Middle Miocene vegetation of the Vallès-Penedès Basin (NE Iberian Peninsula), as inferred from fossil pollen records: state of the art and future prospects

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Abstract

In the Mediterranean region, the study of fossil pollen has provided a comprehensive spatiotemporal paleoclimatic and paleovegetational picture of the Neogene flora and vegetation. The NW Mediterranean sector is a reference area for the study of vertebrate evolution, especially during the Middle Miocene, but paleofloristic and paleovegetational patterns are much less known, which hinders placing faunal evolution in the appropriate paleoenvironmental context. Here, the existing palynological evidence for this area is reviewed to identify the main knowledge gaps and to devise possible future developments. The few palynological records available have provided quantitative paleotemperature and paleoprecipitation estimates, along with general paleovegetation reconstructions, using a modern-analog (MA) approach. The suitability of this method is discussed here and the use of a complementary fossil-community (FC) approach, which has been demonstrated to be useful in other areas and time intervals, is proposed and illustrated using the available raw data. The MA approach is consistent with the available paleoclimatic evidence but special care should be placed on the reliability of overly precise quantitative estimates and the latent danger of circularity when analyzing the biotic responses to climatic changes. The FC approach is considered to be more suitable for reconstructing past communities because it requires less unwarranted assumptions. Additional fieldwork efforts are needed in the search for new pollen records, with an emphasis on more complete ecosystem reconstructions using both floral and faunal evidence.

Keywords: Pollen, vegetation, paleoecology, Middle Miocene, Mediterranean, Iberian Peninsula

1. Introduction

The Neogene flora, vegetation and climate of the Iberian Peninsula, as part of the Mediterranean region, have been reconstructed using primarily palynological evidence (e.g., Suc, 1984; Suc et al., 1999, 2018; Jiménez-Moreno and Suc, 2007; Fauquette et al., 2007; Postigo-Mijarra et al., 2009; Barrón et al., 2010; Jiménez-Moreno et al., 2010; Carrión et al. 2022). These analyses have been focused on the definition of a number of floristic groups representing broad biome categories – notably megathermic (tropical), mega-mesothermic (subtropical), mesothermic (warm-temperate), meso-microthermic (cool-temperate), microthermic (boreal), Mediterranean and steppic – and their use as proxies for estimating paleotemperature and paleoprecipitation patterns, along with their spatiotemporal gradients over time (Fauquette et al., 2007; Suc et al., 2018). Regarding vegetation, a regional reconstruction of the main features has been attempted by defining broad categories such as *Avicennia* mangroves, *Taxodium/Glyptostrobus* coastal swamps, *Artemisia* steppes or Mediterranean sclerophyll forests, among others, and their latitudinal and longitudinal shifts over time. A general north–south retreat of mangroves and megathermic elements was documented between 16.5 Ma (Middle Miocene) and 5.6 Ma (latest Miocene), followed by a westward expansion of *Artemisia* steppes, which reached the Iberian Peninsula at the beginning of the Pleistocene (2.6 Ma) (Fig. 1). In the Iberian Peninsula, the Mio-Pliocene biotic turnover was manifested in the expansion of the northern temperate Arctotertiary flora/vegetation and the disappearance of many Paleotropical taxa and the corresponding plant formations, which has been linked to global climatic shifts, notably cooling and aridification (Postigo-Mijarra et al., 2009; Barrón et al., 2010).

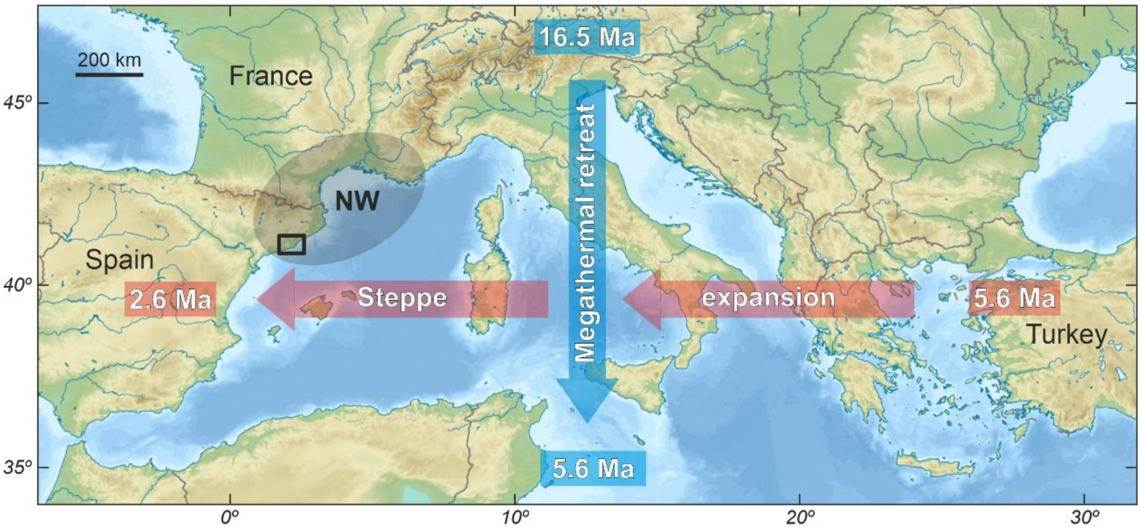

Figure 1. Map of the Mediterranean region showing the main Neogene vegetation trends. The study area of this paper is highlighted by a black box within a shaded spot indicating the NW Mediterranean subregion. Based on Suc et al. (2018).

In the NW Mediterranean subregion (presently NE Spain and SE France) (Fig. 1), the megathermic flora was present until the Serravallian (Middle Miocene), whereas the replacing mega-mesothermic tropical/subtropical flora persisted until the Pliocene (3 Ma) in SE France and the Pleistocene (2 Ma) in SE Spain, just before the establishment of *Artemisia* steppes. Of particular interest in this region is the expansion of sclerophyll vegetation similar to its present Mediterranean counterpart since the Early/Late Pliocene boundary (3.6 Ma), which would have represented the onset of the modern Mediterranean biome and climate. Based on pollen data, mean annual temperature (MAT) and precipitation (MAP) values 2-8 °C and 400-700 mm higher than today were estimated for the Middle Miocene in the NW Mediterranean area. Regionally, the north–south thermic gradient was weaker than today and increased to values similar to the present (0.6 °C per degree in latitude) during the Late Miocene, when NW climates were still warmer (3-4 °C higher than today) and wetter (200 mm higher than today).

These estimates, as well as the ensuing bioclimatic classification (megathermic, mesothermic, microthermic, etc.), were based on the climate amplitude method, a modern analog (MA) approach based on the assumption that the Neogene taxa (usually identified at the genus and family levels) have the same climatic requirements as their extant representative species (Fauquette et al., 1998). The reliability of this approach was discussed by its own proponents, who consider that the hypothesis of Miocene to present climatic niche conservatism remains to be demonstrated and needs future studies for its validation (Fauquette, 2017). In spite of this, this approach constitutes the main source of paleoclimatic information available for the

Mediterranean region. Another MA-based approach, the coexistence approach (Mosbrugger & Utescher, 1997; Utescher et al., 2014), has also been used in the Iberian Peninsula and some circum-Mediterranean regions (e.g., Casas-Gallego et al., 2021; Mahler et al., 2022), but not as extensively as the climate amplitude method.

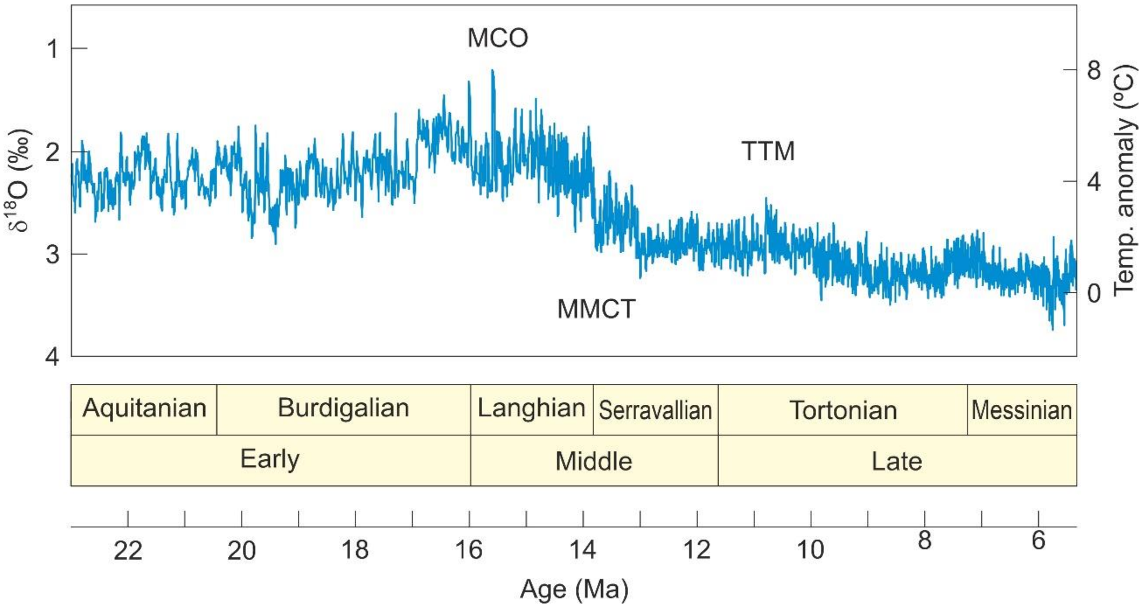

Figure 2. Miocene global paleotemperature reconstruction based on oxygen isotope records. Temperatures expressed as anomalies with respect to present values. MCO, Miocene Climatic Optimum; MMCT, Middle Miocene Climatic Transition; TTM, Tortonian Temperature Maximum. Raw data from Westerhold et al. (2020).

The development of mangrove vegetation was specifically analyzed within a Northern Hemispheric context (Popescu et al., 2021). In Europe, the maximum extent of the *Avicennia* mangroves occurred during the global Miocene Climatic Optimum (MCO; ~17-14 Ma) (Fig. 2), when the northernmost latitudinal boundary of this tropical/subtropical vegetation was approximately 45°, ~15° more northern than the present. Popescu et al. (2021) distinguished three types of *Avicennia* mangroves, as reconstructed from fossil pollen evidence: (i) diversified and well-developed mangroves, or *Avicennia*-dominated mangroves with >5% pollen from other mangrove taxa and high diversity of megathermic flora; (ii) scrawny but diversified mangroves, or *Avicennia*-dominated mangroves with lower values of other mangrove taxa and less diverse megathermic flora; and (iii) *Avicennia*-only mangroves. According to these authors, during the MCO, when maximum regional development of this vegetation took place, type iii was the dominant Mediterranean mangrove between 33°N and 45°N. This vegetation has been considered to be similar to that living today in the northernmost latitudinal mangrove edge, characterized by the absence of other important mangrove elements, notably *Rhizophora* (Quisthoudt et al., 2012). Therefore, *Avicennia*-only mangroves could have marked the northern latitudinal mangrove boundary in the Mediterranean region during the Miocene (Popescu et al., 2021).

