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Phylogenetic diversity in the Iberian flora through the Cenozoic☆

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ABSTRACT

Phylogenetic diversity reflects both community assembly and evolutionary diversification processes. Communities with low phylogenetic diversity might be the outcome of environmental filters favouring the occurrence and/or the diversification of lineages from particular clades. This rationale applies for regional assemblages. Here we propose to integrate phylogenetic diversity into paleobotanical studies aimed to reconstruct temporal shifts in plant assemblages in the past. To do so we first compiled a fossil dataset of 619 vascular plant taxa occurring through the Cenozoic in the Iberian flora, then we reconstructed their phylogenetic relationships, and finally we calculated temporal changes in phylogenetic diversity. The results reveal high phylogenetic diversity in the early Cenozoic (Danian to Lutetian) followed by an abrupt decline around 40 million years ago and a time interval of lower values during the Oligocene and the Miocene. A decreasing trend of phylogenetic diversity was also detected over the Piacenzian and the Early Pleistocene. Early values of high phylogenetic diversity were not explained by null models, and we speculate on putative causes related to climate. Overall, we propose to combine paleobotanical and phylogenetic information for detecting evolutionary changes that shaped our biodiversity across relevant geological scales.

1. Introduction

Plant composition of current communities is the outcome of evolutionary and ecological processes. These processes imprint a characteristic phylogenetic signature that can be used to untangle the ecological and evolutionary mechanisms behind them. Phylogenetic diversity accounts for the historical legacy of the species assembly and integrates the variability of morpho-functional diversity evolved through time. Thus, phylogenetic diversity has been used to understand the assembly mechanisms underlying extant assemblages (Webb et al., 2002). However, little has been performed to understand the changes in phylogenetic diversity through paleontological times (but see Eiserhardt et al., 2015). In this temporal framework, both local diversification and community assembly simultaneously operate to structure local communities (Verdú and Pausas, 2013); and both may leave a signature in the phylogenetic diversity. The gain of species in a given region can be produced by speciation or by colonization. *In situ* speciation tends to increase the number of closely-related species, and thus reduce phylogenetic diversity (Pausas and Verdú, 2008). Such a clade-biased diversification leaves a signature on the topology of the phylogenetic tree, making it more asymmetric (Mooers and Heard, 1997). However, the phylogenetic signature of the colonizers depends on their relatedness with the resident species. The species losses in a given region can be the consequence of extinction processes or of exclusion by local community processes. For instance, extinction reduced phylogenetic diversity of northern temperate tress during the late Cenozoic by extirpating whole clades of cold intolerant species (Eiserhardt et al., 2015) but had no effect on the phylogenetic pattern of regional plant assemblages from the Mediterranean Basin (Verdú and Pausas, 2013). Local processes such as competitive exclusion leading to local extinction are of little relevance at large (regional) scale.

The Iberian flora is a paleophytogeographic assemblage evolved in

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southern Europe that is well bounded by the Pyrenees, Gibraltar strait, Mediterranean Sea and Atlantic Ocean. This geographical situation linked to the relatively well-known paleobotanical record over the Cenozoic, the last 66 Ma (Pais, 1986; Bessais and Cravatte, 1988; Barrón et al., 2010; González Sampériz et al., 2010; Jiménez-Moreno et al., 2010; Carrión et al., 2013) provides an appropriate scenario to track phylogenetic changes through time. Dramatic floristic changes associated to paleogeographic and paleoclimatic changes (mainly cooling, aridification, and increased flammability) occurred through this Era (Portero and Aznar, 1984; López-Martínez, 1989; Alonso-Zarza et al., 2002; Civis, 2004; CIESM, 2008; Postigo-Mijarra et al., 2009, 2010; Barrón et al., 2010; Keeley et al., 2012). Consequently, during the Cenozoic, Iberia witnessed the local extinction of some taxa and the immigration and evolution of others. For instance, Arctotertiary elements migrated from northern latitudes, many Paleotropical lineages became extinct, and Mediterranean elements diversified over the Quaternary (Herrera, 1992; Postigo-Mijarra et al., 2009, 2010; Barrón et al., 2010; Verdú and Pausas, 2013).

Our aim is to evaluate to what extent floristic changes through the Cenozoic have left a phylogenetic signature that can be interpreted in similar terms as community phylogenetics interprets community assembly. We hypothesize that the global cooling and increased aridity occurred through the Cenozoic imposed an environmental filter to the Iberian flora and constrained the diversification favouring some clades over others; consequently, we predict a reduction of the phylogenetic diversity through the Cenozoic. To test this hypothesis, we first compiled an extensive fossil database of the Iberian flora for 22 geological stages and substages in the Cenozoic (see e.g. Calvo et al., 1993; Barrón et al., 2010; Grandstein et al., 2012), then we assembled a phylogenetic tree for the whole dataset and quantified the phylogenetic diversity (MPD, Mean Phylogenetic Distance) for each time slice. To detect abrupt changes in phylogenetic diversity we evaluate the departure of the observed phylogenetic diversity from those expected under a null model following an evolutionary birth-death process.

