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23 **Abstract**

24

25 Phylogenetic diversity is a metric that reflects both community assembly and
26 evolutionary diversification processes. Communities with low phylogenetic diversity
27 might be the outcome of environmental filters favouring the occurrence and/or the
28 diversification of lineages from particular clades. This rationale may also apply for
29 regional assemblages. Here we propose to integrate phylogenetic diversity into
30 paleobotanical studies aimed to reconstruct temporal shifts in plant assemblages in the
31 past. To do so we compiled a fossil dataset of 619 vascular plant taxa occurring through
32 the Cenozoic in the Iberian flora, reconstructed their phylogenetic relationships, and
33 calculated temporal changes in phylogenetic diversity. The results suggest a time span
34 of high phylogenetic diversity in the early Cenozoic (Danian to Lutetian) followed by
35 an abrupt decline around the Bartonian and lower values during the Oligocene and the
36 Miocene. Finally, an abrupt decrease in phylogenetic diversity may also be detected over
37 the Piacenzian and the Early Pleistocene. Early values of high phylogenetic diversity
38 were not explained by null models, and we speculate on putative causes related to
39 climate. Overall, we propose that by combining paleobotanical and phylogenetic
40 information it is possible to detect evolutionary changes that shaped our biodiversity
41 across relevant geological time spans.

42

43 **Keywords:** Cenozoic, Diversification, Iberian flora, Paleoclimate, Phylogenetic
44 Diversity

45 **Introduction**

46
47 Plant taxa inhabiting current communities are the outcome of evolutionary and
48 ecological processes. These processes imprint a characteristic phylogenetic signature
49 that can be used to untangle the ecological and evolutionary mechanisms behind them.
50 Phylogenetic diversity accounts for the historical legacy of the species assembly and
51 integrates the variability of morpho-functional diversity evolved through time. Thus,
52 phylogenetic diversity has been used to understand the assembly mechanisms
53 underlying extant assemblages (Webb et al., 2002). However, little has been
54 performed to understand the changes in phylogenetic diversity through
55 paleontological times (but see Eiserhardt et al., 2015). In this temporal framework, both
56 local diversification and community assembly simultaneously operate to structure
57 local communities (Verdú & Pausas, 2013); and both may leave a signature in the
58 phylogenetic diversity. The gain of species in a given region can be produced by
59 speciation or by colonization. *In situ* speciation tends to increase the number of
60 closely-related species, and thus reduce phylogenetic diversity (Pausas & Verdú,
61 2008). Such a clade-biased diversification leaves a signature on the topology of the
62 phylogenetic tree, making it more asymmetric (Mooers & Heard, 1997). Similarly, the
63 appearance of colonizers may reduce or increase phylogenetic diversity depending on
64 the relatedness between colonizers and resident species. The species losses in a given
65 region can be the consequence of extinction or exclusion by local community
66 processes. Extinction has been shown to reduce phylogenetic diversity of northern
67 temperate trees during the late Cenozoic by extirpating whole clades of cold intolerant
68 species (Eiserhardt et al., 2015). In contrast, regional plant assemblages from the
69 Mediterranean Basin do not show any phylogenetic pattern in the extinction process
70 (Verdú & Pausas, 2013). Local processes such as competitive exclusion leading to

71 local extinction are of little relevance at large (regional) scale.

72

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

89

90 Our aim is to evaluate to what extent floristic changes through the Cenozoic have left
91 a phylogenetic signature that can be interpreted in similar terms as community
92 phylogenetics interprets community assembly. We hypothesize that the global cooling
93 and increased aridity occurred through the Cenozoic imposed an environmental filter
94 to the Iberian flora and constrained the diversification favouring some clades over
95 others; consequently, we predict a reduction of the phylogenetic diversity through the
96 Cenozoic. To test this hypothesis, we first compiled an extensive fossil database of the

97 Iberian flora for 22 stages and substages in the Cenozoic (see e.g. Calvo et al., 1993;
98 Barrón et al., 2010; Grandstein et al., 2012), then we assembled a phylogenetic tree for
99 the whole dataset and quantified the phylogenetic diversity (MPD, Mean Phylogenetic
100 Distance) for each time span. To detect abrupt changes in phylogenetic diversity we
101 evaluate the departure of the observed phylogenetic diversity from those expected
102 under a null model following an evolutionary birth-death process.
103 The application of this model allows us to infer gains and losses of diversity over the
104 Cenozoic. The role of the climate as an environmental filter reducing phylogenetic
105 diversity was tested by correlating the MPD curve with a paleoclimatic curve validated
106 for the study area using independent sources of information (see e.g., Mosbrugger et
107 al., 2005; Utescher et al., 2011). Constrained diversification as a mechanism that
108 results in reduced phylogenetic diversity was tested by correlating MPD with the level
109 of asymmetry of the phylogenetic trees (a measure of non-random diversification). We
110 finally discuss putative causes related to the observed changes in floristic diversity and
111 address caveats of the methodology used.

