterraneennes a partir de la palynologie*. Unpublished PhD dissertation, Université des Sciences et Techniques du Langedoc, Montpellier.

Bessedik, M. & Cabrera, L. 1985: Le couple récif-mangrove à Sant Pau d'Ordal (Vallès-Pénédès, Espagne), témoin du maximum transgressif en Méditerranée nord occidentale (Burdigalian supérieur – Langhien inférieur). *Newsletter on Stratigraphy 14*, 20–35.

Biltekin, D., Popescu, S.-M., Suc, J.-P., Quézel, P., Jiménez-Moreno, G., Yavuz, N. & Namik Çağatay, M. 2015: Anatolia: a long-time plant refuge area documented by pollen records over the last 23 million years. *Review of Palaeobotany and Palynology 251*, 1-22.

Birks, H.J.B. & Birks, H.H. 1980: *Quaternary Palaeoecology*. Edward Arnold, London.

Birks, H.J.B., Lotter, A.F., Juggins, S. & Smol, J.P. 2012: *Tracking Environmental Change Using Lake Sediments. Vol. 5: Data Handling and Numerical Techniques*. Kluwer, Dordrecht.

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

Botsyun, S., Ehlers, T.A., Koptev, A., Böhme, M., Methner, K., Risi, C., Stepanek, C., Mutz, S.G., Werner, M., Boateng, D. & Mulch, A. 2022: Middle Miocene climate and stable oxygen isotopes in Europe based on numerical modelling. *Paleoceanography and Paleoclimatology 37*, e2022PA004442.

Bouchal, J.M. & Denk, T. 2020: Low taxonomic resolution of papillate Cupressaceae pollen (former Taxodiaceae) impairs their applicability for palaeo-habitat reconstruction. *Grana 59*, 71-93.

Bradley, R.S. 2015: *Paleoclimatology. Reconstructing Climates of the Quaternary*. Elsevier-Academic Press, Oxford.

Bystriakova, N., Schnedier, H. & Coomes, D. 2011: Evolution of the climatic niche in scaly tree ferns (Cyatheaceae, Polypodiopsida). *Botanical Journal of the Linnean Society 165*, 1-19.

Crisp, M.D., Arroyo, M.T.K., Cook, L.G., Gandolfo, M.A., Jordan, G.J., McGlone, M.S., Weston, P.H., Westoby, M., Wilf, P. & Linder, H.P. 2009: Phylogenetic biome conservatism on a global scale. *Nature 485*, 754-756.

Crisp, D. & Cook, L.G. 2012: Phylogenetic niche conservatism: what are the underlying evolutionary and ecological causes? *New Phytologist 196*, 681-694.

Cronin, T.H. 2009: *Paleoclimates. Understanding Climate Change Past and Present*. Columbia University Press, New York.

Delcourt, H.R. & Delcourt, P.A. 1991: *Quaternary Ecology*. Chapman and Hall, London.

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., Lee, S.Y., Kristensen, E. & Twilley, R.R. (eds), *Mangrove Ecosystems: A Global Biogeographic Perspective*, 17-53. Springer, Berlin.

Fauquette, S. 2017: *Paléoenviroments en Europe et Región Méditerranéene au Cenozoic*. Universtité Montpellier, Montpellier.

Fauquette, S., Quézel, P., Guiot, J. & Suc, J.-P. 1998a: Signification bioclimatique des taxons-guides du Pliocèce Mediterranéen. *Geobios 31*, 151-169.

Fauquette, S., Guiot, J. & Suc, J.-P. 1998b: A method for climatic reconstruction of the Mediterranean Pliocene using pollen data. *Palaeogeography, Palaeoclimatology, Palaeoecology 144*, 183–201.

Fernández-Mazuecos, M. & Glover, B.J. 2025: Climatic and edaphic niche shifts during plant radiation in the Mediterranean biodiversity hotspot. *Annals of Botany 135*, 717-734.