The application of this model allows us to infer gains and losses of diversity over the Cenozoic. The role of the climate as an environmental filter reducing phylogenetic diversity was tested by correlating the MPD curve with a paleoclimatic curve validated for the study area using independent sources of information (see e.g., Mosbrugger et al., 2005; Utescher et al., 2011). Constrained diversification as a mechanism that results in reduced phylogenetic diversity was tested by correlating MPD with the level of asymmetry of the phylogenetic trees (a measure of non-random diversification). We finally discuss putative causes related to the observed changes in floristic diversity and address caveats of the methodology used.

2. Methods

2.1. Fossil database

We compiled a comprehensive database with all the paleobotanical information available for the Cenozoic of the Iberian Peninsula and the Balearic Islands. We included the occurrence of the fossil plant taxa, families and genera, recorded from micro- (pollen and spores; Fig. 1B–C, E–G), meso- (seeds, fruits, flowers; Fig. 1 J) and macroremains (cones of conifers, winged seeds, inflorescences, leaves and wood remains; Fig. 1A, D, H, I. K) in Cenozoic (Paleocene–Quaternary) sedimentary successions that outcrop across the study area. The database grew from Postigo-Mijarra et al. (2009) by adding new data from Oligocene (Casas-Gallego, 2018; Moreno-Domínguez et al., 2015), Early Miocene (Barrón and Postigo-Mijarra, 2011; Postigo-Mijarra and Barrón, 2013), and Late Miocene ages (Casas-Gallego et al., 2015; Barrón et al., 2016) (Fig. S1, Appendix 1 and 2). Dubious taxa that were not considered for the database included a) fossils with ambiguous morphology (e.g., *Cercis*, from the Oligocene of Mallorca; Colom, 1983); b) Gondwanan genera (*Banksia, Conospermum, Dryandroides* and *Protea*) identified only from leaves and likely to be confused with taxa belonging to the family Myricaceae or Juglandaceae (see e.g. Menéndez Amor, 1955; Jungwirth, 2004); and c) other untrusted taxa whose occurrence in the study area or botanical affinity have not been confirmed confidently (Cavagnetto, 2002). The chronostratigraphic framework used follows Calvo et al. (1993) and Gradstein et al. (2012). The base of the Pleistocene at 2.58 Ma allows the inclusion of areas considered to be of Plio-Pleistocene or Tiglian age within the early Quaternary (Pillans, 2004; Clague, 2006). Following the version 2019/05 of the International Chronostratigraphic Chart (http://stratigraphy.org/ICSchart/ChronostratChart2019-05), we subdivided the Cenozoic into 22 geological units that correspond to the following stages and substages: Danian, Selandian, Thanetian, Ypresian, Lutetian, Bartonian, Priabonian, Rupelian, Chattian, Aquitanian, Burdigalian, Langhian, Serravallian, Tortonian, Messinian, Zanclean, Piacenzian, Gelasian, Calabrian, Middle Pleistocene, Upper Pleistocene and Holocene. When a taxon occurred in two non-consecutive stages (i.e. *Lazarus* taxon *sensu* Flessa and Jablonski, 1983), we assumed that it was also present in between them, even if we lacked fossil evidence. Data on the occurrence of taxa in the 22 time units and the corresponding sources of information are available in the Supporting Material (Appendix 2).