112

113 **Methods**

114

115 *Fossil database*

116

117 We compiled a comprehensive database with all the paleobotanical information
118 available for the Cenozoic of the Iberian Peninsula and the Balearic Islands. We
119 included the occurrence of the fossil plant taxa, families and genera, recorded from
120 micro- (pollen and spores; Fig 1 B–C, E– G), meso- (seeds, fruits, flowers; Fig 1 J)
121 and macroremains (cones of conifers, winged seeds, inflorescences, leaves and wood
122 remains; Fig 1 A, D, H, I. K) in Cenozoic (Paleocene–Quaternary) sedimentary
123 successions that outcrop across the study area. The database was initiated by Postigo-

124 Mijarra et al. (2009), and has been updated for this study with data from Oligocene
125 (Casas-Gallego, 2018), Early Miocene (Barrón & Postigo-Mijarra, 2011; Postigo-
126 Mijarra & Barrón, 2013; Moreno- Domínguez et al., 2015), and Late Miocene ages
127 (Casas-Gallego et al., 2015; Barrón et al., 2016) (Fig S1, Appendix 1 and 2). Dubious
128 taxa that were not considered for the database include a) fossils that show ambiguous
129 morphology (e.g., *Cercis*, from the Oligocene of Mallorca; Colom, 1983); b)
130 Gondwanan genera (*Banksia*, *Conospermum*, *Dryandroides* and *Protea*) identified
131 only from leaves and likely to be confused with taxa belonging to the family
132 Myricaceae or Juglandaceae (see e.g. Menéndez Amor, 1955; Jungwirth, 2004); and c)
133 other untrusted taxa whose occurrence in the study area or botanical affinity have not
134 been confirmed confidently (Cavagnetto, 2002). The chronostratigraphic framework
135 used was that proposed by Calvo et al. (1993) and Gradstein et al. (2012). The base of
136 the Pleistocene at 2.58 Ma allows the inclusion of areas considered to be of Plio-
137 Pleistocene or Tiglian age within the early Quaternary (Pillans, 2004; Clague, 2006).
138 Following the version 2019/05 of the International Chronostratigraphic Chart
139 (<http://stratigraphy.org/ICSchart/ChronostratChart2019-05>), we subdivided the
140 Cenozoic into 22 stages and substages that correspond to the temporal units of the
141 present study (Danian, Selandian, Thanetian, Ypresian, Lutetian, Bartonian,
142 Priabonian, Rupelian, Chattian, Aquitanian, Burdigalian, Langhian, Serravallian,
143 Tortonian, Messinian, Zanclean, Piacenzian, Gelasian, Calabrian, Middle Pleistocene,
144 Upper Pleistocene and Holocene). When a taxon occurred in two non-consecutive
145 stages (i.e. *Lazarus* taxon *sensu* Flessa & Jablonski, 1983), we assumed that it was
146 also present in between them, even if we lacked fossil evidence. Data on the
147 occurrence of taxa in the 22 studied time spans and the sources of information are
148 available in the Supporting Material (Appendix 2).

149 *Phylogenetic tree*

150

151 We assembled a phylogenetic tree for each stage/substage using the “S.Phylomaker” R
152 function (Qian & Jin, 2016). This function generates phylogenies of seed plants from a
153 particular ecological or biogeographical assemblage by using an updated and corrected
154 version of the mega-tree built by Zanne et al. (2014) that contains ca. 32,000 species
155 with branch lengths representing chronological time (Million years). Missing taxa in
156 Zanne et al. (2014) can be added to a particular node of the tree on the basis of their
157 taxonomic affinity with the taxa contained in the phylogeny. Our fossil taxa were
158 added at the genus, family, order or class node they belong. As such additions
159 generated polytomies, we randomly solved and calibrated them following the Scenario
160 3 described in Qian & Jin (2016). This procedure, analogous to Phylomatic (Webb &
161 Donoghue, 2005) and BLADJ (Webb et al., 2008), assigns an age to the new nodes
162 generated after randomly resolving the polytomies caused by grafting taxa not
163 contained in Zanne’s original tree. The assigned age to the node is the result of
164 distributing the age of undated nodes evenly between nodes of known ages in Zanne’s
165 tree. Finally, the taxa that were not present in the Iberian flora were pruned from the
166 tree. Phylogenies of regional plant assemblages constructed following this procedure
167 provide estimates of community phylogenetic diversity metrics strongly correlated to
168 those obtained with fully resolved phylogenies at the species level (Qian & Jin 2016).
169 The phylogenetic tree of each time interval was scaled to the midpoint; e.g., the first
170 phylogenetic tree (i.e., the Danian tree) was scaled to have a total height of 63.60
171 Million years less than a contemporary tree.