Ghahraman, A., Nourbakhsh, N., Mehdigoli, K. & Attar, F. 2007: Pollen morphology of *Artemisia* L. (Asteraceae) in Iran. *Iran Journal of Botany 13*, 21-29.

Gilson, M.E., McCoy, J., O'Keefe, J.N.K., Nuñez Otaño N.B. & Pound, M.J. 2022: Resconstructing terrestrial paleoclimates: a comparison of the co-existence approach, Bayesian and probability reconstruction techniques using the UK Neogene. *Paleoceanography and Paleoclimatology 37*, e2022PA004358.

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.

Grimm, G.W. & Potts, A.J. 2016: Fallacies and fantasies: the theoretical underpinnings of the Coexistence Approach for palaeclimate reconstruction. *Climate of the Past 12*, 611-622.

Hayat, M.Q., Ashraf, M., Khan, M.A., Yasmin, G., Shaheen, N. & Jabeen, S. 2010: Palynological study of the genus Artemisia (Asteraceae) and its systematic implications. *Pakistan Journal of Botany 42*, 751-763.

Herold, N., Huber, M. & Müller, R. D. 2011: Modeling the Miocene climate optimum. Part I: Land and atmosphere. *Journal of Climate 24*, 6353–6372.

Hussain, A., Potter, D., Hayat, M.Q., Sahreen, S. & Bokhari, S.A.I. 2019: Pollen morphology and its systematic implication on some species of *Artemisia* L. from Gilgit-Baltisan Pakistan. *Bangladesh Journal of Plant Taxonomy 26*, 157-168.

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.

Jiang, L., Qin,W. & Ye, L.-Z. 2005: Pollen morphology of *Artemisia* L. and its systematic significance. *Wuhan University Journal of Natural Sciences 10*, 448-454.

Jiménez-Moreno, G. 2005: *Utilización del análisis polínico para la reconstrucción de la vegetación, clima y estimación de paleoaltitudes a lo largo del arco alpino europeo durante el Mioceno (21-8 Ma)*. Unpublished PhD dissertation, Universidad de Granada, Granada.

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.

Jiménez-Moreno, G., Fauquette, S. & Suc, J.-P. 2010: Miocene to Pliocene vegetation reconstruction and climate estimates in the Iberian Peninsula from pollen data. *Review of Palaeobotany and Palynology 162*, 403-415.

Kendel, A. & Zimmermann, B. 2020: Chemical analysis of pollen by FT-Raman and FTIR secpteroscopies. *Frontiers in Plant Science 11*, 352.

Krassilov, V.A. 2000: Factors of palynomorphological evolution. *Paleontological Journal 34*, S2-S13.

Kvaček, Z. 2007: Do extant relatives of thermophile European Cenozoic plant elements reliably reflect climatic signal? *Palaeogeography, Palaeoclimatology, Palaeoecology 253*, 32-40.

Liu, Y., Wiens, J.J., Luo, A., Xu, X., Dimitrov, D., Su, X., Li, Y., Lyu, T., Pellissier, L., Zimmermann, N.E., Soltis, D.E., Soltis, P.S. & Wang, Z. 2025: Global patterns of climatic niche evolution in angiosperms. *Global Ecology and Biogeography 34*, e70049.

Loera, I., Sosa, V. & Ickert-Bond, S.M. 2012: Diversification in North American arid lands: Niche conservatism, divergence and expansion of habitat explain speciation in the genus *Ephedra*. *Molecular Phylogenetics and Evolution 65*, 437-450.

Lososová, Z., Divíšek, J., Chytrý, M., Götzenberger, L., Těšitel, J. & Mucina, L. 2020: Macroevolutionary patterns in European vegetation. *Journal of Vegetation Science 32*, e12942.

Lu, L.-L., Jiao, B.-H., Qin, F., Xie, G., Lu, K.-Q., Li, J.-F., Sun, B., Li, M., Ferguson, D.K., Gao, T.-G., Yao, Y.-F. & Wang, Y.-F. 2022: *Artemisia* pollen dataset for exploring the potential ecological indicators in deep time. *Earth System Science Data 14*, 3961-3995.