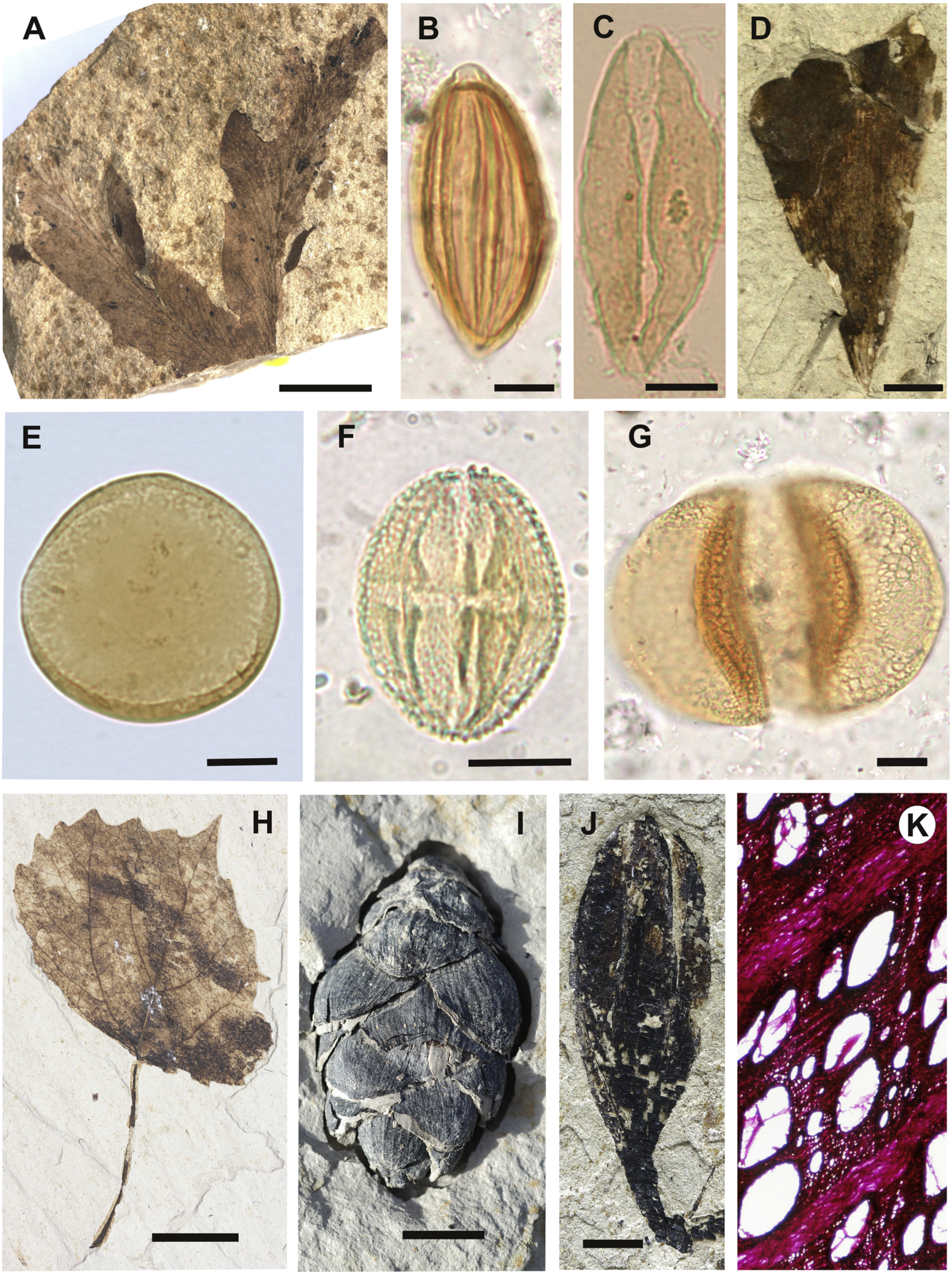
2.2. Phylogenetic tree

We assembled a phylogenetic tree for each time slice (stage/substage) using the “S.Phylomaker” R function (Qian and Jin, 2016). This function generates phylogenies of seed plants from a particular ecological or biogeographical assemblage by using an updated and corrected version of the mega-tree built by Zanne et al. (2014) that contains ca. 32,000 species with branch lengths representing chronological time (Million years). Missing taxa in Zanne et al. (2014) can be added to a particular node of the tree on the basis of their taxonomic affinity with the taxa contained in the phylogeny. Our fossil taxa were added at the genus, family, order or class node they belong. As such additions generated polytomies, we randomly solved and calibrated them following the Scenario 3 described in Qian and Jin (2016). This procedure, analogous to Phylomatic (Webb and Donoghue, 2005) and BLADJ (Webb et al., 2008), assigns an age to the new nodes generated after randomly resolving the polytomies caused by grafting taxa not contained in Zanne's original tree. The assigned age to the node is the result of distributing the age of undated nodes evenly between nodes of known ages in the mega-tree. Finally, the taxa that were not present in the Iberian flora were pruned from the tree. Phylogenies of regional plant assemblages constructed following this procedure provide estimates of community phylogenetic diversity metrics strongly correlated to those obtained with fully resolved phylogenies at the species level (Qian and Jin, 2016). The phylogenetic tree of each time interval was scaled to the midpoint; e.g., the first phylogenetic tree (i.e., the Danian tree) was scaled to have a total height of 63.60 Million years less than a contemporary tree.

2.3. Phylogenetic diversity

For each of the 22 time slices, we computed the Mean Phylogenetic Distance (MPD) as an indicator of the phylogenetic diversity traditionally used in community ecology to compare how different communities are, or which mechanisms, as environmental filtering, are assembling them (Tucker et al., 2017). Phylogenetic distance between two terminal taxa is the sum of branch lengths connecting them through their most recent common ancestor in the phylogenetic tree. MPD is the average phylogenetic distance between all the pairs of species co-occurring in a particular time span, and because it is a mean value, it is relatively robust to the number of species and more sensitive to the structure of the phylogenetic tree. MPD was calculated as the mean value of the paired phylogenetic distances obtained with the *cophenetic* function in the “ape” package for R (Paradis et al., 2004). To check whether the temporal changes in MPD were due to a phylogenetically structured extinction, we recalculated the MPD of each time slice, but without considering the newly emerging taxa. Thus, we obtained the MPD of these "surviving taxa" and compared it to that of the previous stage/substage through a paired-t test. If the MPD of the "surviving taxa" is significantly lower than that of the previous stage/substage, it would indicate that extinction erodes phylogenetic diversity.