In addition to the abovementioned regional latitudinal temperature and precipitation gradients, the Neogene zonal vegetation of the western Mediterranean (Iberian Peninsula) has been proposed to be constrained by local factors (moisture availability, edaphic features, slope orientation), thus developing a complex spatial mosaic (Jiménez-Moreno et al., 2010). In mountain areas, a characteristic elevational gradient was suggested to be formed by six main altitudinal belts (Fig. 3):

1. Coastal *Avicennia* mangroves (of the impoverished type), with halophytes such as Chenopodiaceae/Amarantheceae, *Armeria* and *Tamarix*.
2. Open lowland subdesertic steppes with *Nitraria*, *Neurada*, *Ephedra*, *Convolvulus*, *Lygeum*, *Prosopis*, Caesalpiniaceae and *Acacia*.
3. Lowland (coastal plain to ~700 m) broad-leaved evergreen forests with *Taxodium/Glyptostrobus*, *Myrica*, *Rhus*, Theaceae, Cyrillaceae-Clethraceae, *Bombax*, Euphorbiaceae, *Distylium*, *Castanopsis*, Sapotaceae, Rutaceae, Rubiaceae, *Mussaenda*, *Ilex*, *Hedera*, *Ligustrum*, *Jasminum*, Hamamelidaceae, *Engelhardia* and *Rhoiptelea*.
4. Mid-elevation (700-1000 m) evergreen-deciduous mixed forests characterized by deciduous *Quercus*, *Engelhardia*, *Platycarya*, *Carya*, *Pterocarya*, *Fagus*, *Liquidambar*, *Parrotia*, *Carpinus*, *Celtis* and *Acer*, with Ericaceae, *Ilex* and Caprifoliaceae in the understory. Riverine forests of *Salix*, *Alnus*, *Carya*, *Zelkova*, *Ulmus* and *Liquidambar* grew along water courses.
5. Montane/highland (1000-1800 m) conifer-deciduous mixed forests with *Betula*, *Fagus*, *Cathaya*, *Cedrus* and *Tsuga*.
6. Highland (>1800 m) conifer forests with *Abies* and *Picea*.

These vegetation patterns were based on the similarity of the Neogene Iberian flora with the present subtropical/temperate forests from SE China, where species from a number of genera/families that have already disappeared from Europe still occur and follow the above elevational arrangement (Wang, 1961). Lowland vegetation was deduced from floristic similarities with coastal regions of the Red Sea, the Canary Islands, California and Mexico, especially because of the common occurrence of *Avicennia* mangroves and numerous xerophytic taxa, which would also be present in the Iberian Neogene (review in Jiménez-Moreno, 2005). Therefore, vegetation reconstruction was also based on a MA approach, which assumes that extant plant communities have been present and constant in composition throughout the Neogene. This idea of the Miocene to present community constancy is as hypothetical as the notion of climatic niche conservatism.

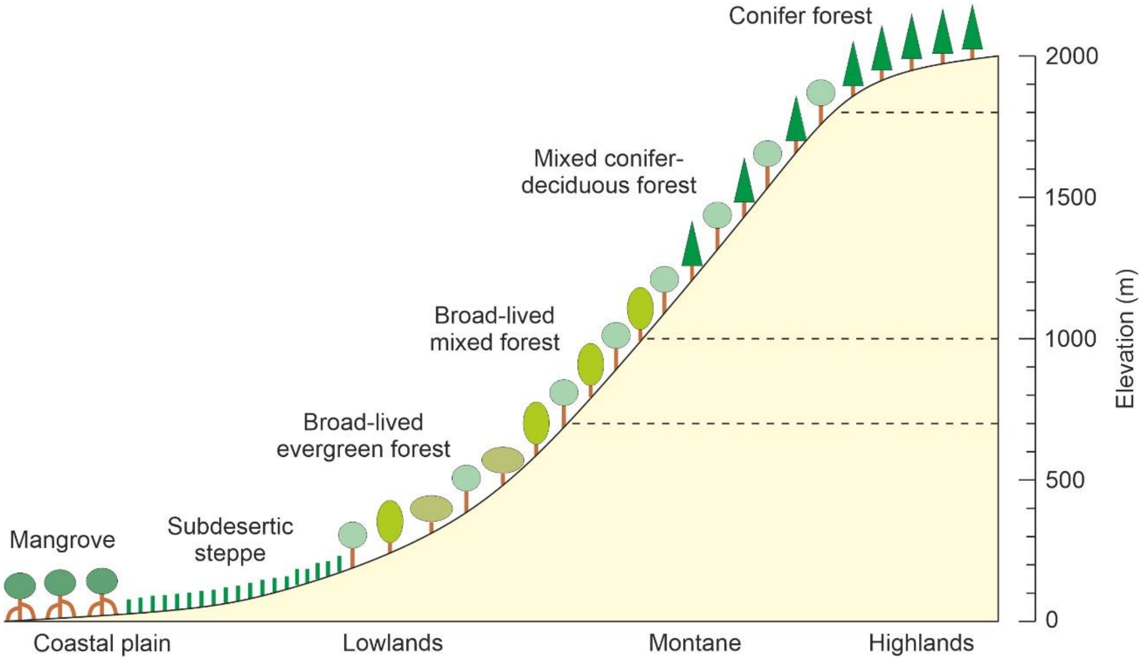

Figure 3. Altitudinal gradient of Neogene vegetation in the Iberian Peninsula, as representative of the western Mediterranean. Raw data from Jiménez-Moreno et al. (2010).

Another MA approach attempted in the Mediterranean Miocene is the biomization method, which uses the botanical affinities of fossil pollen with extant species to assign fossil taxa to the currently known plant functional types and biomes (Mahler et al., 2022). In this way, zonal plant communities such as warm-temperate evergreen conifer forests, temperate deciduous forests or cool conifer forests, along with other azonal vegetation types, such as riparian forests and wetlands, have been defined and mapped for some Iberian regions (Altoaguirre et al., 2023). The biomization method is similar to the so-called integrated plant record (IPR) analysis, a procedure previously developed for central Europe that assigns paleobotanical remains (leafs, fruits, pollen) to their nearest living relatives and the extant vegetation types they form (Kovar-Eder et al., 2008). This method has recently been used in the Iberian Peninsula together with the coexistence approach, as quoted above (Casas-Gallego et al., 2021). Both biomization and IPR methods also assume community constancy over the Neogene.

The Vallès-Penedès Basin (VPB), which is the target of this paper, is part of the NW Mediterranean subregion and lies on the NE Iberian Peninsula (Fig. 1). The few available macrobotanical records suggested tropical to subtropical vegetation and climates between 20 and 17 Ma shifting to more arid environments between 16 and 14 Ma, coinciding approximately with the Miocene Climatic Optimum, or MCO (Sanz de Siria, 1993, 2001). Palynological information is also scarce and consists of a few records suggesting the dominance of relatively open vegetation with scattered low-mid elevation forests (Bessedik, 1984, 1985; Bessedik and Cabrera, 1985; Jiménez-Moreno et al., 2010). Within a peninsular context, the VPB has been considered to be a transitional zone between the forested landscapes of the northern regions and the more open arid environments of southern and inner Iberia during most of the Miocene. To date, the available palynological information has been used primarily for the reconstruction of Middle Miocene floras and their use as paleoclimatic proxies using the abovementioned MA approach (Jiménez-Moreno et al., 2010).

In contrast, the Miocene faunal record is very rich, and the VPB has become a keystone area for the study of mammal evolution in Europe. The VPB is well known for its dense, continuous, and well-dated record of Miocene continental vertebrates, which includes hundreds of localities that have yielded tens of thousands of remains (for recent reviews, see Casanovas-Vilar et al., 2016, 2022a). Indeed, the VPB is a reference area for the European continental Miocene and even the type area for the Vallesian European Mammal Age (Crusafont, 1950; Crusafont and Truyols, 1960; Agustí et al., 1997). Most localities have been precisely dated using a combination of methods that allow constraining their age with an accuracy of 0.1–0.3 Ma, a resolution rarely achieved in continental records. The VPB record covers almost the entire Miocene but it is especially good for key intervals such as the MCO (Early/Middle Miocene; ~17–15 Ma), the Aragonian/Vallesian transition (Middle/Late Miocene; ~12.5–11 Ma) and the Vallesian faunal turnover event (early/late Vallesian, Late Miocene; ~10–8.5 Ma) (Agustí et al., 1997; Casanovas-Vilar et al., 2016, 2022a). Such good and dense record, coupled with excellent chronologic control allows for the study of terrestrial vertebrate paleobiodiversity dynamics and test its correlation with global and regional paleoenvironmental changes. These trends and events have been well studied, particularly for the Vallesian, which primarily implied the extinction of forest-dwelling mammal taxa of Middle Miocene origin, including hominoid primates (Agustí and Moyà-Solà, 1990; Agustí et al., 1997, 1999, 2003; Casanovas-Vilar et al., 2014, 2016; Madern et al., 2018). In general, the faunal record agrees with the occurrence of transitional forested to arid environments in the VPB during the Miocene (Casanovas-Vilar and Agustí, 2007; Casanovas-Vilar et al., 2008, 2010; Jovells-Vaqué and Casanovas-Vilar, 2021; Madern et al., 2018; Van den Hoek et al., 2021). However, independent palynological evidence is still insufficient for a basin-wide paleoenvironmental and paleoecological reconstruction aimed at identifying the potential drivers of the observed faunal extinction and turnover patterns.

This paper reviews the available palynological information for the study area to provide a first overview, aimed at identifying the main knowledge gaps and suggesting studies to be developed in the future, in the way toward a robust regional vegetation reconstruction. First, a brief summary of the state of the art is provided based on the few localities studied to date using MA-based paleoclimatic and paleovegetation approaches. Then, a complementary perspective is provided by using the same raw data to attempt a vegetation reconstruction based on fossil pollen assemblages defined quantitatively using statistical methods before considering the botanical affinities of the involved pollen types and the corresponding environmental assumptions. This is called the fossil community (FC) approach and has been successfully used in paleoecological reconstruction of Paleogene and Neogene tropical environments with mangroves and other coastal vegetation types (e.g., Rull, 1997, 1998, 1999, 2001, 2003). The results of both MA and FC approaches are then compared, with emphasis on the Middle Miocene, from which most records proceed. Finally, a research plan is suggested for a landscape reconstruction able to provide a regional paleoenvironmental framework for mammal evolution.

