1 **Modern pollen representation of the vegetation of the Tagus Basin (central Iberian Peninsula)**

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Abstract

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18   The study of modern vegetation-pollen relationships has long been recognized as crucial for the

19   proper interpretation of fossil pollen records. Despite the quickly growing number of palynological

20   studies from central Iberia and its adjacent Atlantic margin, comprehensive studies about modern

21   pollen representation at broad spatial scales were still lacking. In this paper, we have studied the

22   vegetation-pollen relationships in the Tagus Basin in 62 sites located along a wide environmental

23   gradient from Thermomediterranean evergreen mixed thermophilous woodlands by the Atlantic coast

24   to Oromediterranean shrublands above the treeline in the Guadarrama Mountains (central Spain). At

25   each site, we analysed pollen from moss polsters and conducted vegetation surveys. Most forested

26   vegetation types (pinewoods, oak woods, evergreen mixed thermophilous woodlands) presented

27   rather distinct pollen assemblages dominated by the pollen equivalents of the major tree species.

28   Nevertheless, enhanced taxonomic resolution within *Pinus* and *Quercus ilex*-type would represent

29   significant progress, e.g. enabling to separate Mediterranean and mountain pinewoods. Pollen spectra

30   from shrubland and steppic communities are in general less differentiated, due to high regional pollen

31   input associated to low local pollen production and/or the dominance of insect-pollinated species (e.g.

32   *Cytisus oromediterraneus* in mountain shrublands). The results presented here will readily assist the

33   interpretation of regional fossil pollen records from small mires/bogs/lakes and forest hollows, given

34   their comparable pollen catchments. Comparison of modern pollen assemblages with pollen records

35   from larger lakes and marine settings is not so straightforward, but our results suggest that marine

36   pollen assemblages might average the pollen signature of the entire basin.

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1. Introduction

Pollen-stratigraphic records from sedimentary archives represent one of the most powerful and widely used tools to reconstruct vegetation changes on long (decadal to millennial) timescales (e.g. van Zeist and Wright, 1963; Birks, 1965; Lotter, 1999; Tinner et al., 1999; Sánchez Goñi et al., 2008; Rey et al., 2019). The Iberian Peninsula and its margin is one of the European regions where the amount of palynological investigations has increased most significantly in recent times, stimulated by its diverse landscape, complex land-use history and sensitivity to climate change (Carrión et al., 2010; Sánchez Goñi et al., 2018). Palaeoecology has particularly developed in central Iberia, with the publication of a number of new multi-proxy studies addressing diverse ecological questions like vegetation dynamics, fire history, fire ecology, human impact, or herbivore-vegetation interactions (e.g. Franco Múgica et al., 1998; López-Merino et al., 2010; Abel-Schaad and López-Sáez, 2013; Morales-Molino et al., 2017a, 2019, Luelmo-Lautenschlaeger et al., 2019). Likewise, pollen-based palaeoclimatic research on marine sediments with strong influence of the River Tagus and River Sado plumes has largely moved forward in recent years (e.g. Sánchez Goñi et al., 1999, 2008, 2019; Roucoux et al., 2006; Oliveira et al., 2017).

Studies on the modern pollen representation of extant plant communities have long been recognized as playing a central role in assisting the interpretation of fossil palynological records, helping disentangle challenging issues concerning differential pollen production, dispersal and preservation (e.g. Davis and Goodlett, 1960; Wright, 1967; Stevenson, 1985; Bell and Fletcher, 2016). During the last decades, several studies have addressed modern vegetation-pollen relationships all over the Mediterranean region (e.g Davies and Fall, 2001; Finsinger et al., 2007; Fall, 2012; Bell and Fletcher, 2016; López-Sáez et al., 2018), including the Iberian Peninsula (e.g. Stevenson, 1985; Díaz-Fernández, 1994; Andrade Olalla et al., 1994; Aranbarri et al., 2015). The latter research has provided very valuable insights into the pollen representation of Iberian plant communities, but its geographical scope was usually rather narrow, i.e. transects across single mountain ranges (Díaz Fernández, 1994; Andrade Olalla et al., 1994; Sánchez Goñi and Hannon, 1999; Cañellas-Boltà et al., 2009; Aranbarri et al., 2015). In central Iberia, the main focus has been on specific plant communities such as *Pinus sylvestris*, *Quercus ilex* and *Quercus pyrenaica* woodlands (López-Sáez et al., 2010, 2013, 2015), or