To detect unexpected changes in phylogenetic diversity we compared the observed temporal changes in MPD *versus* the expected values under a null model following a constant rate evolutionary birth- death



(caption on next page)

Fig. 1. Selected specimens of Cenozoic Spanish plant assemblages.
A- Lygodium gaudinii Heer (Arènes & Depape 1954), Burdigalian, Early Miocene, Mallorca
Burdigalian, Early Miocene, Mallorca. Specimen MBCN-2693, Museu Balear de Ciències Naturals, Sóller, Mallorca. Bar: 10 mm.
B-*Distachyapites* cf. *eocenipites* (Wodehause 1933) Grabowska and Ważyńska 2002.
Poliplicate pollen grain produced by an *Ephedra* (Gnetophyta). Burdigalian, Early Miocene, Rubielos de Mora Basin, Teruel. Bar: 10 μm.
C-*Cycadopites* sp. Monosulcate pollen grain produced by a gymnosperm of the divisions Cycadophyta or Ginkgophyta. Burdigalian, Early Miocene, Rubielos de Mora Basin, Teruel. Bar: 10 μm.
D-*Ginko adiantoides* (Unger 1845) Heer 1878. Flabelliform leaf remain with dichotomous venation. Tortonian, Late Miocene, La Cerdaña Basin, Lérida. Specimen MGBV-10154, Museu de Geologia de Barcelona. Bar: 5 mm.
E-*Proxapertites operculatus* (Van der Hammen 1954) Van der Hammen 1956. Zono- operculate pollen grain produced by tropical palms retated to the extant genus *Astrocaryum*. Early Eocene, Porciles, Asturias. Bar: 10 μm.
F-*Rhuspollenites striaticus* Grabowska 2014. Tricolporate and striate-reticulate pollen grain produced by an angiosperm of the genus *Rhus*. Rupelian–Chattian, Oligocene, As Pontes Basin, La Coruña. Bar: 10 μm.
G-*Cathayapollis potoniei* (Sivak 1976) Ziembińska-Tworzydło 2002. Basaccate pollen grains produced by a conifer of the extant genus *Cathaya* which today inhabits China. Burdigalian, Early Miocene, Rubielos de Mora Basin, Teruel. Bar: 10 μm.
H-*Populus populina* (Brongniart 1822) Knobloch 1964. Orbiculate and long-petiolate leaf of a poplar. Burdigalian, Early Miocene, Ribesalbes-Alcora Basin, Castellón. Specimen MSV- 003, Museo de La Baronía, Ribesalbes, Castellón. Bar: 10 mm.
I-cf. *Tsuga* sp. Female cone of a conifer now extinct of Europe. Tortonian, Late Miocene, La Cerdaña Basin, Lérida. Specimen MGSB-69390, Museo del Seminari de Barcelona. Bar: 10 mm.
J-*Trigonobalanopsis exacantha* (Mai 1970) Kvaček and Walther 1988. Cupule of an extinct tropical Fagaceae. Burdigalian, Early Miocene, Ribesalbes-Alcora Basin, Castellón.
Specimen JAGV-346, Museo de La Baronía, Ribesalbes, Castellón. Bar: 5 mm.
K- Transversal anatomical preparation of a wood of *Quercus* sp. showing its vessels. Calabrian (lower Pleistocene), Cal Guardiola, Tarrasa, Barcelona. Sample 631, Universidad Autónoma de Barcelona. ×500.

process (Nee et al., 1994). We use constant rates as a simplification of more complex models allowing diversification rate-shifts in different portions of the phylogeny that explain better the diversification dynamics (Landis et al., 2018; Smith and Brown, 2018). For example, Landis et al. (2018) identified 334–530 shifts in diversification rates on Zanne et al. (2014) phylogeny, what broadly agrees with the 471 rate shifts found by Smith and Brown (2018) in their phylogeny. These results come from hundreds of different models but evaluating the likelihood of such a high number of alternative models goes beyond our objective. Instead, we have tested that our results are robust to a wide range of birth, death and incomplete sampling rates under a constant-rate evolutionary, as discussed below.