172

173 *Phylogenetic diversity*

174

175 For each stage/substage, we computed the Mean Phylogenetic Distance (MPD) as an
176 indicator of the phylogenetic diversity traditionally used in community ecology to

177 compare how different communities are or which mechanisms, as environmental
178 filtering, are assembling them (Tucker et al., 2017). Phylogenetic distance between
179 two terminal taxa is the sum of branch lengths connecting them through their most
180 recent common ancestor in the phylogenetic tree. MPD is the average phylogenetic
181 distance between all the pairs of species co-occurring in a particular time span, and
182 because it is a mean value, it is relatively robust to the number of species and more
183 sensitive to the structure of the phylogenetic tree. MPD was calculated as the mean
184 value of the paired phylogenetic distances obtained with the *cophenetic* function in
185 the “ape” package for R (Paradis et al., 2004). To check whether the temporal
186 changes in MPD were due to a phylogenetically structured extinction, we
187 recalculated the MPD of each stage/substage after removing the newly emerging
188 taxa. Thus, we obtained the MPD of these “surviving taxa” and compared it to that of
189 the previous stage/substage through a paired-t test. If the MPD of the “surviving
190 taxa” is significantly lower than that of the previous stage/substage, it would indicate
191 that extinction erodes phylogenetic diversity.

192

193 To detect unexpected changes in phylogenetic diversity we compared the observed
194 temporal changes in MPD *versus* the expected values under a null model following
195 a constant rate evolutionary birth- death process (Nee et al., 1994). We use this
196 process as a simplification of more complex models allowing diversification rate-
197 shifts in different portions of the phylogeny. For example, Landis et al. (2018)
198 identified 334-530 shifts in diversification rates on this phylogeny, what broadly
199 agrees with the 471 rate shifts found by Smith and Brown (2018) in their
200 phylogeny. These results come from hundreds of different models but evaluating
201 the likelihood of such a high number of alternative models goes beyond our

202 objective. Instead, we have tested that our results are robust to a wide range of
203 birth, death and incomplete sampling rates under a constant-rate evolutionary, as
204 discussed below.

205

206 For each stage/substage we estimated a null model by simulating a phylogenetic
207 tree with the same number of taxa as the observed fossil taxa on that time span.
208 Birth and death parameters for the simulation were obtained from the tree of the
209 previous interval of time with the help of the `bd.time` function of the “ape”
210 package for R (Paradis et al., 2004); no null model was simulated for the first
211 stage. One thousand trees per stage/substage were simulated with the
212 `sim.bd.taxa.age` function in the R package “TreeSim” (Stadler, 2017). This
213 function simulates constant rates birth-death trees allowing for incomplete
214 sampling by assigning fixed probability for each species to be included in the final
215 tree (Stadler, 2009). Incomplete sampling is a very common feature in fossil data
216 that can be assessed through likelihood models. We obtained the fraction of
217 sampling rate (the *frac* parameter in the `sim.bd.taxa.age` function) through Foote
218 (1997) likelihood function to model sampling and extinction rates for taxonomic
219 duration datasets with the help of the `make_durationFreqDisc` and `sProb2sRate`
220 functions in PaleoTree package for R (Bapst, 2012). This approach can deal with
221 regional stratigraphic datasets where the observed frequency of taxon durations is
222 known for discrete time intervals. Mean phylogenetic distance for each simulated
223 tree was calculated as explained above and null expectations constructed by
224 obtaining the mean and 95% confidence interval of the 1,000 MPDs calculated per
225 each time stage/substage. Since the estimation of death rates and sampling rates
226 with phylogenies are prone to error (Rabosky, 2010; Bapst, 2014), we repeated the

227 analysis with different rates to check for the robustness of the results.