2. Geological setting

The VPB is an elongated half graben parallel to the Catalan coastline and bounded by the Catalan Coastal Ranges that formed during the opening of the Western Mediterranean by the Late Oligocene (Roca et al., 1999; Cabrera et al., 2004). Its sedimentary record covers most of the Miocene and is mainly continental except for relatively brief episodes of marine transgression. As quoted above, the Vallès-Penedès is well known for its dense, continuous, and well-dated record of Miocene continental vertebrates, which includes hundreds of localities but he paleobotanical record is comparatively scarcer and includes barely a dozen macrofossil sites, particularly of Langhian age (see Sanz de Síria, 1985, 1993, 1996, 2001), and only three palynological records (Fig. 4): La Rierussa, Sant Pau d'Ordal and Vilobí del Penedès. La Rierussa is by far the longest record and the only one for which the detailed stratigraphical provenance of the pollen samples has been reported (Jiménez-Moreno, 2005). For Sant Pau d'Ordal and Vilobí del Penedès sections only the approximate provenance of the pollen samples is given in Bessedik (1985). Palynological sites, as well as most plant macrofossil sites, occur in the marine and transitional sequences deposited during the episodes of marine transgression.

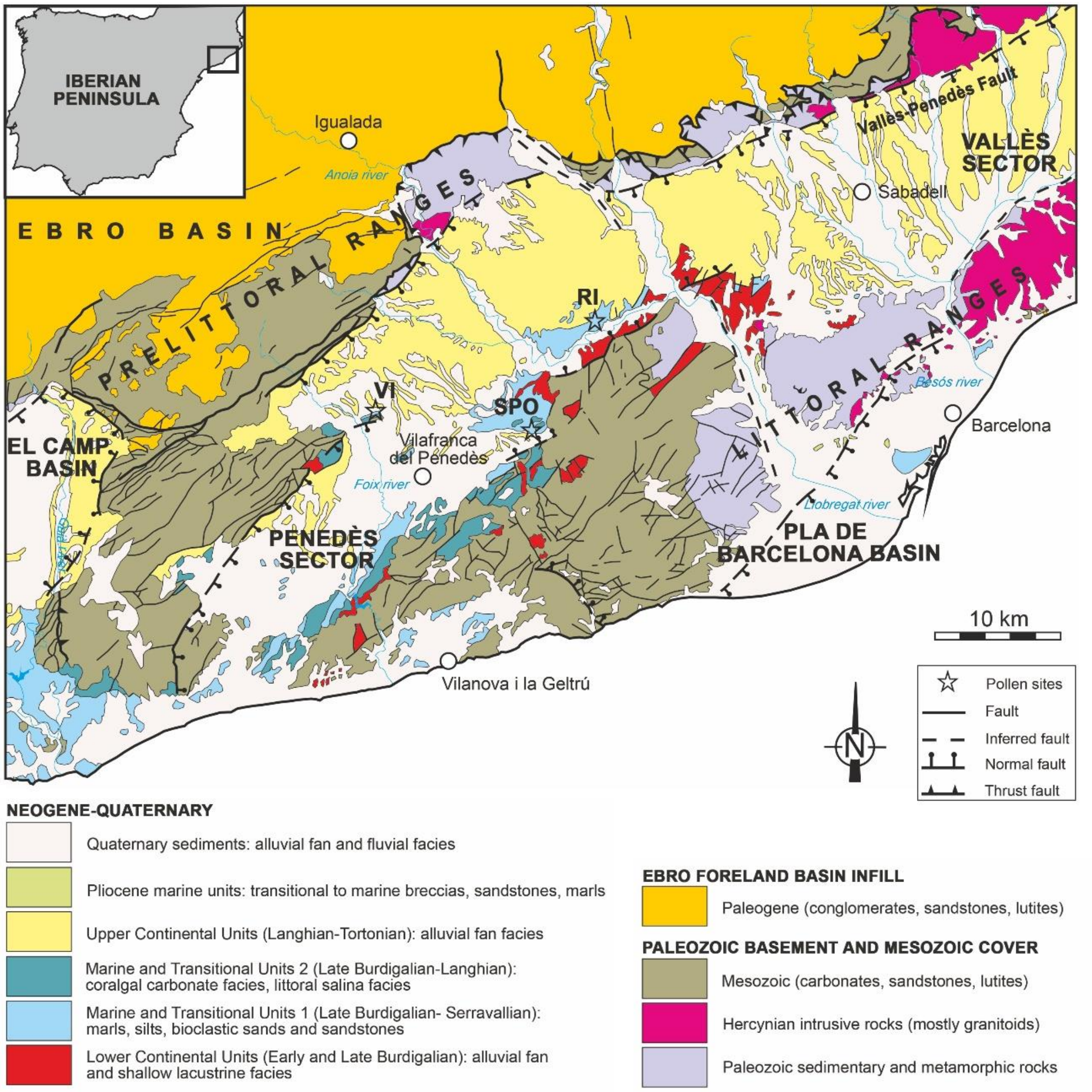

Figure 4. Simplified geological map of the Vallès-Penedès Basin showing the main lithostratigraphic units as well as all known pollen sites. RI = la Rierussa; SPO = Sant Pau d'Ordal; VI = Vilobí del Penedès. Modified from Casanovas-Vilar et al. (2016).

Marine transgressions in the Vallès-Penedès occurred during the late Burdigalian, the Langhian and the early Serravallian (Fig. 5). The sequences deposited at that that time make up the so called marine and transitional units and correspond to shallow marine environments (Cabrera et al., 1991, 2004, Cabrera and Calvet, 1996; Casanovas-Vilar et al., 2016, 2022a). The Littoral Range isolated the VPB from the Mediterranean, but the southwestern end of the basin was connected to the sea, so part of the basin was flooded during sea-level highstands. The Langhian transgression was the most important and most of the southwestern half of the basin (the Penedès Sector) was persistently flooded. Marine deposits in this area correspond to carbonate coralgal platform, marine bay, and transitional fan delta systems. During the Langhian transgressive maxima the sea extended into the northeastern half of the basin (Vallès Sector), reaching Sant Cugat del Vallès and Cerdanyola del Vallès, where poorly developed shallow marine and transitional deposits occur. Known palynological sites are located in the Penedès Sector, which was more continuously occupied by shallow marine environments.

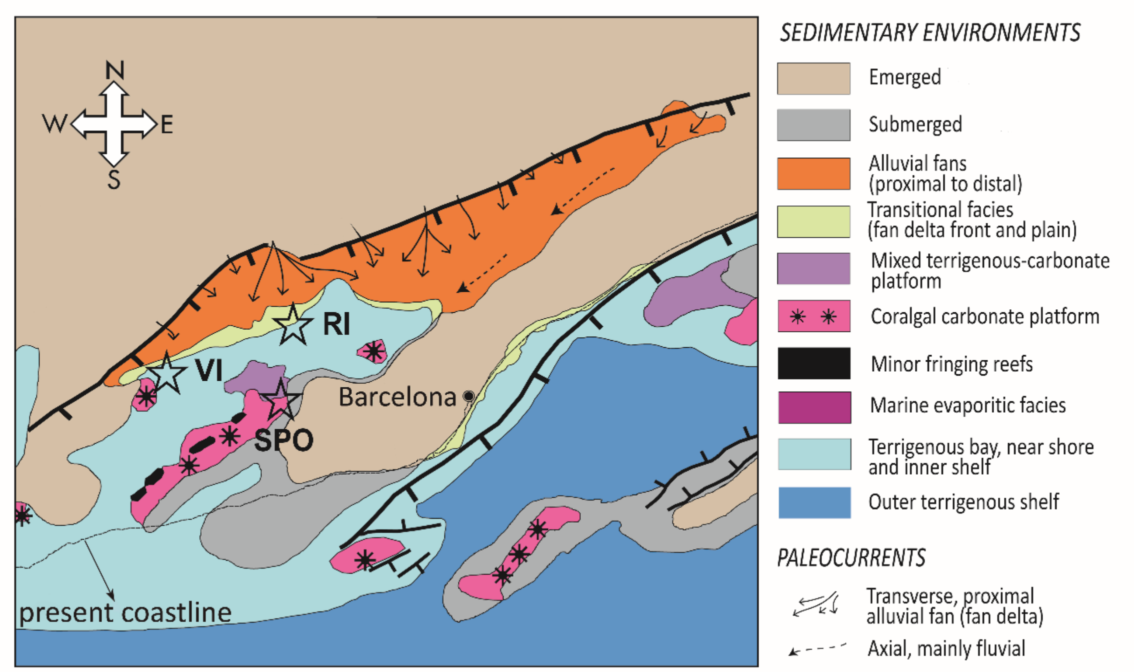

Figure 5. Paleogeographic scheme of the Vallès-Penedès Basin during the Langhian (Middle Miocene) and indicating the different sedimentary environments. The approximate location of the known pollen sites is also indicated. RI, la Rierussa; SPO, Sant Pau d'Ordal; VI, Vilobí del Penedès. Modified from Casanovas et al. (2016, 2022a).

La Rierussa is a 300 m-thick series, situated north of the town of Gelida (41°26'24" N – 01°52'02" E; Fig. 4), that alternates marine and continental sediments. From bottom to top, it has been divided into three parts: Sant Salvador, Can Raimundet (erroneously referred to as "La Rimunder" in Magné, 1978; Bessedik, 1985; and Jiménez-Moreno et al. 2005) and La Pedrera (Casanovas Cladellas et al., 1972; Magné, 1978) (Fig. 6). The lowermost part records the onset of the Langhian transgression in this sector of the basin, marked by calcareous sandstones covering the reddish continental sediments at Sant Salvador. The upper half of the Sant Salvador and Can Raimundet sections consists of blueish marls that are interpreted as shallow bay deposits (Casanovas Cladellas et al., 1972; López, 1984; Cabrera et al., 1991). The upper part of the Can Raimundet section shows the progradation of fan-delta systems, as evidenced by the progressive abundance of ocher silts and sands with ripples and cross lamination (Casanovas Cladellas et al., 1972; López, 1984; Cabrera et al., 1991). The la Pedrera section shows the same pattern, the lowermost part consisting of bay deposits interbedded with littoral bioclastic sandstones and the upper part consisting of fan-delta deposits, mostly defined by ocher sandstones (Casanovas Cladellas et al., 1972; López, 1984; Cabrera et al., 1991; Navas et al., 1994). The bluish marl deposits have yielded a rich and diverse malacofauna that includes a major proportion of tropical taxa (Navas et al., 1994; Domènech et al., 2011). Overall, la Rierussa series records the repeated progradation of fan-delta systems into variably restricted shallow bay environments (Casanovas Cladellas et al., 1972; López, 1984; Cabrera et al., 1991; Navas et al., 1994). The whole la Rierussa section is covered by reddish alluvial fan facies that evidence the retreat of marine and transitional environments. Planktonic foraminifera recovered from the bluish marls at the Sant Salvador and Can Raimundet sections indicate a correlation to zone N8 (Magné, 1978). Calcareous nannofossils have also been recovered at Can Raimundet, indicating a correlation to zone NN4 (Bessedik, 1985). Therefore, the la Rierussa section is correlated to the latest Burdigalian–early Langhian. The pollen samples were taken from the marine bluish marls as well as from the ocher clays of prodelta deposits (Bessedik, 1985; Jiménez-Moreno et al., 2005).