For each time slice, we estimated a null model by simulating a phylogenetic tree with the same number of taxa as the observed fossil taxa on that time slice. Birth and death parameters for the simulation were obtained from the tree of the previous interval of time with the help of the bd.time function of the “ape” package for R (Paradis et al., 2004); no null model was simulated for the first stage. One thousand trees per stime slice were simulated with the sim.bd.taxa.age function in the R package “TreeSim” (Stadler, 2017). This function simulates constant rates birth-death trees allowing for incomplete sampling by assigning fixed probability for each species to be included in the final tree (Stadler, 2009). Incomplete sampling is a very common feature in fossil data that can be assessed through likelihood models. We obtained the fraction of sampling rate (the *frac* parameter in the sim.bd.taxa.age function) through Foote (1997) likelihood function to model sampling and extinction rates for taxonomic duration datasets with the help of the *make_durationFreqDisc* and *sProb2sRate* functions in PaleoTree package for R (Bapst, 2012). This approach can deal with regional stratigraphic datasets where the observed frequency of taxon durations is known for discrete time intervals. Mean phylogenetic distance for each simulated tree was calculated as explained above and null expectations constructed by obtaining the mean and 95% confidence interval of the 1000 MPDs calculated per each time stage/substage. Since the estimation of death rates and sampling rates with phylogenies are prone to error (Rabosky, 2010; Bapst, 2014), we repeated the analysis with different rates to check for the robustness of the results.

2.4. Cenozoic climate in the Iberian Peninsula

Ideally, any correlative analysis of climate versus extinction and remaining diversity should rely on independently obtained climatic data. Thus, climatic information directly inferred from the past presence or abundance of taxa according to their current climatic niches is inappropriate for this purpose. Deep, long-term independent reconstruction of Cenozoic climate has relied on data directly or indirectly related with chemical parameters, such as carbon and oxygen isotopes in deep-sea sediments. These proxies are directly related to ocean temperature and might influence atmosphere temperature when polar oceans are mostly free from ice-sheets (see Zachos et al., 2001, 2008 for details). As such isotope-based methods are usually applied to benthic foraminifera, data are independently obtained from the vegetation present at the corresponding geological periods. The values reported are representative of the global climatic parameters (mostly temperature) and thus there may be a bias due to the different scale of our study (Iberia) and, consequently, validation is required.

For the purpose of correlating phylogenetic diversity values across times with climatic changes, we extracted the longest series of Cenozoic climatic paleoindicators (global averaged oxygen isotope (δ18O) from Zachos et al. (2001) as reported in Utescher et al. (2011) for the last 66 Ma. We used the web based tool WebPlotDigitizer v. 4.1 (Rohatgi, 2018) for extracting the data from published figures. We validated its use at the Iberian scale by correlating Zachos et al. (2001) data with that obtained for Tethyan unrelated fossils (sirenians teeth, including some Iberian specimens) in Clementz et al. (2009). Given that δ18O in sea sediments directly correlated only with sea temperature, we correlated the δ18O curve with that of climatic atmosphere mean annual temperature inferred by climatic tolerance of Nearest Living Relatives (NLR) estimates for central Europe and northern Parathetys palaeoflora (closer to Iberia) in the last 45 Ma (Mosbrugger et al., 2005). Correlations between temporal series were run after binning the data to 1 million year intervals. This approach can be used at a more local/regional scale and adds information on the precipitation regime, for which isotope data are little informative. Altogether, evidence exists for sound correlation between these parameters across geological periods, thus validating their use for testing climatic clues of diversification patterns. It should be noted that our quantitative paleoenvironmental assessment involves only temperature. Precipitation regimes are more difficult to infer and we did not use the values obtained inferred through NLR by Mosbrugger et al. (2005) because we could not validate them against a non-botanical record for the entire Cenozoic.

Thus, interpretation about precipitation was aided by qualitative information coming from sedimentology in the Tethyan-Mediterranean region (García-Castellanos et al., 2003) and also at global scale (Ziegler

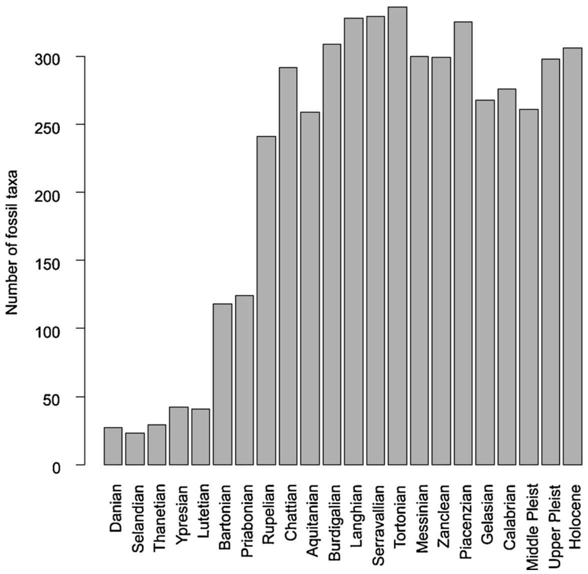


Fig. 2. Temporal distribution of the number of fossil taxa in the study database.