228

229 *Cenozoic climate in the Iberian Peninsula*

230

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

244

245 For the purpose of correlating phylogenetic diversity values across times with climatic
246 changes, we extracted the longest series of Cenozoic climatic paleoindicators (global
247 averaged oxygen isotope ($\delta^{18}\text{O}$) from Zachos et al. (2001) as reported in Utescher et al.
248 (2011) for the last 66 Ma. We used the web based tool WebPlotDigitizer v. 4.1 (Rohatgi
249 2018) for extracting the data from published figures. We validated its use at the Iberian
250 scale by correlating Zachos et al. (2011) data with that obtained for Tethyan unrelated
251 fossils (sirenians teeth, including some Iberian specimens) in Clementz et al. (2009).
252 Given that $\delta^{18}\text{O}$ in sea sediments directly correlated only with sea temperature, we
253 correlated the $\delta^{18}\text{O}$ curve with that of climatic atmosphere mean annual temperature

254 inferred by climatic tolerance of Nearest Living Relatives (NLR) estimates for central
255 Europe and northern Parathetys palaeoflora (closer to Iberia) in the last 45 Ma
256 (Mosbrugger et al., 2005). Correlations between temporal series were done after binning
257 the data to 1 million year intervals. This approach can be used at a more local/regional
258 scale and adds information on the precipitation regime, for which isotope data are little
259 informative. Altogether, evidence exists for sound correlation between these parameters
260 across geological periods, thus validating their use for testing climatic clues of
261 diversification patterns. It should be noted that our quantitative paleoenvironmental
262 assessment involves only temperature. Precipitation regimes are more difficult to infer
263 and we did not use the values obtained inferred through NLR by Mosbrugger et al.
264 (2005) because we could not validate against a non-botanical record for the entire
265 Cenozoic.

266
267 Thus, interpretation about precipitation was aided by qualitative information coming
268 from sedimentology in the Tethyan-Mediterranean region (García-Castellanos et al.
269 2003) and also at global scale (Ziegler et al., 2003), diet composition of sirenians
270 (Clementz et al. 2009), abundance of coral reefs and large foraminifera (Scheibner &
271 Speijer, 2008). A thorough account of the Cenozoic climate of the Iberian Peninsula
272 can be found in Postigo-Mijarra et al. (2009). These independent sources of
273 information point to an increase of aridity and seasonality through the Cenozoic
274 across the whole Tethys Basin, although the particular values of mean annual
275 precipitation and its seasonality are far to be known in detail.

276 **Results and Discussion**

277

278 Our database contains 619 fossil taxa stratigraphically distributed covering all the stages
279 of the Cenozoic. Magnoliophyta (angiosperms) is the best represented group with 568

280 taxa (Fig 1 E–F, H, J– K), followed by Coniferophyta (24 taxa; Fig 1 G, I), Pteridophyta
281 (21 taxa; Fig 1 A), Lycopodiophyta (3 taxa), Cycadophyta (1 taxon; Fig 1 C),
282 Ginkgophyta (1 taxon; Fig 1 D) and Gnetophyta (1 taxon; Fig 1, B). Obviously, the
283 inherent incompleteness of the fossil record means that the database necessarily
284 represents a subset of the plant species that occurred during the Cenozoic. However, it
285 represents the state-of-the-art of the fossil flora in Iberia and Balearic Islands. Taxa
286 richness increases from a few tens in the Danian to ca. 300 taxa in recent ages (Fig 2).
287 This trend could probably be related to the sampling bias since oldest outcrops
288 (Paleocene–Lutetian) are very scarce and concentrated in northern Iberia (Fig S1 A),
289 requiring thus the use of methods controlling for sampling bias for further phylogenetic
290 analyses, as we have used.

291

292 Phylogenetic diversity measures the amount of evolutionary history treasured in a
293 community as the result of processes related to lineage diversification, migration of
294 lineages, stochastic processes and local assembly (Yguel et al., 2016). Tracking
295 temporal trends of phylogenetic diversity may provide useful information on this
296 plethora of processes assembling past communities. According to our null model, Mean
297 Phylogenetic Diversity (MPD) displays two different phases in the Cenozoic of the
298 Iberian Peninsula (Fig. 3): From the Danian to the Lutetian, MPD is higher than
299 expected by the null model, while for the time interval between the Bartonian and the
300 present day (41.2–0 Ma) MPD shows values that lie within the null expectation. The null
301 models, which were constructed from simulated phylogenies with the same number of
302 species than those observed for each stage/substage (18–306) and a range of birth (0.22–
303 0.39), death (0–0.1) and (incomplete) sampling rates (0.089) obtained from the true
304 phylogenies (Fig S2), consistently support the existence of two phases in MPD (Figs S3

305 and S4). In all cases, except those where death rates are similar to birth rates (~ 0.25), a
306 significant high MPD is detected for the early Cenozoic (Danian to Lutetian) followed
307 by an abrupt decrease and a long-term stability.