70   on geographically restricted areas such as the Gredos Mountains (Broothaerts et al., 2018). More

71   general overviews on vegetation-pollen relationships over broad ecological and geographical

72   gradients, i.e. those probably integrated in deep-sea pollen assemblages (Heusser and Balsam, 1977;

73   Dupont and Wyputta, 2003; Mudie and McCarthy, 2006), are therefore lacking so far for the Iberian

74   Peninsula.

75   In this paper, we aim at partially filling this gap by investigating the modern pollen representation of

76   the Tagus Basin (Figure 1). This area of central Iberia is not particularly rich in endemic plant species

77   but it hosts an outstandingly diverse set of plant communities and is home to a diverse flora (Sainz

78   Ollero et al., 2010; Moreno Saiz et al., 2013; Aedo et al., 2017), as a result of the wide environmental

79   gradients and its location at the crossroad of several different floristic regions (Sainz Ollero and

80   Sánchez de Dios, 2011; Moreno Saiz et al., 2013). In this setting, we sampled an array of (semi-

81   )natural plant communities distributed throughout the Tagus Basin, from the Atlantic coast to the

82   Iberian Range (Figure 1). In our sampling, we included not only the most widespread woodlands and

83   shrublands (e.g. pine and oak woods, maquis, garrigue) but also rarer vegetation types of great

84   biogeographical interest such as beech and chestnut stands, *Prunus lusitanica*-dominated riparian

85   forests, juniper woodlands, broom-dominated shrublands and steppic communities on gypsum (Table

86   1). Some of these currently rare vegetation types, for instance steppic communities, were dominant in

87   the Iberian Peninsula during Quaternary cold and dry stages (e.g. Sánchez Goñi et al., 2002). At the

88   study sites, we conducted vegetation surveys and collected surface samples (usually moss polsters) to

89   analyse the modern pollen rain, with the main aim of assessing today's pollen-vegetation relationships

90   and shedding new light into the interpretation of regional fossil pollen sequences.

91

92   **2. Study area**

93   The River Tagus flows south-westwards along more than 1,000 km, from its springs in the Montes

94   Universales at 1,593 m asl to its mouth at the Atlantic Ocean near Lisbon (Figure 1). The Tagus is

95   indeed the longest of the Iberian rivers, and drains a basin of 81,600 km^2 across central Spain and

96   Portugal. Most of the surface of the Tagus Basin is included within the Southern Iberian Plateau,

97   where elevation is highest at the foothills of the Iberian Range on its north-eastern edge (*ca.* 1,000 m

98 asl) and then decreases westwards to *ca.* 200-300 m asl in the region of Extremadura, averaging 600-

99 700 m asl. The mountainous borders of the Tagus Basin include the Iberian Central Range (*'Sistema*

100 *Central Ibérico'* or *'Cordillera Central Ibérica'*) to the north, the Iberian Range (*'Sistema Ibérico'*) to

101 the east, and the Toledo Mountains *sensu lato* (*'Montes de Toledo'*) to the south (Figure 1). The

102 Iberian Central Range is a *ca.* 600-km long mostly west-to-east oriented cordillera that mainly

103 consists on siliceous bedrock (e.g. granite, gneiss, slate) and features notable peaks usually above

104 2,000 m asl, particularly in its central and eastern sectors (e.g. Almanzor 2,591 m asl, Peñalara 2,428

105 m asl, or Pico del Lobo 2,274 m asl). In contrast, although bedrock is outstandingly diverse,

106 calcareous rocks clearly dominate in the section of the Iberian Range that delimits the Tagus Basin.

107 Other major features of this mountainous area are: (i) the massive extension; (ii) the high plateau-like

108 structure with relatively modest elevations mostly ranging between 1,000 and 1,800 m asl and lack of

109 truly prominent peaks; and (iii) the abundance and length of impressive canyons (usually with several

110 hundred metres high cliffs) carved by the River Tagus and its tributaries in the dominant limestone,

111 dolostone and sandstone. Finally, the Toledo Mountains are a hilly landscape of mid-elevation

112 mountains (highest peaks between 1,000 and 1,600 m asl: e.g. Pico Rocigalgo 1,448 m asl and Pico

113 Las Villuercas 1,603 m asl) of usually gentle slopes built on acidic bedrock (e.g. schist, slate,

114 quartzite).