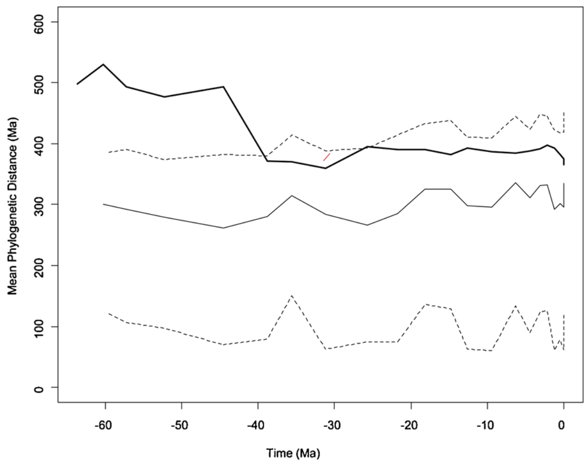


Fig. 3. Observed phylogenetic diversity (thick solid line) along the studied period. The mean and confidence interval obtained under the null birth-death model is also indicated (thin and dashed lines). Two phases according to the null model are shown: the first (66-40 Ma) where MPD is significantly higher than the null model and the second (40 – 0 Ma) where MPD does not depart from the null expectation.

et al., 2003), diet composition of sirenians (Clementz et al., 2009), abundance of coral reefs and large foraminifera (Scheibner and Speijer, 2008). A thorough account of the Cenozoic climate of the Iberian Peninsula can be found in Postigo-Mijarra et al. (2009). These independent sources of information point to an increase of aridity and seasonality through the Cenozoic across the whole Tethys Basin, although the particular values of mean annual precipitation and its seasonality are far to be known in detail.

3. Results and discussion

Our database contains 619 fossil taxa stratigraphically distributed across all the stages of the Cenozoic. Magnoliophyta (angiosperms) is the best represented group with 568 taxa (Fig. 1E–F, H, J–K), followed by Coniferophyta (24 taxa; Fig. 1G, I), Pteridophyta (21 taxa; Fig. 1A), Lycopodiophyta (3 taxa), Cycadophyta (1 taxon; Fig. 1C), Gingkophyta (1 taxon; Fig. 1D) and Gnetophyta (1 taxon; Fig. 1B). The inherent incompleteness of the fossil record means that the database necessarily represents a subset of the plant species that occurred during the Cenozoic. However, it represents the state-of-the-art of the fossil flora in Iberia and Balearic Islands. Taxa richness increases from a few tens in the Danian to ca. 300 taxa in recent ages (Fig. 2). This trend could probably be related to the sampling bias since oldest outcrops (Paleocene–Lutetian) are scarce and concentrated in northern Iberia (Fig. S1 A), requiring thus the use of methods controlling for sampling bias for further phylogenetic analyses, as we have used.

Phylogenetic diversity measures the amount of evolutionary history treasured in a community as the result of processes related to lineage diversification and migration of lineages, stochastic processes and local assembly (Yguel et al., 2016). Tracking temporal trends of phylogenetic diversity may provide useful information on this plethora of processes assembling past communities. According to our null model, Mean Phylogenetic Diversity (MPD) displays two different phases in the Cenozoic of the Iberian Peninsula (Fig. 3): From the Danian to the Lutetian, MPD is higher than expected by the null model, while for the time interval between the Bartonian and the present day (˜40-0 Ma) MPD values lie within the null expectation. The null models, which were constructed from simulated phylogenies with the same number of species than those observed for each stage/substage (23–335) and a range of birth (0.22-0.39), death (0-0.1) and (incomplete) sampling rates (0.089) obtained from the true phylogenies (Fig. S2), consistently support the existence of an early MPD higher than expected followed but a later MPD not departing from random expectation (Figs. S3 and S4). Only under high death rates (˜0.25; bottom right plot in Fig. S4), some of the initial points of the MPD curve fall within the null expectation.

The high MPD during the early Cenozoic is consistent with the composition of the Iberian flora living in a tropical-like climate (Zachos et al., 2001; Barrón et al., 2010) with abundant taxa of paleotropical origin from the Paleocene and Lower Eocene, such as Arecaceae, Ebenaceae, Magnoliaceae, tropical Fagaceae and pteridophytes. Paleomangroves with *Nypa* and laurophyllous forests also occurring in different areas of Iberia (Haseldonckx, 1973; Médus, 1977; Médus and Colombo, 1991; Médus et al., 1992; López-Martínez et al., 1999; Fernández-Marrón et al., 2004; Solé de Porta et al., 2007). Gymnosperms, especially conifers, were also a significant group during this time interval (e.g. Sciadopityaceae or taxodioid conifers). This evergreen vegetation type is consistent with high temperatures and humidity promoting high phylogenetic diversities (Verdú et al., 2003).