308

309 The results show that MPD was high during the early Cenozoic (Danian to Lutetian)
310 (Fig 3). The Iberian flora of the early Cenozoic lived in a tropical-like climate (Zachos
311 et al. 2001; Barrón et al. 2010) with abundant taxa of paleotropical origin from the
312 Paleocene and Lower Eocene, such as Arecaceae, Ebenaceae, Magnoliaceae, tropical
313 Fagaceae and pteridophytes. Paleomangroves with *Nypa* and laurophyllous forests also
314 occurring in different areas of Iberia (Haseldonckx, 1973; Médus, 1977; Médus and
315 Colombo, 1991; Médus et al., 1992; López-Martínez et al. 1999; Fernández-Marrón et
316 al., 2004; Solé de Porta et al., 2007). Gymnosperms, especially conifers, were also a
317 significant group during this time interval (e.g. Sciadopityaceae or taxodioid conifers).
318 This evergreen vegetation type is consistent with high temperatures and humidity
319 promoting high phylogenetic diversities (Verdú et al., 2003).

320

321 The Early Eocene was the warmest stage of the Cenozoic and was punctuated by
322 various warming events or 'hyperthermals', including the Paleocene-Eocene Thermal
323 Maximum (PETM; ~ 56 Ma), the Eocene Thermal Maximum 2 (ETM2; ~ 54 Ma) and
324 the Early Eocene Climatic Optimum (EECO; 52 – 50 Ma) (Sloan and Morrill, 1998;
325 Lear et al., 2000; Cramwinckel et al., 2018). The latter is usually regarded as a crucial
326 turning point in the global climate dynamics, which was succeeded by a long-term,
327 progressive cooling leading to the development of polar ice-sheets (Zachos et al., 2008).
328 According to our results, the MPD remained high during the Lutetian in the study area,
329 after the EECO, probably reflecting the prevalence of a warm climatic regime and

330 favourable conditions for sustaining a high MPD. The sharp decrease in MPD observed
331 in the Bartonian could therefore be related to intensified cooler conditions after the
332 short-duration Middle Eocene Climatic Optimum (MECO) at ca. 41.5 Ma. (Mai, 1989;
333 Zachos et al., 2001, 2008; Mosbrugger et al., 2005; Postigo-Mijarra et al., 2009). The
334 MPD curve continues dropping during the Priabonian. At this time, families such as
335 Anacardiaceae, Cupressaceae (non taxodioids), Ephedraceae, Fabaceae and
336 Plumbaginaceae spread in the north-eastern part of the Iberian Peninsula due to their
337 cooler and drier ecological requirements (Cavagnetto & Anadón, 1996). The Eocene-
338 Oligocene transition is marked by a further global decrease in temperature (Liu et al.,
339 2009; Zanazzi et al., 2007). At a local scale, this climatic trend is reflected in NW Iberia
340 by a significant decrease in the proportion and diversity of thermophilous taxa (Postigo-
341 Mijarra et al., 2009; Casas-Gallego, 2018) consistent with the decrease in MPD
342 observed for the Rupelian (Fig 3). The Late Oligocene warming is another global
343 climatic event locally reflected in the Iberian paleofloras (Casas-Gallego et al., 2018)
344 which could be associated with the slight increase in MPD observed for the Chattian of
345 the Iberian Peninsula. Subsequently, during the Miocene, the MPD remained relatively
346 constant (Fig. 3). Over the Miocene, Arctotertiary taxa spread in different areas of Iberia
347 as well as different taxa related to open, more or less dry, environments such as
348 Amaranthaceae, Asteraceae, *Combretum*, Linaceae, Poaceae, Thymeleaceae, *Juniperus*
349 and *Quercus* (Rivas-Carballo, 1991; Rivas-Carballo et al., 1994; Valle-Hernández et al.,
350 1995; Barrón et al., 2010).

351

352 At the end of the Cenozoic, the MPD showed a decreasing tendency (Fig 3) which could
353 be related to the development of a dry season coinciding with the warmest period of the
354 year (ca. 3.1–3.2 Ma), thus initiating Mediterranean seasonality (Suc & Cravatte, 1982),

355 and the onset of the Quaternary glaciations (Lisiecki and Raymo, 2005, 2007). A
356 significant set of Paleotropical and Arctotertiary taxa (ca. 40 taxa e.g. Cyatheaceae,
357 Menispermaceae, *Ginkgo*, *Rhizophora*, *Liriodendron*, taxodioids, *Tsuga*, Araliaceae
358 [non *Hedera*], *Engelhardia*, Lauraceae [non *Laurus*], *Liquidambar* or *Parrotia*)
359 disappeared during the middle–late Piacenzian and the Middle Pleistocene Transition
360 (MPT) (Clark et al., 2006; Postigo-Mijarra et al., 2009, 2010). At that time, droughts
361 and fires increased (Keeley et al., 2012) producing the diversification of non-
362 sclerophyllous fire-prone species and the extinction of fire sensitive species (Verdú &
363 Pausas, 2013). However, our methodological framework lacks the resolution required to
364 depict changes at such short time scales, and thus the late decrease in MPD does not
365 depart from the null expectation. Alternatively, stochastic processes may be erasing the
366 phylogenetic trend in this late period or, conflicting processes leading to increase and
367 decrease of MPD simultaneously may be cancelling each other resulting in a non-
368 significant MPD (Ulrich et al., 2016).