Mahler, S., Shatilova, I. & Bruch, A.A. 2022: Neogene long-term trends in climate of the Colchic vegetation refuge in Western Georgia – uplift versus global cooling. *Review of Palaeobotany and Palynology 296*, 104546.

Malik, S., Vitales, D., Hayat, M.Q., Korovkov, A.A., Garnatje, T. & Vallès, J. 2017. Phylogeny and biogeography of *Artemisia* subgenus *Seriphidium* (Asteraceae: Anthemideae). *Taxon 66*, 934-952.

Martín-Hernanz, S., Albaladejo, R.G., Lavergne, S., Rubio, E., Grall, A. & Aparicio, A. 2012: Biogeographic history and environmental niche evolution in the palearctic genus *Helianthemum* (Cistaceae). *Molecular Phylogenetics and Evolution 163*, 107238.

Matthaeus, W.J., Macarewich, S.I., Richey, J., Montañez, I.P., McElwain, J.C., White, J.D., Wilson, J.P. & Poulsen, C.J. 2023: A systems approach to understanding how plants transformed Earth's environment in deep time. *Annual Reviews of Earth and Planetary Sciences 51*, 551-580.

Mosbrugger, V. & Utescher, T. 1997: The coexistence approach: a method for quantitative reconstructions of tertiary terrestrial palaeoclimate data using plant fossils. *Palaeogeography, Palaeoclimatology, Palaeoecology 134*, 61–86.

Ni, J., Yu, G., Harrison, S.P. & Prentice, I.C. 2010: Palaeovegetation in Chinaduring the Late Quaternary: biome reconstructions based on a global scheme of plant functional types. *Palaeogeography, Palaeoclimatology, Palaeoecology 289*, 44-61.

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.

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. & Labrousses, 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 Manzaneque, 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.

Prentice, I.C., Guiot, J., Huntley, B., Jolly, D. & Cheddadi, R. 1996: Reconstructing biomes from palaeoecological data: a general method and its application to European pollen data at 0 and 6 ka. *Climate Dynamics 12*, 185-194.

Qian, H., Qian, S., Zhang, J. & Kessler, M. 2024: Effects of climate and environmental heterogeneity on the phylogenetic structure of regional angiosperm floras worldwide. *Nature Communications 15*, 1079.

Quirk, Z.J., Smith, S., Acosta, R.P. & Poulsen, C.J. 2024: Where did they come from, where did they go? Niche conservatism in woody and herbaceous plants and implications for plant-based paleoclimatic reconstructions. *American Journal of Botany 111*, e16426.

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.

Roberts, N. 2014: *The Holocene: An Environmental History*. Wiley-Blackwell, Hoboken.

Rull, V. 2020: *Quaternary Ecology, Evolution and Biogeography*. Elsevier/Academic Press, London.

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

Rull, V. 2025: Insights on the indicator capacity of *Artemisia* pollen in pre-Holocene paeoecology. *Palynology*, 49, 2499121.

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

Rull, V., Vicente, A., Bouchal, J.M., Casanovas-Vilar, I. 2025: On the use of extant Middle-East mangroves as modern analogs for Miocene Mediterranean-Paratehtyan mangroves. *Palaeobiodiversity and Palaeoenvironments*, https://doi.org/10.1007/s12549-025-00693-y

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.

Sanz, M., Vilatersana, R., Hidalgo, O., Garcia-Jacas, N., Susanna, A., Schneeweiss, G.M. & Vallès, J. 2008: Molecular phylogeny and evolution of floral characters of *Artemisia* and allies (Anthemideae, Asteraceae): evidence from nrDNA ETS and ITS sequences. *Taxon 57*, 66-78.

Smyth, A.P., Seales, B. & Bradley, P.M. 2015: A pollen profile by scanning electron microscopy bracketing the mid-Holocene *Tsuga canadensis* declines at Pouywater Pond Bog, Holden, Massachussetts. *Grana 54*, 263-270.