The Early Eocene was the warmest stage of the Cenozoic and was punctuated by various warming events (‘hyperthermals’), including the Paleocene-Eocene Thermal Maximum (PETM; ˜56 Ma), the Eocene Thermal Maximum 2 (ETM2; ˜54 Ma) and the Early Eocene Climatic Optimum (EECO; 52 – 50 Ma) (Sloan and Morrill, 1998; Lear et al., 2000; Cramwinckel et al., 2018). The latter is usually regarded as a crucial turning point in the global climate dynamics, which was succeeded by a long-term, progressive cooling leading to the development of polar ice-sheets (Zachos et al., 2008). According to our results, the MPD remained high during the Lutetian in the study area, after the EECO, probably reflecting the prevalence of a warm climatic regime and favourable conditions for sustaining a high MPD. The sharp decrease in MPD observed in the Bartonian could therefore be related to intensified cooler conditions after the short-duration Middle Eocene Climatic Optimum (MECO) at ca. 41.5 Ma. (Mai, 1989; Zachos et al., 2001, 2008; Mosbrugger et al., 2005; Postigo-Mijarra et al., 2009). The MPD curve continued dropping during the Priabonian, when families such as Anacardiaceae, Cupressaceae (non taxodioids), Ephedraceae, Fabaceae and Plumbaginaceae spread into the north-eastern part of the Iberian Peninsula due to their cooler and drier ecological requirements (Cavagnetto and Anadón, 1996). The Eocene-Oligocene transition is marked by a further global decrease in temperature (Liu et al., 2009; Zanazzi et al., 2007). At a local scale, this climatic trend is reflected in NW Iberia by a significant decrease in the proportion and diversity of thermophilous taxa (Postigo-Mijarra et al., 2009; Casas-Gallego, 2018) consistent with the decrease in MPD observed for the Rupelian (Fig. 3). The Late Oligocene warming is another global climatic event locally reflected in the Iberian paleofloras (Casas-Gallego, 2018) which could be associated with the slight increase in MPD observed for the Chattian of the Iberian Peninsula. Subsequently, during the Miocene, the MPD remained relatively constant (Fig. 3). Over the Miocene, Arctotertiary taxa spread in different areas of Iberia together with taxa related to open, more or less dry, environments such as Amaranthaceae, Asteraceae, *Combretum*, Linaceae, Poaceae, Thymelaeaceae, *Juniperus* and *Quercus* (Rivas-Carballo, 1991; Rivas-Carballo et al., 1994; Valle-Hernández et al., 1995; Barrón et al., 2010).

At the end of the Cenozoic, MPD showed a decreasing tendency (Fig. 3) which could be related to the development of a dry season coinciding with the warmest season (ca. 3.1–3.2 Ma), thus initiating Mediterranean seasonality (Suc, 1984; Bertoldi et al., 1989), and the onset of the Quaternary glaciations (Lisiecki and Raymo, 2005, 2007). A significant set of Paleotropical and Arctotertiary taxa (ca. 40 taxa e.g. Cyatheaceae, Menispermaceae, *Gingko*, *Rhizophora*, *Liriodendron*, taxodioids, *Tsuga*, Araliaceae [non *Hedera*], *Engelhardia*, Lauraceae [non *Laurus*], *Liquidambar* or *Parrotia*) disappeared during the middle–late Piacenzian and the Middle Pleistocene Transition (MPT) (Clark et al., 2006; Postigo-Mijarra et al., 2009, 2010). At that time, droughts and fires increased (Keeley et al., 2012) producing the diversification of non-sclerophyllous fire-prone species and the extinction of fire sensitive species (Verdú and Pausas, 2013). However, the late decrease in MPD does not depart from the null expectation probably due to the lack of resolution of our methodology to depict changes at such short time scales. Stochastic or antagonistic processes may also be erasing the phylogenetic trend in this late period (Ulrich et al., 2016).

It is tempting to relate the observed phylogenetic diversity trends with climate fluctuations, as closely related species tend to have similar climate and disturbance tolerances (Prinzing et al., 2001; Verdú and Pausas, 2007). Moreover, climate is an indicator of the disturbance regime (Pausas and Paula, 2012). There is correlative evidence that Zachos et al. (2001) world paleo-curve based on the Cenozoic deep sea δ^{18}O signal can be used as a reliable proxy for temperature in Iberia (Fig. S5). For this purpose, we used data on δ18O series obtained in enamel teeth of Tethyan sirenians along the last 54 Ma, including specimens found in Iberian deposits (Clementz et al., 2009). Zachos et al (2001) series is significant and positively correlated with the sirenian data ($r = 0.87$; $p < 0.01$), suggesting that the global climatic trend also reflects a regional (Tethyan) climatic trend in areas close to Iberia. It is also necessary to state that estimated sea temperatures by Clementz et al. (2009) are in some extent reflecting air temperature, which directly affects terrestrial plant life. In fact, δ^{18}O from Tethys sirenians is significantly correlated with the mean temperature estimated from the Nearest Living Relatives (NRL) climatic tolerance of species in paleobotanical records at Central Europe along the last 45 Ma ($r = -0.51$; $p = 0.006$) (Mosbrugger et al., 2005), suggesting that data from δ^{18}O can be extrapolated to temperatures faced by plant assemblages close to Iberia, as it has been found for world climate (Mosbrugger et al., 2005). Altogether, these correlations allow us to use Zachos et al. (2001) paleoclimate curve as a proxy for local Iberian temperature trend along the 66 Ma of the Cenozoic. The same curve is also significantly correlated to that of the phylogenetic diversity in Iberia (Fig. 4). This relationship is driven by two separate clouds of points: both the highest MPD and the warmest period occurred in the early Cenozoic (Danian to Lutetian) and then MPD and temperature abruptly decreased during the Bartonian. This pattern suggests that the climatic conditions that followed the MECO exerted a major influence on the Iberian phylogenetic diversity. Other climatic fluctuations and paleoenvironmental events (e.g., the multiple glacial phases that occurred during the Miocene, the Middle Miocene Climatic Optimum [MMCO] and the Mediterranean Salinity Crisis) seem to have had little effect on MPD, as no clear trend appears within each of the two periods. Probably, fine-tuned climatic record and fossil record are inherently difficult to reconcile due to their different sampling frequency and different sensitivities (including speed of response) of fossil taxa to changing climates (see Corlett and Westcott, 2013 for current climate change). Whereas we admit that the presence of these two disparate clouds of points may limit the resolution of our analysis, it is noteworthy that the strong difference in MPD between them coincides with sharp increase of high frequency and wide variability in δ18O since the Priabonian, probably related with the establishment of the first ice-sheets in the Cenozoic (Zachos et al., 2001). Whether it means a similar effect than that of Pleistocene Ice-Ages remains unknown.