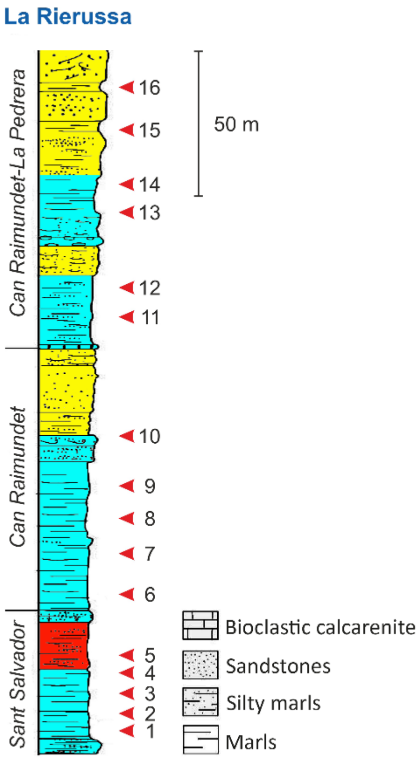

Figure 6. Composite stratigraphic section of la Rierussa outcrop based on Jiménez-Moreno (2005). Red arrows are pollen samples. Sedimentary environments (red, alluvial plain; blue, transgressive and shallow bay; yellow, delta fan) after Casanovas Cladellas et al. (1972;), López (1984), Cabrera et al. (1991) and Navas et al. (1994).

The area between Sant Sadurní d'Anoia and Sant Pau d'Ordal (Subirats) comprises a very continuous succession of the Langhian marine units (Fig. 4). The Langhian marine transgression is marked by an oyster coquina that occurs close to Sant Sadurní, a few meters in series above els Casots continental vertebrate site. The age of els Casots site has been well constrained using bio- and magnetostratigraphy and is correlated to chron C5Br, with an estimated age of 15.9 Ma, corresponding to earliest Langhian (Casanovas-Vilar et al., 2022b). Above the oyster coquina, following the road that leads from els Casots to Sant Pau d'Ordal, the marine succession consists of ocher lutites and gray marls with minor intercalations of conglomeratic sandstones and bioclastic sandstones predominantly containing oyster fragments. These deposits are interpreted as restricted bay and are rich in marine invertebrates and microfossils (Agustí et al., 1990; Cabrera et al., 1991, Domènech et al., 2011). Planktonic foraminifera recovered from these deposits indicate a correlation to zone N8, early Langhian (Magné, 1978; Bessedik and Cabrera, 1985; Agustí et al., 1990). The marine clay deposits are of variable thickness, being thicker (up to several hundred meters) toward the central part of the basin. From this point on, the marine succession includes meter-thick biocalcarenitic packstones mostly consisting of rodoliths. Finally, a small coral patch reef occurs in the succession, at the Can Sala quarry (el Pago, Subirats).

It is generally agreed that the development of reef systems in the VPB coincided with a Langhian marine transgression highstand and therefore represents a warm peak during the MCO. Reefs developed when the southeastern half of the basin was flooded and always occur near the borders of the basin. Two types of reef systems occurred: an important, 20 km-long, fringing reef system was formed bordering the Garraf mountains (Permanyer, 1990); while much smaller patch reefs also developed in small elevations, such as the Can Sala reef (Bessedik and Cabrera, 1985; Agustí et al., 1990; Permanyer, 1990; Cabrera et al., 1991; Casanovas-Vilar et al., 2022a). The Can Sala patch reef is 1 km long by 200–300 m wide, and reef facies have a maximum thickness of just 10 m; its structure and stratigraphy are described in detail in Permanyer (1990) and Cabrera et al. (1991). *Mussismilia*, *Montastrea*, *Tarbellastrea*, and *Porites* are the main coral genera present. The reef framework facies attain a maximum thickness of up to 6 m and are covered by a cap of broken branching *Porites* that would indicate very shallow water. The reef is overlain by sandy clays and sandstones with oyster fragments that are affected by a ferruginous hardground, indicating the transition toward more continental environments. Reef deposits become thinner toward the southwest where they interbed with laterally equivalent blue marls, corresponding to restricted shallow bay environments (Navas et al., 1994).

At the Can Vendrell farmhouse (Sant Pau d'Ordal; 41°27'57" N – 01°47'52" E; Fig. 4) these facies yielded three pollen assemblages (Bessedik, 1985; Bessedik and Cabrera, 1985) as well as planktonic foraminifera, which still indicate an early Langhian age (zone N8; Magné, 1978; Bessedik, 1985; Bessedik and Cabrera, 1985; Agustí et al., 1990). These marine marls are concordantly overlain by prodelta and delta front deposits mostly defined by ocher lutites and sandstones, which are poorer in paleontological content than the blue marls (Navas et al., 1994). Finally, subaerial continental alluvial fan facies cover these deposits and crop out toward the southwest, next to the Garraf reliefs. Unfortunately, a stratigraphic display of this section with the location of samples is unavailable in the literature.

The Vilobí del Penedès outcrop (41°23'03" N – 01°39'42" E; Fig. 4) represents a different geological setting. The succession is situated on an elevated block of the basin that brings to the surface basement rocks, here defined by Cretaceous limestones (Ortí and Pueyo, 1976; Permanyer, 1990). These sediments are unconformably overlain by a 5–10 m succession of continental breccias, gray lutites and lacustrine limestones belonging to the Early Miocene (Ortí and Pueyo, 1976; Agustí et al., 1990; Bitzer, 2004; Sánchez-Román et al., 2023). These units are followed by the thick (~145 m according to Sánchez-Román et al., 2023) Vilobí Gypsum Unit, which mostly consists of secondary gypsum but with primary laminated gypsum at the top. Recent interpretations of the depositional environment of the gypsum unit conclude that alternated between a sabkha and a less restricted coastal salina (Sánchez-Román et al., 2023). The Vilobí Gypsum Unit is covered by a 7 m-thick succession of alternating reddish and grayish continental lutites that are interbeded by with primary gypsum in its lowermost part (for a detailed description of this part of the succession, see Sanjuan et al., 2023). These layers have yielded abundant small oyster fragments, ostracods, charophytes (Sanjuan et al., 2023), planktonic foraminifera (Magné, 1978), small mammals (Jovells-Vaqué and Casanovas-Vilar, 2021) and seven pollen samples (Bessedik, 1984). As it occurs in Sant Pau d'Ordal, a stratigraphic scheme with the location of pollen samples is unavailable. The planktonic foraminifera indicate a correlation to zone N8 (early Langhian; Magné, 1978), which agrees with the recovered rodent fauna indicating a correlation with the Aragonian regional mammal age subzone Cb (i.e., earliest Middle Miocene; Jovells-Vaqué and Casanovas-Vilar, 2021).

These deposits are finally covered by an oyster biocalcarenite, analogous to those observed marking the Langhian marine transgression in other areas of the basin. Sánchez-Román et al. (2023) refined the age of these deposits correlating $^{87}Sr/^{86}Sr$ ratios of the dolomites interbedded with the gypsum layers and oyster shell fragments from the biocalcarenites atop the succession with the global Sr curve. This yielded an age of 18.15 Ma (early Burdigalian) for the bottom of the gypsum unit and 16.05 Ma (terminal Burdigalian) for the oyster biocalcarenite on the top. The recovered charophyte flora provides valuable clues about the existing paleoenvironment. The six samples studied from Vilobí solely include *Lamprothamnium papulosum*, the most halotolerant species of living charophytes (Sanjuan et al., 2023). This indicates that after the deposition of the Vilobí Gypsum Unit, the sedimentary environment still represented a coastal salina with some seasonal decrease in salinity (up to 10‰). Evaporation in these variably restricted coastal salinas was certainly favored by the warm climate associated with the MCO.

In summary, the three studied outcrops date back to the latest Burdigalian–early Langhian and represent marine to transitional environments that were deposited in the Penedès Sector of the VPB basin, in the context of the marine transgressions associated with the MCO. These outcrops are very close in age, although not chronologically equivalent. On the other hand, they are associated with different coastal to shallow marine environments, ranging from restricted bay (Sant Pau d'Ordal, part of la Rierussa section) to delta fan facies (part of la Rierussa section) and coastal salinas (Vilobí del Penedès). These different depositional environments, together with minor age differences, may also account for some differences in pollen composition (see below).

3. Previous palynological studies

The la Rierussa and Sant Pau d'Ordal Langhian records were used in the recent reconstructions of the western Mediterranean region mentioned in the introduction, and their summary pollen diagrams are shown in Fig. 7. The most complete record is la Rierussa, where the pollen spectra were dominated by herbs and shrubs (Poaceae, Asteraceae and halophytes such as Amaranthaceae, Plumbaginaceae). Mega-mesothermic elements (*Taxodium*-type, *Myrica*, Sapotaceae, *Engelhardia* and *Platycarya*) were also abundant, followed by megathermic taxa (*Avicennia*, Rubiaceae, *Mussaenda*-type, Euphorbiaceae, *Croton*, *Bombax*). Mesothermic elements were represented by *Carya*, deciduous *Quercus*, Fabaceae, *Zelkova*, *Acer*, *Salix* and *Liquidambar*. High-elevation elements were scarce and represented only by *Cathaya* and *Sciadopitys* (Jiménez-Moreno, 2005). Using the climate amplitude method, Fauquette et al. (2007) estimated MAT of ~20 °C (~4 °C above the present) and MAP of ~1000 mm (~450 mm above the present) during the MCO. The occurrence of Caesalpiniaceae and Mimosoideae (*Acacia*) was interpreted in terms of high seasonality. The absence of subdesertic taxa such as *Lygeum*, *Nitraria*, *Prosopis*, *Neurada* and *Calligorum* suggested that the climate was less arid and seasonal than in southern Iberia, where these elements were abundant (Jiménez-Moreno and Suc, 2007). The whole assemblage suggested relatively open vegetation with scattered low-mid elevation forests along rivers and around lakes (Jiménez-Moreno and Suc, 2007). The presence of impoverished *Avicennia* mangrove communities on the coasts was deduced from the consistent presence (up to 5%) of pollen from this taxon, especially in the lower half of the section.