369

370 It is tempting to relate the observed phylogenetic diversity trends with climate
371 fluctuations, as closely related species tend to have similar climate and disturbance
372 tolerances (Prinzing et al., 2001; Verdú & Pausas, 2007). Moreover, climate is an
373 indicator of the disturbance regime (Pausas & Paula, 2012). There is correlative
374 evidence that Zachos et al. (2001) world paleo-curve based on the Cenozoic deep sea
375 $\delta^{18}\text{O}$ signal can be used as a reliable proxy for temperature in Iberia (Fig S5). For this
376 purpose, we used data on $\delta^{18}\text{O}$ series obtained in enamel teeth of Tethyan sirenians
377 along the last 54 Ma, including specimens found in Iberian deposits (Clementz et al.,
378 2009). Zachos et al (2001) series is significant and positively correlated with the
379 sirenian data ($r=0.87$; $p<0.01$), suggesting that the global climatic trend also reflects a

380 regional (Tethyan) climatic trend in areas close to Iberia. It is also necessary to state that
381 estimated sea temperatures by Clementz et al. (2009) are in some extent reflecting air
382 temperature, which directly affects terrestrial plant life. In fact, $\delta^{18}\text{O}$ from Tethys
383 sirenians is significantly correlated with the mean temperature estimated from the
384 Nearest Living Relatives (NRL) climatic tolerance of species in paleobotanical records
385 at Central Europe along the last 45 Ma ($r = -0.51$; $p = 0.006$) (Mosbrugger et al., 2005),
386 suggesting that data from $\delta^{18}\text{O}$ can be extrapolated to temperatures faced by plant
387 assemblages close to Iberia, as it has been found for world climate (Mosbrugger et al.,
388 2005). Altogether, these correlations allow us to use Zachos et al. (2001) paleoclimate
389 curve as a proxy for local Iberian temperature trend along the 66 Ma of the Cenozoic.
390 The same curve is also significantly correlated to that of the phylogenetic diversity in
391 Iberia (Fig. 4). This relationship is driven by two separate clouds of points: both the
392 highest MPD and the warmest period occurred in the early Cenozoic (Danian to
393 Lutetian) and then MPD and temperature abruptly decreased during the Bartonian. This
394 pattern suggests that the climatic conditions that followed the MECO exerted a major
395 influence on the Iberian phylogenetic diversity. Other climatic fluctuations and
396 paleoenvironmental events (e.g., the multiple glacial phases that occurred during the
397 Miocene, the Middle Miocene Climatic Optimum [MMCO] and the Mediterranean
398 Salinity Crisis) seem to have had little effect on MPD, as no clear trend appears within
399 each of the two periods. Probably, fine-tuned climatic record and fossil record are
400 inherently difficult to reconcile due to their different sampling frequency and different
401 sensitivities (including speed of response) of fossil taxa to changing climates (see
402 Cortlett & Wescott, 2013 for current climate change). Whereas we admit that the
403 presence of these two disparate clouds of points limits the resolution of our analysis, it
404 is noteworthy that the strong difference in MPD between them coincides with sharp

405 increase of high frequency and wide variability in $\delta^{18}\text{O}$ since the Priabonian, probably
406 related with the establishment of the first ice-sheets in the Cenozoic (Zachos et al.,
407 2001). Whether it means a similar effect than that of Pleistocene Ice-Ages remains
408 unknown.

409

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

425

426 Despite the limitations associated with the fragmentary nature of the fossil record, we
427 provide, for the first time, a general overview of the plant phylogenetic diversity
428 through the Cenozoic in the Iberian Peninsula. Additionally, we propose a
429 methodological approach borrowed from the discipline of community phylogenetics,

430 which can be useful for detecting diversity patterns through time in other regions of the
431 world where appropriate paleontological and paleoenvironmental data were available.
432 Future developments of this approach should include spatial information to identify
433 spatio-temporal hot and cold spots of evolutionary history. For instance, the results
434 based on the fossil record could be incorporated in the comparative historical analysis of
435 biotas with similar current climate, which sometimes have been regarded as a result of
436 convergence (e.g., Mediterranean-type floristic regions: Rundel et al., 2016; subtropical
437 moist broadleaf forest in SE Asia and E North America: Qian et al., 2017). Most of the
438 territory of the Iberian Peninsula currently harbors a Mediterranean-type climate with a
439 particular diversification pattern, which seems to contrast with that of older SW
440 Australia and Cape Mediterranean climate (Rundel et al., 2018). Comparing
441 phylogenies of fossil record across Mediterranean-type climate regions might throw
442 light here. Ultimately, and despite the unprecedented rates of extinction associated to
443 current climatic change, understanding how plant communities faced past climatic
444 fluctuations could help us to forecast the consequences of climatic change on current
445 ecological communities (Thuiller et al., 2011).