115 The climate of the Tagus Basin is predominantly mediterranean, i.e. temperate with mild humid

116 winters and dry and hot summers (climate Csa according to the Köppen-Geiger Climate

117 Classification; AEMET/IMP, 2011). Although summer drought is a consistent feature all over the

118 basin, cooler temperatures and convective rain attenuate it in the mountains (climate Csb), particularly

119 in the Iberian Range where frequent convective rain episodes lead to an absence of dry season

120 (climate Cfb; see P_{summer} values in Table 1). At the highest peaks of the Iberian Central Range, climate

121 is cold with temperate/cool dry summers (climates Dsb and Dsc). Similarly, particularly dry

122 conditions translate into a cold steppe climate (climate BSk) in the lowlands of the central sector of

123 the Tagus Basin. Mean annual temperature ranges from *ca.* 15-17°C close to the Atlantic Ocean and

124 on the Extremaduran plains to *ca.* 5°C at the highest mountains of the Iberian Central Range and the

125 Montes Universales area in the Iberian Range. Mean annual precipitation is also quite variable, from

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126 less than 400 mm in the central section of the River Tagus valley bottom to more than 1000 mm at the

127 highest elevations of the Iberian Central Range (Table 1). In general, mean annual precipitation

128 follows two main gradients: (i) decreasing rainfall with increasing distance to the Atlantic coast, and

129 (ii) increasing precipitation at higher elevation in the mountains due to orographic rain.

130 Today's vegetation cover of the Tagus Basin, like elsewhere in the Mediterranean region, is heavily

131 disturbed after millennia of human activities, and the landscape is mainly dedicated to rather intensive

132 farming and industrial activities. Natural and semi-natural vegetation is mostly restricted to

133 mountainous terrain where agricultural activities and livestock raising were always extensive and

134 have been largely abandoned during the last decades. Despite these constraints, the Tagus Basin

135 currently hosts a unique richness of plant species and communities. This paper does not intend to

136 provide a detailed description of the many different plant communities that currently inhabit this

137 region of central Iberia. We will rather describe briefly the main plant communities thriving in each of

138 the four major vegetation belts represented in the Tagus Basin, i.e. the Thermomediterranean, the

139 Mesomediterranean, the Supramediterranean, and the Oromediterranean, based on Costa et al. (2005),

140 Loidi (2017) and the authors' field expertise. The Thermomediterranean belt consists of a narrow strip

141 of land along the Atlantic coast where the most relevant woody plant communities are evergreen

142 thermophilous woodlands and maquis (with *Quercus coccifera*, *Ceratonia siliqua*, *Pistacia lentiscus*,

143 *Phillyrea latifolia*, *Arbutus unedo*, *Olea europaea* and *Erica arborea* among others), Mediterranean

144 pinewoods (*Pinus pinaster*, *Pinus pinea*) on coastal dunes and sand sheets, psammophilous

145 communities on the coastal dunes, and some *Quercus suber*-dominated *'dehesas'* (*'montados'* in

146 Portuguese; open oak woods with agro-silvo-pastoral use). Evergreen oak (*Quercus ilex* subsp.

147 *ballota*, *Quercus suber*) woods and *'dehesas'* are the most frequent forest communities in the

148 Mesomediterranean belt, widespread in the central and western sectors of the study area, with notable

149 variations in the floristic composition of their understory driven by local soil features, climatic

150 conditions, historical biogeography, and land-use history. At the foothills of the Iberian Central Range

151 and the Iberian Range, evergreen oaks mixed with Mediterranean pines (mostly *Pinus pinaster* and to

152 a lesser extent *Pinus pinea* and *Pinus halepensis*) and deciduous oaks (*Quercus pyrenaica*, *Quercus*

153 *faginea* subsp. *faginea*). The Supramediterranean belt covers extensive mid-elevation areas of the

154   Iberian Central Range and the Iberian Range, and the highest areas of the Toledo Mountains. This

155   vegetation belt hosts the highest diversity of wooded plant communities of the entire Tagus Basin,

156   namely deciduous oak woods (*Quercus pyrenaica* on siliceous bedrock, and *Quercus faginea* subsp.