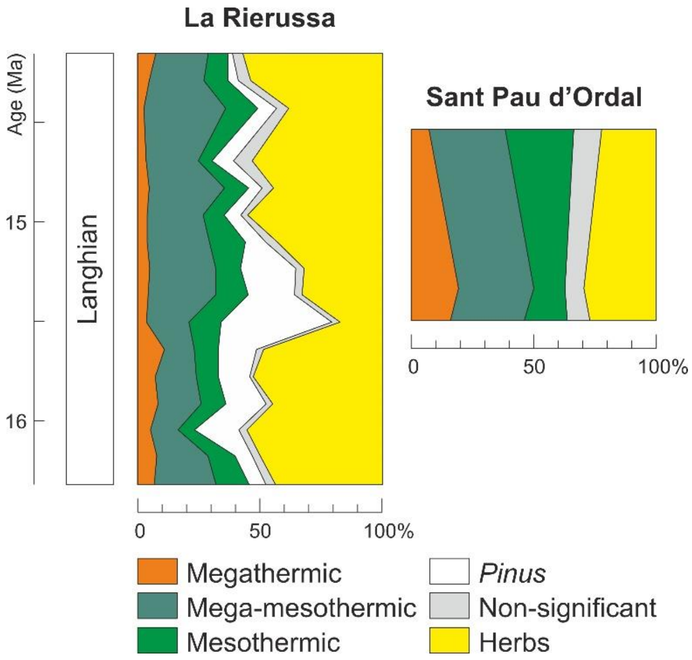

Figure 7. Synthetic pollen diagrams of la Rierussa and Sant Pau d'Ordal. Redrawn from Jiménez-Moreno et al. (2010) and carrion et al. (2022). The nonsignificant group gathers the pollen types with unclear bioclimatic meaning.

The Sant Pau d'Ordal section yielded similar results, but *Pinus* was not a major component, and micro-mesothermic elements, especially *Alnus*, were more abundant. *Avicennia* was also present in percentages up to 3% (Bessedik, 1985; Bessedik and Cabrera, 1985). Vegetational and climatic patterns similar to la Rierussa were inferred for this section (Jiménez-Moreno and Suc, 2007). In the Vilobí sequence (Late Burdigalian-Early Langhian), the trends were also similar, but *Ephedra* was more abundant and *Avicennia* was present in a single sample with values below 1%, which suggested a more inland setting than in the former localities (Bessedik, 1984, 1985). In the three sections, the most productive palynological samples corresponded to marls deposited in shallow marine environments. The presence of coastal *Avicennia* mangroves is supported by studies of modern pollen sedimentation showing that the pollen of this genus is underrepresented with respect to the abundance and cover of its parent plants. *Avicennia* pollen is abundant (25-40%) only locally under the mangrove canopy, and its percentages rapidly decline (1-5%) in shallow marine settings in front of coastal mangroves and disappear further offshore. As this pollen is transported mostly by rivers, it is usually absent in inland environments situated upstream of mangroves (Muller, 1959; Rull, 2022a).

It is important to highlight that only the climate amplitude method of paleoclimatic estimation (Fauquette et al., 1988) and the elevational vegetation model displayed in Fig. 3 (Jiménez-Moreno et al., 2010) have been used to date in the VPB. Other MA-based methods of paleoclimatic estimation and vegetation reconstruction mentioned above, such as the coexistence approach (Utescher et al., 2014), the biomization (Mahler et al., 2022) or the IPR methods (Kovar-Eder et al. 2008), have not yet been attempted in the area.

4. A fossil community approach

4.1. Raw data and statistical methods

This section uses the raw data from the above studies, which are available in publications and public databases, to identify the quantitative fossil pollen assemblages before making inferences based on their botanical affinities with extant counterparts. In this way, the possibility of past associations different from present ones representing vegetation types with no modern analogs is preserved. Numerical data (pollen counts) are available for two sections, la Rierussa and Sant Pau d'Ordal, whereas the Vilobí results are available only as a percentage diagram (Bessedik, 1984). Raw data from la Rierussa were retrieved from the Dryad database (Suc et al., 2022), and the same type of data from Sant Pau d'Ordal were taken from Bessedik (1985). Some old taxonomical terms have been replaced by their present equivalents. For example, the former families Taxodiaceae, Abietaceae, Chenopodiaceae and Mimosaceae are now subfamilies (Taxodioideae, Abietoideae, Chenopodioideae and Mimosoideae) of the families Cupressaceae, Pinaceae, Amaranthaceae and Fabaceae, respectively. Other terms have also been updated to fit with the formal botanical nomenclature; for example, Gramineae has been changed to Poaceae, Compositae to Asteraceae, Labiatae to Lamiaceae and Leguminosae to Fabaceae. In la Rierussa, fossil pollen assemblages were obtained by cluster analysis using the linear correlation and the unweighted pair-group method with arithmetic mean (UPGMA) on taxa above 0.5% of the total. Details on these statistical methods are available in Hammer and Harper (2005). Other multivariate techniques may be used to define fossil assemblages (Rull, 2003), but the reasoning behind is the same, i.e., defining fossil assemblages per se with no prior reference to modern analogs. Statistical analyses were performed with Past 4.12 (Hammer et al., 2001). The software psimpoll 4.27 was used for diagram plotting and zonation, which was performed by optimal splitting by information content (OSIC) and the brocken-stick method (Bennett, 1996). In the Sant Pau d'Ordal and Vilobí sections, pollen assemblages were established visually, in the absence of a statistically significant number of samples in the former and the lack of numerical data, in the latter.

4.2. La Rierussa

This is the most extensive section regarding pollen analysis. Unfortunately, the depth and age of each sample are unavailable in the corresponding publications/databases, although it is known that the whole record corresponds to the Langhian. The diagram is dominated by *Pinus* and Taxodioideae (trees) and Poaceae (herbs) (Fig. 8). Stratigraphic shifts in these and the other taxa defined three pollen zones, from bottom to top: RI-1, codominated by trees (*Pinus*, Taxodioideae) and herbs (Poaceae, Amaranthaceae, Cichorioideae); RI-2, dominated by trees (*Pinus*, *Taxodium*, *Engelhardia*); and RI-3, which is similar to RI-1 but with higher amounts of *Taxodium* to the detriment of *Pinus*.

Two major groups and six pollen assemblages were defined by cluster analysis using the same pollen types of the diagram (Fig. 9). Group A is formed mainly by herbaceous taxa, and group B is composed mainly of trees and shrubs. Group A was subdivided into three assemblages: A1, mostly herbs and dominated by Poaceae; A2, with herbs and trees, including mangrove taxa (*Avicennia* and Amaranthaceae); and A3, with a mixture of herbs and trees. Assemblage A2 was further subdivided into A2a and A2b, the first dominated by Amaranthaceae and other herbs, and the second dominated by *Avicennia*. Notably, *Plantago*, also part of A2, did not fit with either A2a or A2b. Group B was subdivided into two assemblages: B1, characterized by trees and shrubs (notably Taxodioideae, *Platycarya*), and B2, characterized by *Pinus* and other trees (*Engelhardia*, *Mussaenda*).

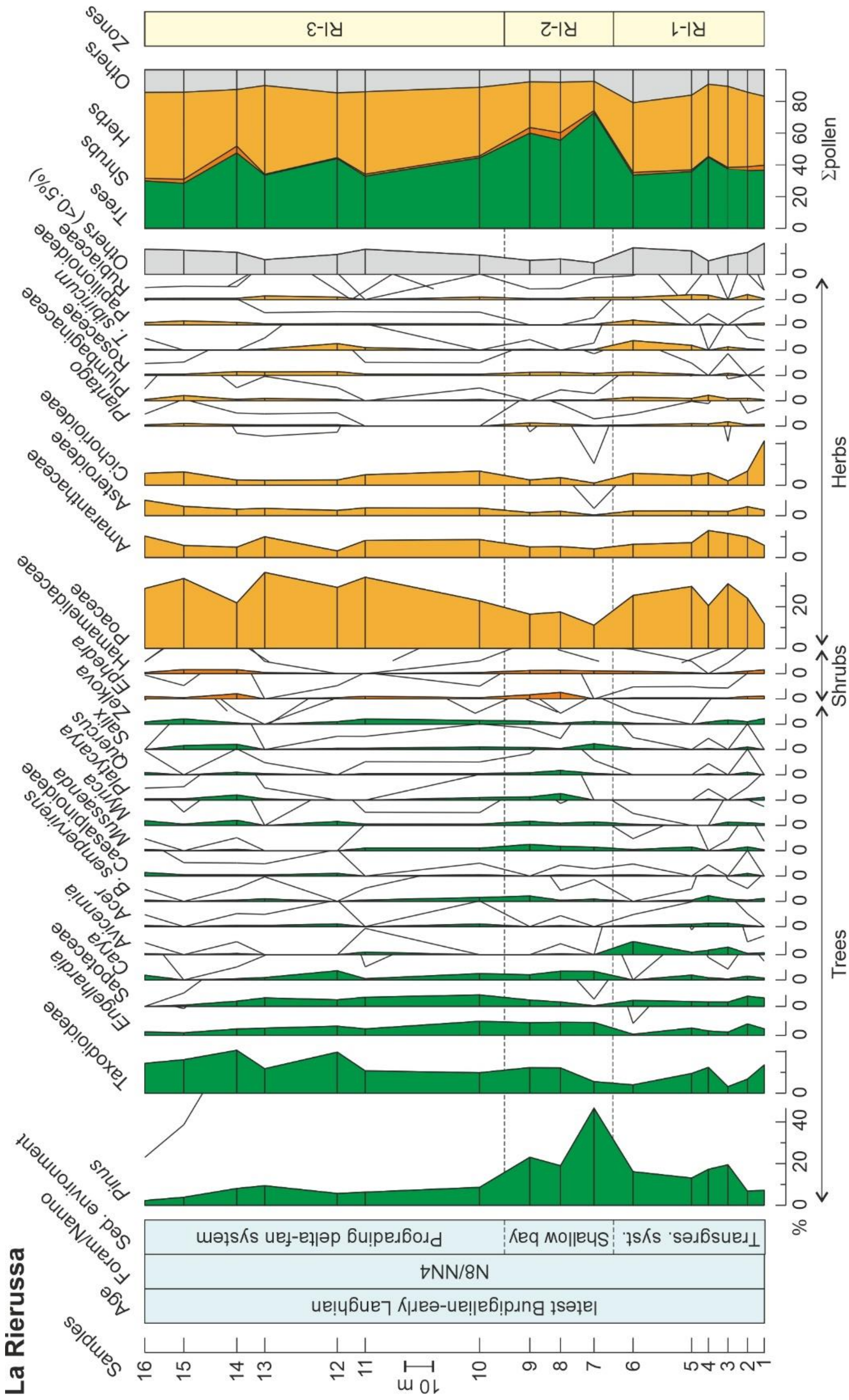

Figure 8. Percentage pollen diagram of the la Rierussa section using the taxa above 0.5% of the total (taxa below this boundary are grouped as "others"). See Fig. 6 for the location of samples. *T. sibiricum*, *Tricolporopollenits sibiricum*.