446

447

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449

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455 **References**

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Figure legends

Fig 1. Selected specimens of Cenozoic Spanish plant assemblages.

- A-*Acrostichum lanzaeanum* (Visiani 1908) Reid and Chandler 1926, fragment of frond.
Burdigalian, Early Miocene, Mallorca. Specimen MBCN-2693, Museu Balear de Ciències Naturals, Sóller, Mallorca. Bar: 10 mm.
- B-*Distachyapites* cf. *eocenipites* (Wodehouse 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-*Ginkgo 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 related 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 potonieii* (Sivak 1976) Ziemińska-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 Pliocene), Cal Guardiola, Tarrasa, Barcelona. Sample 631, Universidad Autónoma de Barcelona. X500.

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

Figure 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.

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

Supplementary Material

Figure S1. Paleogene (A) and Neogene (B) fossil plant sites of the Iberian Peninsula. Information about them and fossil taxa identified for this study can be found in Appendix 1 and 2.

Fig S2. Tree assembling the phylogenetic relationships of the 619 taxa in the whole database (top) and in each time period studied (bottom)

Fig S3. Observed phylogenetic diversity (thick solid line) along the studied period against a null model (thin and dashed lines) constructed with different fractions of sampling rates of the simulated phylogenies.

Fig S4. Observed Phylogenetic diversity (thick solid line) along the studied period against a null model (thin and dashed lines) constructed with different death rates of the simulated phylogenies.

Fig S5. Cenozoic paleoclimatic curves reconstructed from data on a) deep sea $\delta^{18}\text{O}$ signal (Zachos et al., 2001), b) $\delta^{18}\text{O}$ signal in enamel teeth of Tethyan sirenians and c) mean annual temperature from fossil Cenozoic floras of central Europe (Mosbrugger et al., 2005).

Appendix 1. List of references used to construct the database.

Appendix 2. Database of fossil taxa in the Iberian flora through the Cenozoic.