157   *faginea* on calcareous bedrock and gypsum), mountain pinewoods (*Pinus nigra* subsp. *salzmannii*,

158   *Pinus sylvestris*), *Pinus pinaster* woodlands, juniper (*Juniperus thurifera*) woodlands, sweet chestnut

159   (*Castanea sativa*) stands, and evergreen oak woodlands (*Quercus ilex*), just to mention the most

160   broadly distributed ones. Finally, *Pinus sylvestris* woods are the dominant forest communities at the

161   highest elevations of the central and eastern sectors of the Iberian Central Range and the Iberian

162   Range, i.e. in the Oromediterranean belt, both on siliceous and calcareous bedrock. The understory of

163   these Oromediterranean mountain pinewoods is usually dominated, particularly near the timberline

164   and at the tree line ecotone, by creeping shrubs like *Juniperus communis* subsp. *alpina*, *Juniperus*

165   *sabina* and *Cytisus oromediterraneus*, which are actually the most frequent species in the shrublands

166   located above the tree limit. The Oromediterranean belt of the Iberian Central Range, specifically on

167   the Ayllón Mountains, is also home to some of the southern-edge populations of *Fagus sylvatica* in

168   western Europe, where European beech is accompanied by a diverse set of mesophilous trees like

169   *Quercus petraea*, *Ilex aquifolium*, *Betula pendula*, *Sorbus aria* or *S. aucuparia*. Another differential

170   feature of the vegetation of the Ayllón Mountains, partially shared with the westernmost massifs of

171   the Central Iberian Range (e.g. Serra da Estrela), is the abundance of Ericaceae (e.g. *Calluna vulgaris*,

172   *Erica arborea*, *Erica australis*, *Arctostaphylos uva-ursi*) in the understory of the deciduous forests

173   typical of the Supra- and Oromediterranean vegetation belts, above the timberline, and in the serial

174   shrublands. Riparian vegetation is very diverse in the Tagus Basin (Lara et al., 2007), with *Salix* spp.,

175   *Populus* spp., *Fraxinus angustifolia* and *Ulmus minor* as the usually dominant taxa and also the

176   remarkable presence of some communities dominated by the rare Tertiary evergreen broadleaved

177   *Prunus lusitanica*, particularly in the western sector of the Toledo Mountains (Calleja et al., 2009).

178   Concerning non-forested vegetation, the shrublands that have replaced forests and woodlands

179   following anthropogenic or natural intense and/or frequent disturbance mostly consist of *Cistus* spp.,

180   *Erica* spp., *Calluna vulgaris* and different genera of Genisteae (e.g. *Cytisus*, *Genista*, *Pterospartum*)

181   and Lamiaceae (e.g. *Lavandula*, *Thymus*, *Salvia*, *Satureja*). Finally, it is noteworthy the presence of

182   steppic communities with abundant *Macrochloa (Stipa) tenacissima*, Amaranthaceae

183   (Chenopodiaceae), *Ephedra* spp., *Helianthemum squamatum* and *Artemisia herba-alba* on gypsum in

184   some areas of the central Tagus Basin.

185

186   **3. Material and Methods**

187   *3.1 Fieldwork: sample collection and vegetation surveys*

188   In November 2016, we conducted fieldwork throughout the Tagus Basin, collecting 62 samples from

189   the coastal dunes and sand sheets close to the River Tagus estuary to the headwaters of the River

190   Tagus and its main tributaries (Figure 1). Fieldwork planning aimed at sampling a wide set of the

191   extant (semi-)natural plant communities of central Iberia (Table 1), from the Thermomediterranean to

192   the Oromediterranean vegetation belt. The environmental gradients covered were thus notably broad,

193   with the sampling sites located along a large elevation gradient (from sea level to *ca.* 1900 m asl),

194   under contrasting climatic conditions (from the mild Atlantic shore to one of the coldest and most

195   seasonal area of the Iberian Peninsula, the central Iberian Range), and on diverse bedrock (e.g.

196   granite, schist, limestone, sandstone).

197   The sampling sites were classified in thirteen groups according to their present *'vegetation type'* to

198   facilitate the latter representation and discussion of the results (see Table 1, Figure 2): (1)

199   *'Mediterranean pinewoods'* includes forest and woodland communities dominated by *Pinus pinea*,

200   *Pinus halepensis* and/or *Pinus pinaster* (*n*=10); (2) *'Mountain pinewoods'* consists of *Pinus sylvestris*-

201   and/or *Pinus nigra*-dominated forests and woodlands (*n*=8); (3) *'Deciduous oak woods'* comprises

202   woodlands where *Quercus pyrenaica* and/or *Quercus faginea* dominate (*n*=12); (4) *'Evergreen oak*