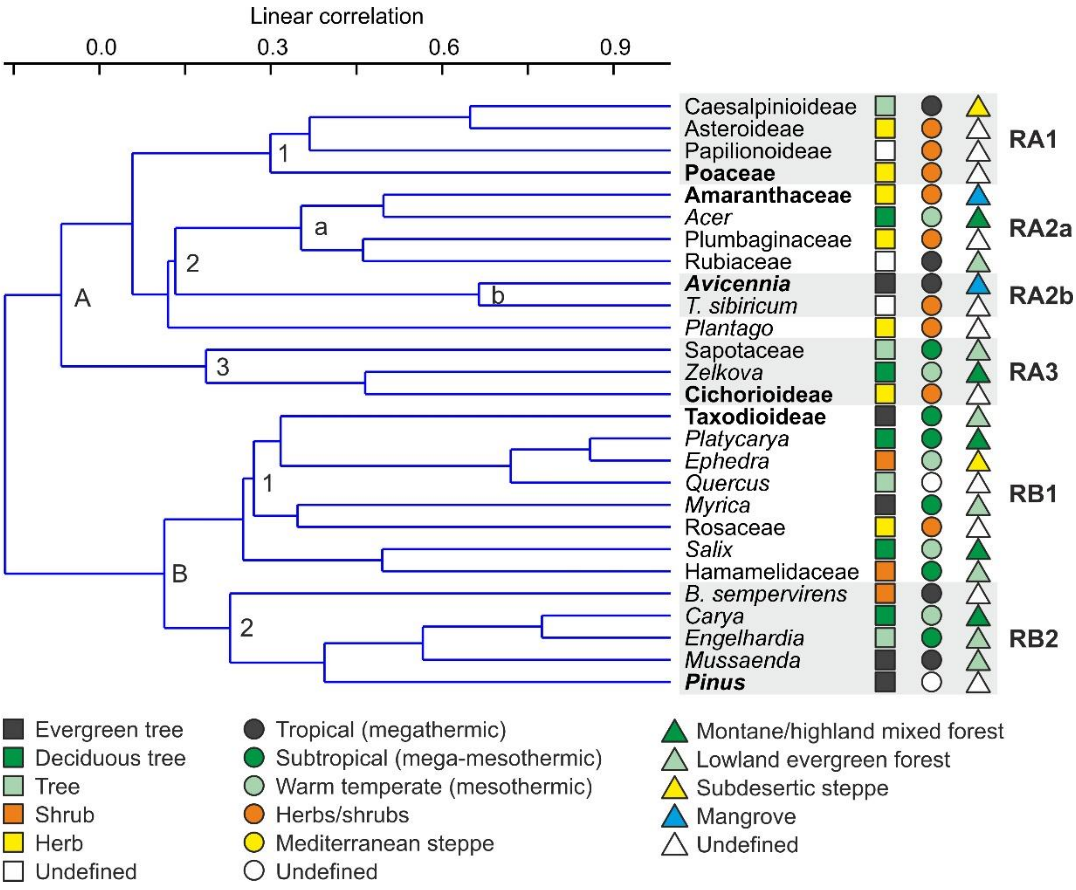

Figure 9. Cluster analysis using the taxa above 0.5% of the total pollen counts from the la Rierussa section. The dominant types of each assemblage are in bold. Squares indicate the habit according to the modern plant representatives, circles are the floristic groups established for the Mediterranean region (Suc et al., 2018), and triangles correspond to the vegetation types defined previously using modern analogs (Jiménez-Moreno et al., 2010). *B. sempervirens, Buxus sempervirens*; *T. sibiricum*, *Tricolporopollenits sibiricum*.

Using only the general features (notably the habit) of the involved taxa, with no reference to the specific environmental requirements of their assumed modern counterparts, these pollen assemblages are tentatively considered to represent the following vegetation types: A1, grass meadows with Asteroideae; A2a, open amaranth stands; A2b, *Avicennia* mangroves; A3, Sapotaceae-Cichorioideae mosaic/parkland vegetation; B1, Taxodioideae woodlands (likely swamps); and B2, pine forests with *Engelhardia*. The stratigraphic arrangement of these vegetation types can be seen in Fig. 10. The better represented assemblages in Zone RI-1 are grass meadows and pine forests. The abundance of *Avicennia* (5-10%) is consistent with the presence of mangrove communities dominated by this tree in the adjacent coasts. Notably, the fossil species *Tricolporopollenites sibiricum*, of unknown botanical affinity (Jiménez-Moreno, 2005), is well associated statistically with *Avicennia*, suggesting that its parent plant may be a mangrove-related element. A significant shift occurred in Zone RI-2, when pine forests began to dominate to the detriment of herbaceous communities and mangroves, coinciding with the presence of blue marls deposited in shallow-bay environments. It is possible that the mangrove decline is due to the shift to more marine sediments and the ensuing decrease in *Avicennia* pollen, which is known to settle close to the coast and rapidly decline offshore (Muller, 1959; Rull, 2022a). Taxodioideae swamps also increased, indicating a general increase in regional forest cover. In Zone RI-3, the situation reverts to former vegetation patterns (RI-1) but with a relevant reduction in mangroves, which end by disappearing toward the top, and the increasing importance of Taxodioideae swamps. Whether this could be linked to the dominance of inland environments, where mangrove pollen is mostly absent, or to a regional cooling, as suggested by former MA-based studies, or both, remains to be attested.

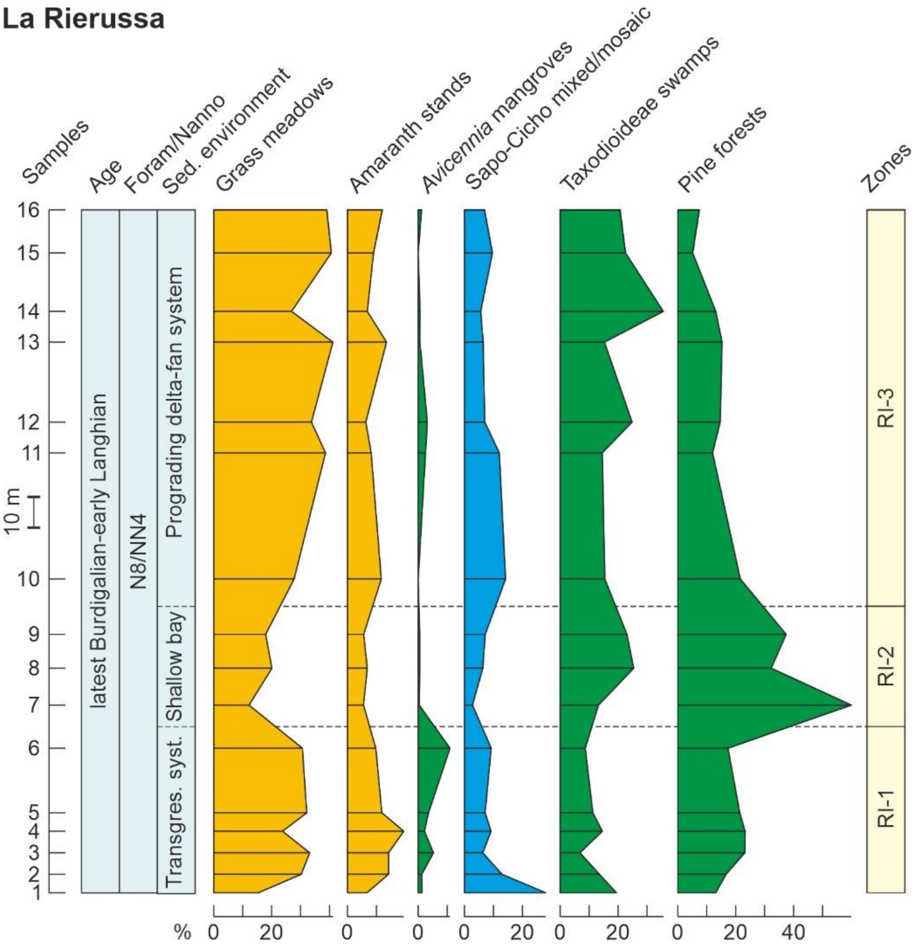

Figure 10. Stratigraphic arrangement of pollen assemblages obtained by cluster analysis (Fig. 8).

4.3. Sant Pau d'Ordal

According to Bessedik (1985), only three samples from this section contained enough pollen to calculate reliable percentages, which is insufficient to define statistical associations. However, the homogeneity among the three samples (Fig. 11) suggests the existence of a single assemblage (OA1) representing the same vegetation type. The assemblage is dominated by trees (80% or more), which indicates a forested community codominated by Abietoideae, *Engelhardia*, *Dodonaea* and *Alnus*. Secondary elements are Sapotaceae, *Platycarya*, *Carya* and *Olea*. Elements that were dominant in the la Rierussa forests, notably Taxodioideae and *Pinus*, are not important here, which suggests the existence of very different vegetation types. Given the well-known wind dispersal ability of pollen types such as *Pinus* and Abietoideae, these differences could be of regional extent, which is remarkable in localities separated by barely 10 km. Another difference is the comparatively lower percentage of *Avicennia* (up to 3%) compared with the maximum in la Rierussa (up to 6%). These percentages are in the range of shallow-marine environments not far from the coastal mangrove communities, which coincides with the presence of blue marls and delta front deposits. It is possible that the time interval covered by the Sant Pau d'Ordal record does not coincide with that represented in the la Rierussa record, but the available dating resolution is not enough for a definite answer. The vegetation type defined by the Sant Pau d'Ordal pollen record will be tentatively called mixed (evergreen-deciduous) Abietoideae-*Engelhardia*-*Dodonaea* forest. It is also possible that the

Sant Pau d'Ordal record is a mixture of more than one vegetation type, but this cannot be confirmed with the available evidence. However, even in this case, the regional picture represented in the Sant Pau d'Ordal and la Rierussa records is significantly different in both vegetation types and forest cover.