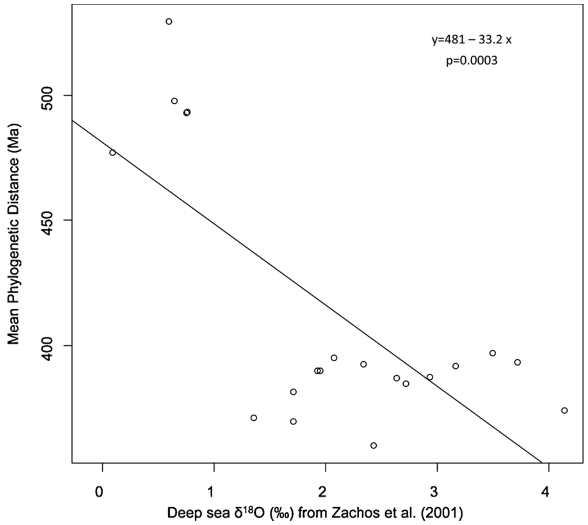


Fig. 4. Relationship between the plant phylogenetic diversity in the Iberian Peninsula and the global temperature reconstructed from deep-sea oxygen isotope records by Zachos et al. (2001).

High phylogenetic diversity associated with high temperatures has been observed in extant communities, such as North American trees (Hawkins et al., 2014) and worldwide island ecosystems (Weigelt et al., 2015). These results have been explained by the poor adaptations of angiosperms to cold temperatures due to their tropical ancestry. Later on, climatic cooling and aridification might have led to an environmental filtering eroding the phylogenetic diversity of plant communities, constraining the diversification and favouring some clades over others (Valiente-Banuet et al., 2006; Verdú and Pausas, 2013). Our analyses to test whether extinction is phylogenetically structured showed that the MPD of the “surviving taxa” was significantly higher than the one obtained in the previous time period ($t = -3.7$, $df = 20$, p-value $= 0.001$; paired-t test). This result suggests that extinction increases phylogenetic diversity, probably by extirpating closely related species from different clades across the phylogeny. Then, we cannot attribute the observed decreasing trend in MPD to a depauperating effect of extinction but to explosive radiation of some clades adapted to the new conditions.

Despite the limitations associated with the fragmentary nature of the fossil record, we provide, for the first time, a general overview of the plant phylogenetic diversity through the Cenozoic in the Iberian Peninsula. Additionally, we propose a methodological approach borrowed from the discipline of community phylogenetics, which can be useful for detecting diversity patterns through time in other regions of the world where appropriate paleontological and paleoenvironmental data were available. Future developments of this approach should include spatial information to identify spatio-temporal hot and cold spots of evolutionary history. For instance, the results based on the fossil record could be incorporated in the comparative historical analysis of biotas with similar current climate, which sometimes have been regarded as a result of convergence (e.g., Mediterranean-type floristic regions: Rundel et al., 2016; subtropical moist broadleaf forest in SE Asia and E North America: Qian et al., 2017). Most of the territory of the Iberian Peninsula currently harbors a Mediterranean-type climate with a particular diversification pattern, which seems to contrast with that of older SW Australia and Cape Mediterranean climate (Rundel et al., 2018). Comparing phylogenies of fossil record across Mediterranean-type climate regions might throw light here. Ultimately, and despite the unprecedented rates of extinction associated to current climatic change, understanding how plant communities faced past climatic fluctuations could help us to forecast the consequences of climatic change on current ecological communities (Thuiller et al., 2011).

Declaration of Competing Interest

The authors declare that there is no conflict of interest.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.envexpbot.2019.103888.

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