203   *woods'* groups the *Quercus ilex* subsp. *ballota*- and/or *Quercus suber*-dominated woodlands and

204   *'dehesas'* (*n*=10); (5) *'Evergreen mixed thermophilous woodland'* refers to shrub and forest

205   communities dominated by several species of Mediterranean evergreen trees and shrubs (often

206   referred to as sclerophyllous) like *Quercus coccifera*, *Pistacia lentiscus*, *Olea europaea*, *Ceratonia*

207   *siliqua*, *Phillyrea latifolia*, *Arbutus unedo*, *Erica arborea*, *Juniperus phoenicea* or *Viburnum tinus*

208   (*n*=5); (6) *'Chestnut stands'* are communities with *Castanea sativa* as the dominant tree (*n*=2); (7)

209   *'Riparian forest with* Prunus lusitanica*'* sites are within stands of *Prunus lusitanica* inhabiting narrow

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gorges of the Toledo Mountains surrounded by *Quercus pyrenaica* woodlands (*n*=2); (8) *'Beech stands'* site was located in one of the three main *Fagus sylvatica* sub-populations of the Iberian Central Range (*n*=1); (9) *'Juniper woodlands'* refers to more or less open woodlands dominated by *Juniperus thurifera* with an understory rich in chamaephytes (*n*=3); (10) *'Mountain shrublands'* are located above the modern tree line and the dominant species are usually *Cytisus oromediterraneus* and *Juniperus communis* subsp. *alpina* (*n*=4); (11) *'Lowland shrublands'* includes communities resulting from the degradation of mid-elevation woodlands where Cistaceae and Lamiaceae are dominant (*n*=2); (12) *'Steppic vegetation'* refers to *Macrochloa (Stipa) tenacissima*-dominated communities growing on gypsum in particularly dry settings, where other typical steppic plants such as *Artemisia*, *Ephedra*, *Helianthemum* and Amaranthaceae (Chenopodiaceae) are relevant (*n*=2); and (13) *'Coastal dunes'* includes a single site from a dune system on the Portuguese coast (*n*=1). Surface samples mostly consisted of moss polsters but in some cases some litter and/or the topmost soil layer were also collected. At each site we picked up several moss fragments (usually 5) within a plot of *ca.* 20×20 m^2 following the recommendations in Pardoe et al. (2010). The only exception was at Site no. 1, where we collected the uppermost soil layer. In these plots we recorded vegetation structure and composition, with a particular focus on the woody taxa (i.e. trees, shrubs, dwarf shrubs, and lianas). Local tree cover (%) and, in some cases, shrub cover (%) were also visually estimated in most cases. We also recorded the extra-local vegetation (some hundred metres around the sampling site) when this was different from the local.

3.2 Pollen analysis

In the laboratory, we carefully homogenized each sample to prevent overrepresentation of plants growing next to each individual moss polster. Moss sub-samples of *ca.* 5-10 cm^3 then underwent physical (wet sieving with a 150 μm mesh, decanting) and chemical (HCl, HF, KOH, acetolysis) to concentrate pollen. We finally mounted slides using glycerol as mounting medium and counted pollen and spores using an optical microscope at 400× magnification. Terrestrial pollen sum (excluding spores and pollen from aquatic plants) was always above 500 pollen grains (Mean ± SE: 531 ± 35) with the exception of Sample no. 1 (*n*=413) due to poorer pollen preservation. For pollen

238   identification we used photographic atlases (e.g. Reille, 1992), identification keys (e.g. Punt et al.,

239   1976-2009; Beug, 2004) and the reference collection at the University of Bordeaux (UMR EPOC).

240   The Tilia software (https://www.tiliait.com/) was used for pollen data handling and plotting of

241   percentage pollen diagrams.

242

243   *3.3 Numerical analyses*

244   We grouped the sampling sites according to the similarity of their modern pollen assemblages using

245   Ward's minimum-variance agglomerative clustering (Ward, 1963; Legendre and Birks, 2012a)

246   running in PAST 3.18 (Hammer et al., 2001). We then used ordination to summarize and assess the

247   compositional variation of the pollen data-set (Legendre and Birks, 2012b). First, we ran detrended

248   correspondence analysis (DCA) on untransformed pollen percentages to quantify the compositional

249   turnover in the surface pollen sample dataset in standard deviation (SD) units and to assess whether

250   ordination methods based on linear or unimodal response models were better suited for further

251   analysis (ter Braak and Prentice, 1988; Šmilauer and Lepš, 2014). As the length-of-gradient of the

252   first axis of the DCA was 2.11 SD, we selected the linear method for unsupervised ordination, i.e.