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

Subally, D. & Quézel, P. 2002: Glacial or interglacial: *Artemisia*, a plant indicator with dual responses. *Review of Palaeobotany and Palynology 120*, 123-130.

Subally, D., Bilodeau, G., Tamrat, E., Ferry, S. & Debard, E. 1999: Cyclic climatic records during the Olduvai subchron (uppermost Pliocene) on Zakynthos Island (Ionia Sea). *Geobios 32*, 793-803.

Suc J.-P. 1984: Origin and evolution of the Mediterranean vegetation and climate in Europe. *Nature 307*, 429-432.

Suc, J.-P., Fauquette, S. & Popescu, S.-M. 2004: L'investigation palynologique du Cénozoïque passe par les herbiers, 67-87. *In*: Pierrel, R. & Reduron, J.-P. (eds), *Actes du Colloque 'Les Herbiers : un Outil d'Avenir, Tradition et Modernité'*. Villeurbanne, France.

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.

Suc, J.-P., Fauqquette, S., Popescu, S.-M. & Robin, C. 2020: Subtropical mangrove and evergreen forest reveal Paleogene terrestrial climate and physiography at the North Pole. *Palaeogeography, Palaeoclimatology, Palaeoecology 551*, 109755.

Svenning, J.-C. 2003: Deterministic Plio-Pleistocene extinctions in the European cool-temperate flora. *Ecology Letters 6*, 646-653.

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.

Utescher, T., Bruch, A.A., Erdei, B., François, L., Ivanov, D., Jacques, F.M.B., Kern, A.K., Liu, Y.-S.C., Mosbrugger, V. & Spicer, R.A. 2014: The coexistence approach–theoretical background and practical considerations of using plant fossils for climate quantification. *Palaeogeography, Palaeoclimatology, Palaeoecology 410*, 58–73.

Vieira, M., Zetter, R., Grímsson, F. & Denk, T. 2023: Niche evolution versus niche conservation and habitat loss determine persistense and extirpation in the Late Neogene European Fagaceae. *Quaternary Science Reviews 300*, 107896.

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.

Wang, W. 2004: On the origin and development of *Artemisia* (Astearaceae) in the geological past. *Botanical Journal of the Linnean Society 145*, 331-336.

Weeks, A., Zapata, F., Pell, S.K., Daly, D.C., Mitchell, J.D. & Fine, P.V.A. 2014: To move or to evolve: contrasting patterns of intercontinental connectivity and climatic niche evolution in 'Terebinthaceae' (Anacardiaceae and Burseraceae). *Frontiers in Genetics 5*, 409.

Westerhold, T., Marwan, N. Drury, A.J., Liebrand, D., Agnini, G., Anagostou, E., Barnet, J.S.K., Bohaty, S.M., De Vleesschouwer, 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.

Wiens, J.J., Ackerly, D.D., Allen, A.P., Anacker, B.L., Buckley, L.B., Cornell, H.V., Damschen, E.I., Davies, J.T., Grytnes, J.-A., Harrison, S.P., Hawkins, B.A., Holt, R.D., McCain, C.M. & Stephens, P.R. 2010: Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters 13*, 1310-1324.

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.

Zagwijn, W.H. 1960: Aspects of the Pliocene and early Pleistocene vegetation in The Netherlands. *Mededelingen van de Geologische Stichting C 3*, 1-78.

Zhang, J., Lenz, O.K., Wang, P. & Hornung, J. 2021: The Eco-Plant model and its implication on Mesozoic dispersed sporomorphs for Bryophytes, Pteridophytes, and Gymnosperms. *Review of Palaobotany and Panlynology 293*, 104503.

Zhang, Z.-Y., Cheng, D.-M., Li, C.-S., Hu, W., Zhan, X.-H., Ji & H.-L. 2019: The complexity of climate reconstructions using the coexistence approach on Qinghai-Tibetan Plateau. *Journal of Palaeogeography 8*, 5.