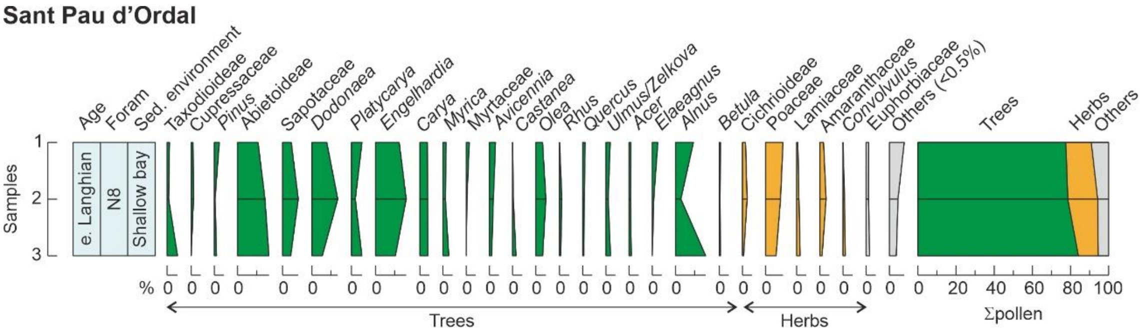

Figure 11. Percentage pollen diagram of the Sant Pau d'Ordal section using pollen types above 0.5% of the total (taxa below this boundary are grouped as "others").

4.4. Vilobí del Penedès

No raw data were found for this section, and only a percentage pollen diagram is available in the corresponding publications (Bessedik, 1984, 1985; Bessedik and Cabrera, 1985). Therefore, the fossil pollen assemblages were defined visually according to the stratigraphic arrangement of these abundances considering only the pollen types above 1%, which is the information provided in these publications (Fig. 12). In general, the diagram is dominated by herbs (Poaceae, Asteraceae and Amaranthaceae), with the most important tree taxa corresponding to Abietoideae, Sapotaceae, *Platycarya*, *Enegelhardia*, and locally *Croton*. Additionally, noteworthy is the consistent presence of *Ephedra* (which was absent or scarce in the la Rierussa and Sant Pau d'Ordal sections) in abundances of approximately 10%, along with the absence of *Avicennia*, which is present in a single sample from Vilobí in negligible percentages (<1%). The defined pollen assemblages and the potential parent vegetation types are listed in Table 1.

The sequence began with mosaic parkland vegetation of herbs (Asteraceae) with tree (*Croton*) stands (VA5) and rapidly shifted to grass meadows with different trees (*Platycarya*, *Engelhardia*) and shrubs (*Ephedra*) (VA4). Then, the herbaceous vegetation became less grassy and dominated by other herbs (Asteraceae and amaranths) with scattered *Ephedra* shrubs (VA2) to return to grass meadows of the VA4 type, but that time had fewer shrubs and enhanced tree diversity (Abietoideae, *Platycarya*, *Engelhardia*, Taxodioideae). Then, the open vegetation also diversified with the increase in Asteraceae and amaranths and the dominance of *Engelhardia* in the arboreal stratum (VA3) after returning to the VA2 type with more *Platycarya* and fewer *Ephedra*. The sequence ends with amaranth-dominated herbaceous communities with trees (Abietoideae, Sapotaceae) and shrubs (*Ephedra*) (VA1). These associations were more similar to those defined in la Rierussa, especially the grass meadows and amaranth stands, which resembled the RA1 and RA2a assemblages of Zone RI-3. The main difference was the abundance and diversity of conifers and deciduous trees, which was greater in Vilobí, and the absence in this section of pine and Taxodioideae swamps, as well as the lack of *Avicennia* mangroves and Sapotaceae-Cichorioideae mixed communities. In general, the scarcity of forested vegetation (including mangroves), along with the importance of amaranth stands and the consistent presence/abundance of *Ephedra*, may suggest the dominance of herbaceous halophytic vegetation typical of arid coastal environments, which is consistent with the sedimentological evidence indicating continental evaporitic settings.

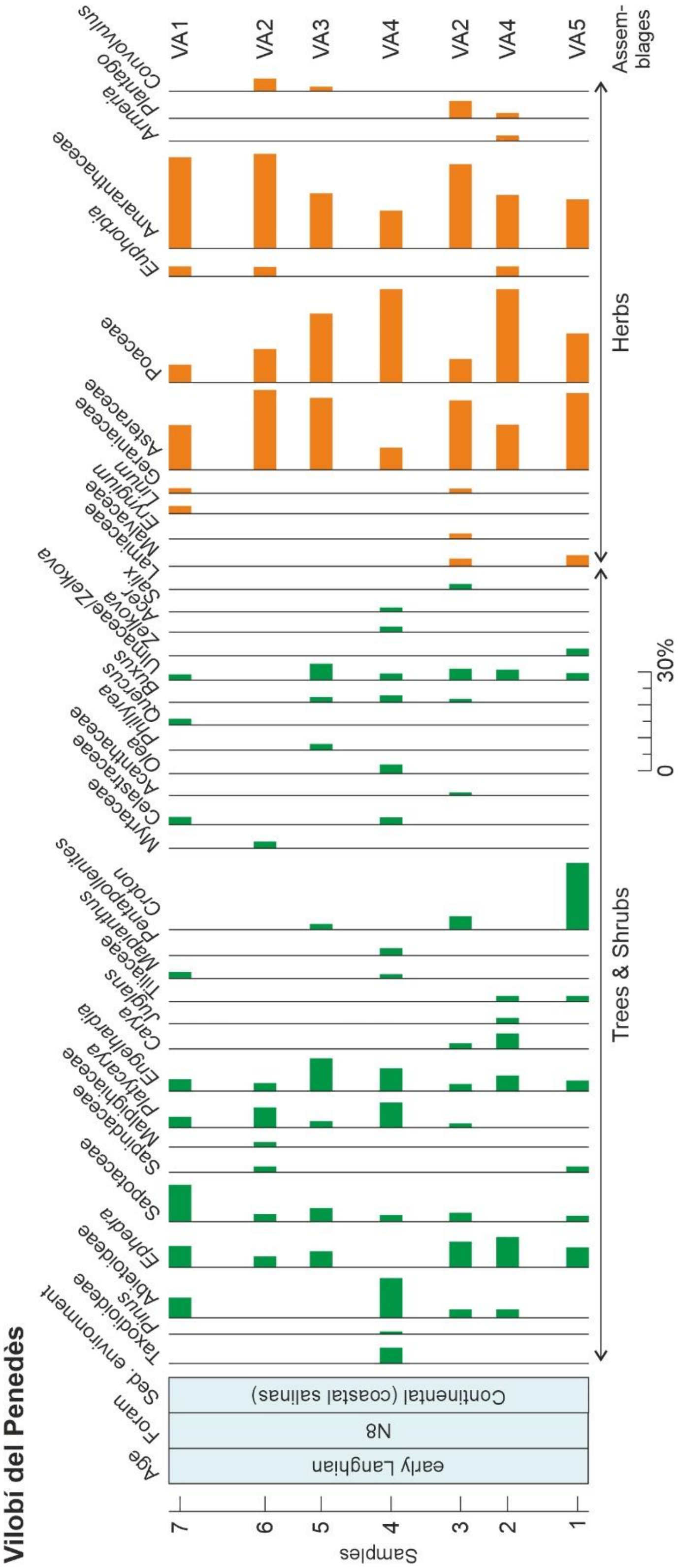

Figure 12. Percentage pollen diagram of the Vilobí outcrop considering only the types above 1% of the total pollen sum. Trees/shrubs are in green, and herbs are in orange. Redrawn and simplified from Bessedik (1984). See Table 1 for the definition of assemblages VA1 to VA5.

Table 1. Pollen assemblages defined in the Vilobí record by visual analysis considering the dominant-subdominant pollen types (see Fig. 12 for details).

Assemblage	>20%	15-20%	1-10%	Vegetation
VA1	Amaranthaceae	Asteraceae Sapotaceae	Abietoideae *Ephedra* Poaceae	Open amaranth stands with trees and shrubs
VA2	Amaranthaceae Asteraceae	Poaceae	*Ephedra* *Platycarya* *Plantago*	Open amaranth-Asteraceae stands with trees and shrubs
VA3	Asteraceae Poaceae	Amaranthaceae *Engelhardia*	*Ephedra* Sapotaceae Ulmaceae/*Zelkova*	Open diverse meadows with scattered trees
VA4	Poaceae	Abietoideae Amaranthaceae Asteraceae	*Platycarya* *Engelhardia* Asteraceae Taxodioideae	Grass meadows with trees and shrubs
VA5	Asteraceae *Croton*	Amaranthaceae Poaceae	*Ephedra*	Mosaic/parkland vegetation

4.5. Overall assessment

In summary, little coincidence has been observed among pollen assemblages and vegetation types in the three studied localities, except for some open plant communities from la Rierussa and Vilobí. Whether this is due to abrupt environmental changes across short spatial sedimentary gradients, lack of synchrony among the pollen records, or both, remains to be established with future studies. The most forested communities were documented in the Sant Pau d'Ordal record, with 80% or more arboreal pollen, and the most open landscapes were reported in the Vilobí area, with herbs typically attaining >60% of the total pollen sum. The la Rierussa record showed fluctuating values of forest cover, with maxima in Pollen Zone RI-2 and minima at the top of the record. Regarding mangroves, the la Rierussa record attained maximum values consistent with the presence of communities of this type near the sampling site, whereas the Vilobí record was characterized by the absence of mangrove pollen, likely due to its more continental setting, as already suggested by sedimentological studies (Bessedik, 1985). In the Sant Pau d'Ordal section, mangrove pollen displayed intermediate values, characteristic of shallow-marine environments. The low chronological resolution prevents us from establishing more detailed correlations among the three sections.

5. Comparison of modern analog and fossil community approaches

This section compares the results of the MA and FC approaches in the three studied sections. The modern analog information for the Neogene has been taken from Suc et al. (2018), in reference to biomes and climatic niches, and Jiménez-Moreno et al. (2010), for community arrangement and composition. The first part compares the results of both approaches in each sequence, while the second part highlights some methodological aspects that may be important for the interpretation of these and other Neogene pollen records.