253   Principal Component Analysis (PCA; Legendre and Birks, 2012b). One surface pollen sample from

254   the Tagus Estuary (*'Barreiro'*) and another marine core-top sample from the Iberian margin off-

255   Portugal (*'MD95-2042'*; Fig. S1; Naughton et al., 2007) were added passively to the ordination plots

256   to explore the relationships between the modern pollen spectra at these sites and the pollen

257   representation of extant plant communities of central Iberia. Ordination analyses were conducted in

258   Canoco 5 (ter Braak & Šmilauer, 2012).

259

260   **4. Results**

261   *4.1 Pollen data*

262   The most striking feature of the pollen spectra from Mediterranean pinewoods is the dominance of

263   *Pinus* pollen (*ca.* 60-85%), in some cases accompanied by pine stomata (Figure 2). *Quercus* pollen is

264   usually relevant in these pollen assemblages, with the main *Quercus* pollen type (type=t.) changing

265   according to the elevation (i.e. *Quercus suber*-t. on coastal communities, *Quercus ilex*-t. at mid-

266   elevation, and *Quercus pyrenaica/faginea*-t. further up). Tree pollen percentages are therefore rather

267   high (70-95%) and there are few shrubs and herbs truly important (Ericaceae undiff./*Corema*, *Cistus*,

268   Poaceae; Figures 2, 3). Mountain pinewoods show a very similar picture, with *Pinus* pollen largely

269   dominating the assemblages (*ca.* 60-90%) and regular findings of *Pinus* stomata (Figure 2). *Quercus*

270   *pyrenaica/faginea*-t. pollen is relatively abundant (>10%) in some samples, and it is worth to note the

271   representation of *Juniperus*-t. in some samples from the Iberian Range (5-10%; Figure 2). In

272   summary, tree pollen percentages are very high (*ca.* 85-95%) and the pollen representation of herbs is

273   extremely reduced (3-5%).

274   Pollen assemblages of deciduous oak woods are characterized by high percentages of tree pollen (75-

275   95%), mostly corresponding to *Quercus pyrenaica/faginea*-t. (usually 30-75%) but with notable

276   representation of *Quercus ilex*-t. (usually *ca.* 5-20%) and *Pinus* (*ca.* 5-40%; Figure 2). Ericaceae

277   undiff./*Corema* and *Alnus* are well represented in several samples from the western sector of the

278   Tagus Basin with >5%. Another remarkable feature of the western deciduous oak woods is the

279   relative abundance of *Plantago lanceolata*-t. (*ca.* 2-5%; Figure 3). Tree pollen percentages are also

280   high in samples from evergreen oak woods (70-95%), mainly *Quercus ilex*-t. (*ca.* 30-80%) but also

281   *Pinus*, especially to the east of the study area (15-45%), and *Quercus pyrenaica/faginea*-t., also in the

282   central and eastern sectors of the Tagus Basin (5-25%; Figure 2). The abundance of Cichorioideae

283   pollen (*ca.* 10%) in a pair of samples from *'dehesas'* is highly remarkable, together with moderate

284   abundances of *Plantago lanceolata*-t. (2-4%; Figure 3). Evergreen mixed thermophilous woodland

285   pollen assemblages are also dominated by tree pollen (*ca.* 70-85%), with a moderate representation of

286   shrub pollen (*ca.* 10-25%; Figure 2). *Quercus ilex*-t. is usually the most abundant pollen type (*ca.* 40-

287   65%) with the exception of Site no. 9 where *Pinus* is dominant (*ca.* 40%) alongside *Olea europaea*

288   (*ca.* 20%). But the most remarkable feature of the pollen assemblages of this vegetation type is

289   probably the diversity and moderate abundances of evergreen woody taxa (broadleaved and conifers),

290   e.g. *Juniperus*, *Ceratonia*, *Phillyrea*, *Pistacia*, *Smilax aspera* or *Viburnum tinus*-t.