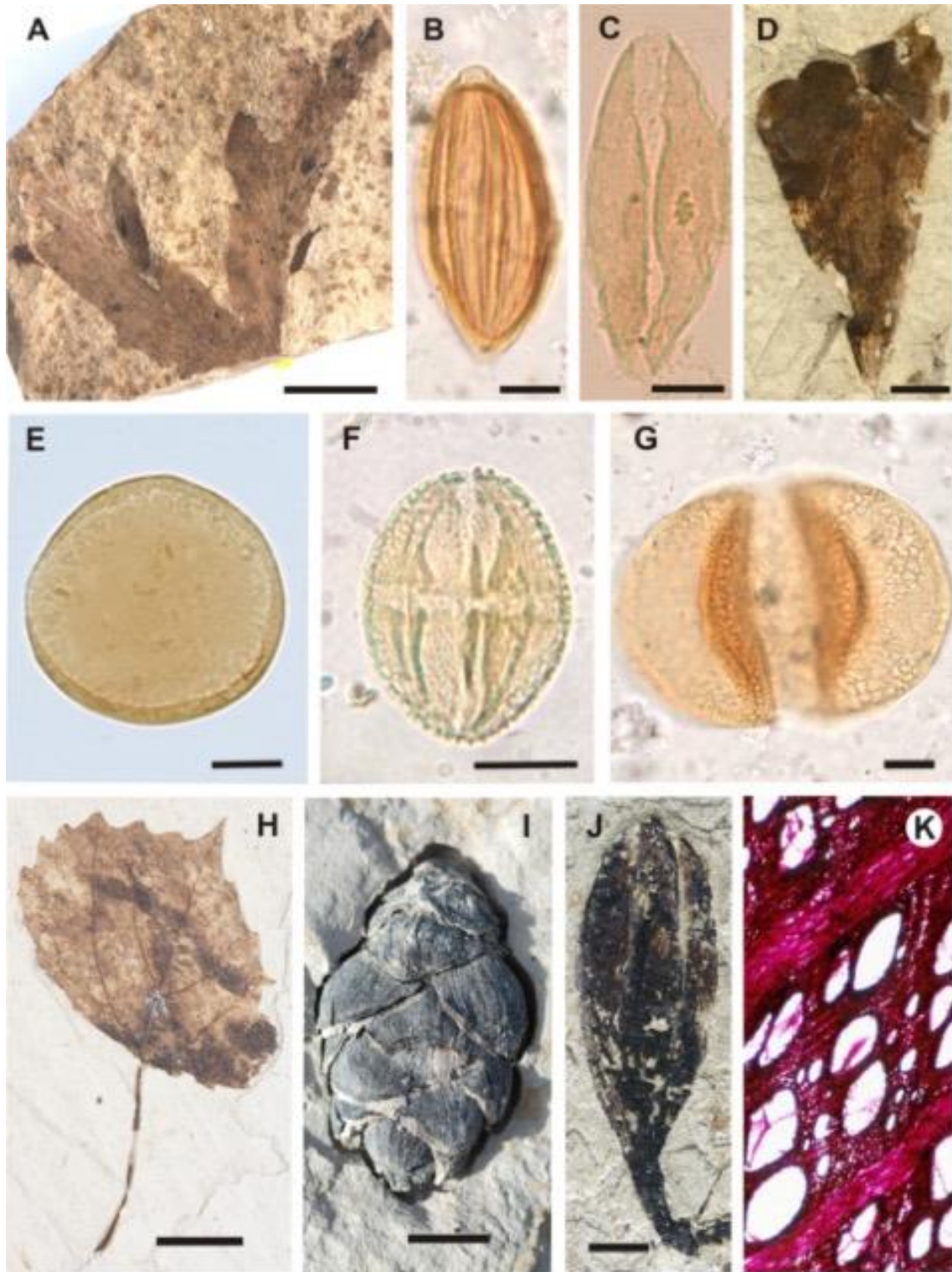


Fig. 1

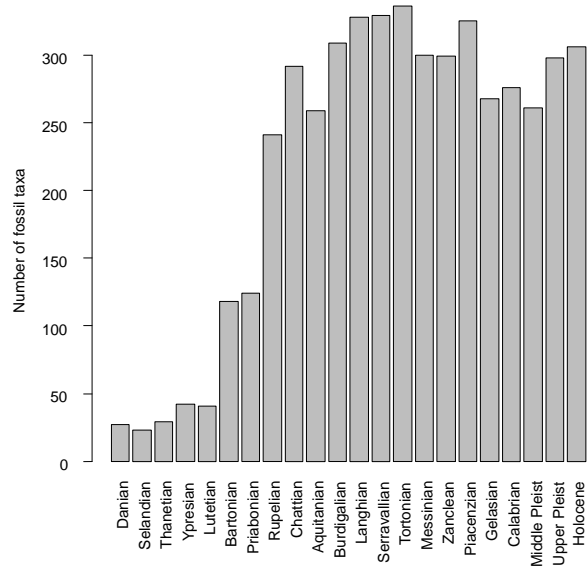


Fig. 2

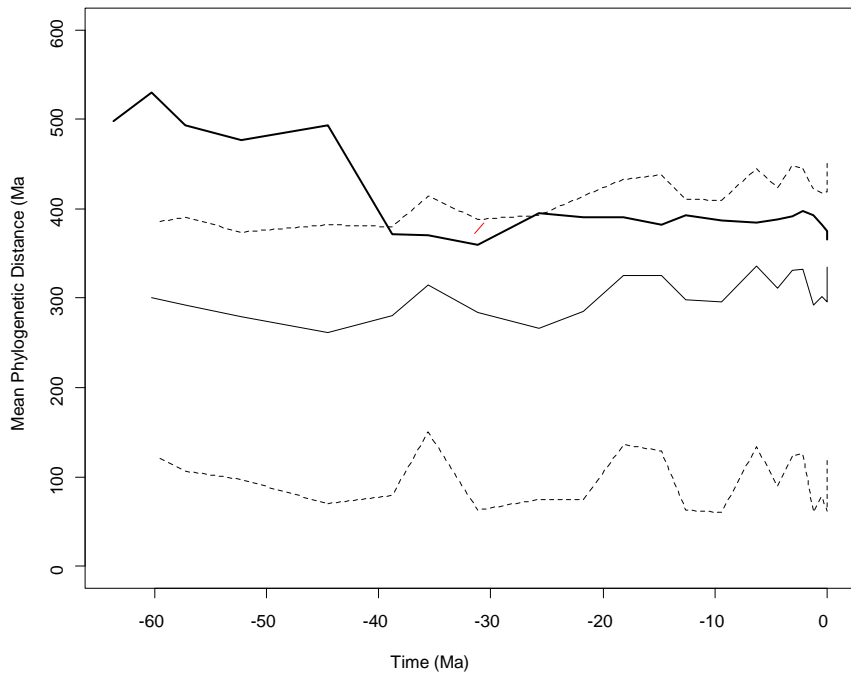


Fig. 3