5.1. Ad hoc comparisons

In the la Rierussa sequence, this information has been placed close to the dendrogram to facilitate visualization (Fig. 9). In general, the open communities represented by RA assemblages were dominated by elements of the herb/shrub biome with some megathermic (tropical) trees, especially in the mangrove assemblage (RA2b). Forest assemblages (RB) were characterized mostly by tropical, subtropical and warm temperate trees. The scarcity of elements from Mediterranean steppes and sclerophyll vegetation is noteworthy, which indicates that these biomes were still absent from the region during the time interval studied (Langhian). Within RB assemblages, tropical elements were restricted to RB2 (pine forests), and subtropical elements were more characteristic of RB1 (Taxodioideae swamps), whereas warm-temperate taxa were represented in both groups. The decline in *Avicennia* mangroves and the increase in Taxodioideae swamps across the RI-1/RI-2 boundary would be consistent with former interpretations suggesting a regional replacement of megathermic mangroves by mesothermic *Taxodium/Glyptostrobus* swamps in coastal environments during the general southward retreat of the megathermic biome after the MCO (Suc et al., 2018; Popescu et al., 2021) (Figs. 1 and 2). Regarding vegetation types, little coincidence existed among the assemblages defined by the FC approach utilized here (Fig. 9) and the former vegetation units defined on the basis of modern analogs (Fig. 7).

The most abundant taxa of the Sant Pau d'Ordal forest assemblage (Fig. 11) belong to a wide range of floristic groups – mega-mesothermic/subtropical (*Dodonaea*, *Engelhardia*, *Platycarya*, Sapotaceae), mesothermic/warm-temperate (*Alnus*, *Carya*) microthermic/cool-temperate (Abietoideae) and Mediterranean (*Olea*) biomes – and vegetation types – lowland broad-leaved evergreen forests (*Engelhardia*, Sapotaceae), lowland sclerophyll vegetation (*Olea*), montane evergreen/deciduous forests (*Carya*, *Platycarya*) and highland conifer forests (Abietoideae). Once more, steppe dominants (*Artemisia*, *Ephedra*) were scarce or absent. In the case of Vilobí, all the dominant taxa of open communities were from the herb/shrub floristic group, and one of them was characteristic of coastal halophytic vegetation (Amaranthaceae), whereas the others (Poaceae, Asteraceae) were present in a diversity of open communities. Among the main tree elements, some were subtropical (Sapotaceae, *Platycraya*, *Engelhardia*), and others were warm and cool-temperate (Taxodioideae, Abietoideae). In this case, a steppe element (*Ephedra*) was already present, although the dominance of this biome (*Artemisia*) was still absent. These taxa represented two main lowland vegetation types: broad-lived evergreen forests (*Engelhardia*, *Platycarya*, Sapotaceae, Taxodioideae) and subdesertic open communities of halophytic vegetation (Amaranthaceae, *Ephedra*). As in the former sections, *Artemisia* remained absent.

In summary, some coincidences existed among the FC-based vegetation types established here and some of the traditional modern analog groups, especially in the la Rierussa record. However, little agreement has been found with the previously established vegetation types based on botanical affinities of fossil pollen taxa, except in the case of the Vilobí record. This suggests that there is still room for improvement in these research fields.

5.2. Methodological and conceptual insights

As stated above, MA approaches largely rely on the concepts of niche conservatism and community constancy, whereas the FC approach considers the possibility of past taxa having contrasting autecological requirements with their present botanical equivalents and forming different ecological communities. The principle of niche conservatism has been considered relevant in the case of long-lasting ecosystems (Wiens et al., 2010) and important for the assembly of European biomes, including the Mediterranean (Lososová et al., 2020). However, in modern ecology, it is known that environmental niches are species specific (Rull, 2020), which represents a handicap for paleoecological reconstruction using pollen, usually identified at the genus/family level at most. To circumvent this drawback, the climate amplitude method considers the niches of all modern species from each genus/family. However, this does not account for the possibility of modern species being of more recent origin, past species having different autecological requirements, and/or both having experienced adaptive evolutionary changes. Indeed, inferences about the ecological requirements of past taxa assume identity with their present counterparts based solely on pollen morphology, which is a conservative character that is less affected by evolution than other phenotypic features directly influencing species-environmental relationships, notably ecophysiological traits (Krassilov, 2000). In summary, taxonomic resolution, speciation, extinction and physiological evolution are serious drawbacks for the a priori application of the niche conservatism hypothesis. In addition, taxonomic affinity between fossil and extant species decreases with time due to evolution, which progressively reduces the possibility of extant species being reliable modern analogs for older fossils. Establishing a chronological boundary for this reliability is not possible with the available information (Matthaeus et al., 2023).

The developers of the climate amplitude method for paleotemperature estimation are aware of these weaknesses and asked two fundamental questions in relation to climatic niche conservatism: have the ecological requirements of plants varied over time?, and how far back can we go (using this approach)? According to the same authors, answering these questions is fundamental to evaluate the reliability of their own results, but they remain to be answered (Fauquette, 2017). Unfortunately, the above issues cannot be resolved solely by theoretical considerations based on the principle of uniformitarianism (Romano, 2015). Rather, the climatic requirements of past plant taxa should be sought on empirical evidence, that is, on the case-by-case analysis of their fossils in relation to independent paleoclimatic proxies, usually of physico-chemical nature, such as elemental analysis, stable isotopes or biomarkers or leaf-margin analysis, among others (Elias, 2020). For example, paleoclimatic reconstructions using leaf-margin analysis have recently been carried out in the Late Miocene of the nearby La Cerdanya Basin (Tosal et al., 2021) and could be attempted in the VPB. The same is true for the taxonomic composition of past communities, which should be derived from the analysis of fossils themselves – for which the FC approach is able to provide direct evidence – rather than from extant assemblages.

In vegetation reconstruction, there is an additional consideration, as the idiosyncratic nature of species' response to environmental shifts leads to substantial changes in community composition, even during periods when the taxonomic identity and autecological requirements of past and present taxa are highly reliable, such as the Quaternary (Rull, 2020). Therefore, special care is needed when using the principle of niche constancy in palynology, in terms of vegetation reconstruction. Finally, the possibility of paleoenvironmental reconstruction using pollen evidence leading to circularity is also worth mentioning. Indeed, pollen-based paleoclimatic estimates cannot be used to infer vegetation responses to climatic drivers using the same palynological evidence. For example, in our case, it is not possible to infer arid climates from the presence of dry steppes and then claim that aridity favored the expansion of steppe vegetation. This may seem trivial, but it is a latent danger, especially when a paleoclimatic framework becomes established with time and the actual proxies used to generate it are not considered. These considerations do not invalidate the use of modern environmental and vegetational analogs but call for careful use of this approach.

In our case – and in the Mediterranean region, in general – climatic niche conservatism seems better supported by the available evidence than community constancy. Indeed, the presence and abundance of today's tropical/subtropical taxa is consistent with globally warmer climates during the Middle Miocene, especially in the MCO. However, accurate quantitative paleoclimatic estimates using modern individual parameters seem still premature and need more studies of the involved taxa in relation to independent empirically-based paleoclimatic reconstructions derived from the same fossiliferous sediments. Regarding community composition, the coincidence of presently tropical, subtropical and temperate elements in the same Miocene pollen associations calls for a methodological reconsideration based on the raw information provided by fossils, rather than on modern analog inferences from an array of distant and biogeographically diverse areas. In summary, from a methodological point of view, the MA approach used in the VPB could be considered a first step useful to set the bases for the study of the Miocene flora and vegetation, which can be complemented with other approaches, of which the FC approach, as implemented in this paper, is only an example.

6. Conclusions and prospects for future studies

From the above discussion, we can conclude that the main handicaps for a robust basin-wide vegetational and landscape reconstruction in the Vallès-Penedès area are (i) the few localities studied using palynology and their concentration in a reduced geographical area; (ii) the low chronostratigraphic and sampling resolution; and (iii) the lack of studies combining palynological and fossil mammal records on the same outcrops/wells. After the discussion provided here, we can add a fourth drawback: (iv) the strong emphasis of the available palynological studies on floristic aspects, as deduced from botanical affinities of fossil pollen with extant plant taxa, rather than on vegetation reconstruction using the FC approach in the first place. The main guidelines for future research include (i) a basin-wide sampling campaign including as many Miocene sequences as possible; (ii) more intensive sampling within each section for pollen analysis and dating, able to provide well-dated high-resolution records; (iii) the development of joint vegetation-faunal analyses on the same samples whenever possible; and (iv) the use of the FC approach and its comparison with the MA approach. These new studies should include resampling and reanalysis of the three sections discussed here. At more regional level, the results of these new FC-based studies in the VPB could be compared with other areas of the Iberian Peninsula (see Carrión et al., 2022 for a review), provided FC-based approaches are developed on them in the future. Comparisons using MA approaches are already available in a number of studies mentioned in this paper (e.g., Jiménez-Moreno & Suc, 2007; Fauquette et al., 2007; Jiménez-Moreno et al., 2010; Suc et al., 2018).

As advanced in the introduction, the FC approach is viewed as a complementary, rather than an opposed, method to the MA approaches, and it is expected that improved paleoecological and paleoenvironmental reconstructions will emerge from constructive comparisons between the respective outputs. Both approaches have pros and cons that should be properly considered for a balanced view in each case study. Some general features of each of these approaches are highlighted below.

The MA approaches seem to be more useful for defining large-scale biogeographical and bioclimatic patterns, whereas the FC approach may be better suited for identifying intra-biome spatiotemporal heterogeneities, at the vegetation type/formation and ecosystem levels. However, this does not hinder the ability of the FC approach to provide large-scale biogeographic patterns after the compilation of appropriate databases. The MA approach seems able to provide relatively rich and detailed information but requires more undemonstrated assumptions, notably individual niche conservatism and community constancy from the Miocene to the present. The FC approach seems to be less informative but is more evidence-based, and therefore less speculative. Epistemologically, the MA approach may be viewed as a physics-like top-down method in which general inferences come from predictions based on axiomatic laws (Lipton, 2005). The main difference between the MA approach and predictive induction is that the ideas of niche conservatism and community constancy over the Neogene are untested hypotheses (Fauquette, 2017), rather than physics-like laws. In contrast, the FC approach is a bottom-up procedure, which is more usual in biology, where inductive generalizations come from the progressive accumulation of evidence-based knowledge after recurrent hypothesis testing (Rull, 2022b).

In addition to helping to understand vertebrate evolution and paleobiogeography, an integrated plant-animal approach has the potential to provide more complete ecosystem reconstructions that may help to understand not only the composition of the Miocene biota of the VPB but also their main functional traits at the ecosystem level, which a fundamental paleoecological target (Rull, 2012). If such integration would also be able to furnish paleoclimatic data from biotic-independent fossil evidence, then a major ecological driver, the external environment, would be incorporated for a more complete ecological reconstruction.

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