291   The two samples from chestnut stands have very different pollen signatures, as one of them bears a

292   strong dominance of *Castanea sativa* pollen (no. 13, *ca.* 85%) while the other has a minimum

293   representation of this pollen type (no. 20, *ca.* 2%; Figure 2). Sample no. 20 has actually a rather mixed

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294 composition with *Alnus* (*ca.* 15%), *Pinus* (*ca.* 10%) and *Quercus pyrenaica/faginea*-t. (*ca.* 30%) as

295 best represented taxa. Similarly, pollen assemblages from riparian communities where *Prunus*

296 *lusitanica* is dominant or co-dominant record low proportions of *Prunus* pollen (0.5 and 3.5%), and

297 are rather dominated by *Quercus pyrenaica/faginea*-t. (*ca.* 15-35%) and Ericaceae undiff./*Corema*

298 (*ca.* 15-20%; Figure 2). *Pinus* (*ca.* 10%) and *Quercus ilex*-t. (*ca.* 5-15%) are also important taxa of the

299 assemblages, while *Frangula alnus* and *Cistus* reach *ca.* 5% and 3-4% of the terrestrial pollen sum

300 respectively. In Sample no. 49, *Osmunda regalis* spores reach an outstanding 15% (Figure 3). The

301 only sample collected from *Fagus sylvatica*-dominated stands show co-dominance of *Fagus* (*ca.*

302 35%) and *Pinus* (*ca.* 30%) in a pollen assemblage where other relevant woody taxa are *Quercus*

303 *pyrenaica/faginea*-t. (*ca.* 10%), *Ilex aquifolium* (*ca.* 3%), *Sorbus* (1%) and Ericaceae undiff./*Corema*

304 (*ca.* 5%; Figure 2). Open juniper woodland (Sample no. 52) shows moderate tree pollen percentage

305 (65%) while the closed stands of *Juniperus thurifera* (Samples no. 55 and 57) reach *ca.* 85% of tree

306 pollen (Figure 2). *Juniperus*-type is the most abundant pollen type (*ca.* 20-45%) with notable

307 percentages of *Pinus* (*ca.* 25%), *Quercus pyrenaica/faginea*-t. (7-15%) and *Quercus ilex*-t. (*ca.* 5%).

308 In Sample no. 52, *Helianthemum* and Lamiaceae 6-colpate are remarkably well-represented, 7% and

309 4% respectively.

310 Mountain shrubland samples feature rather low tree pollen percentages (*ca.* 35-55%) and usually low

311 proportions of shrub pollen (2-8(25)%; Figure 2). The representation of trees is quite variable

312 depending on the site but, in general, *Pinus*, *Quercus* and *Alnus* are the main ones. *Juniperus*-t. (0.5-

313 7%), Ericaceae undiff./*Corema* (1-24%) and *Genista*-t. (0.5-4%) are the most relevant shrubs. Among

314 the herbs, Poaceae (*ca.* 10-40%), *Rumex acetosa/acetosella*-t. (1-1.5%, and 20% in Sample no. 16)

315 and *Anthemis*-t. (1-3%) are the best represented (Figure 3). Lowland shrubland samples are very

316 different (Figures 2, 3): Sample no. 25 is dominated by *Cistus* (30%) and regional tree pollen (*Pinus*

317 20%, *Quercus ilex*-t. 15%, *Quercus pyrenaica/faginea*-t. *ca.* 10%), whereas tree pollen dominates in

318 Sample no. 40 (*Pinus* 40%, *Quercus ilex*-t. 20%, *Quercus pyrenaica/faginea*-t. 10%) with the

319 remarkable abundance of *Gypsophila*-t. (*ca.* 10%). Pollen assemblages from steppic communities

320 show the lowest values of tree pollen (35-50%) because herbs dominate (*ca.* 45-65%). It is important

321 to note the relative abundance of regional wind-pollinated trees such as *Pinus*, *Quercus ilex*-t. and

12

Quercus pyrenaica/faginea-t. (Figure 2). Important taxa are Poaceae (*ca.* 10-20%), Chenopodiaceae

(5-20%), *Gypsophila*-t. (>20% in Sample no. 37) and to a lesser extent *Artemisia*, Apiaceae, Cerealia-

t. and *Helianthemum* (Figures 2, 3). Finally, Sample no. 1, from the coastal dunes of Portugal, shows

relatively low proportion of tree pollen, mostly *Pinus* (*ca.* 30%; presence of stomata) and *Salix* (*ca.*

10%), and rather high abundances of herbaceous pollen, mostly of Poaceae (10%) and other plants

typical of coastal environments such as Chenopodiaceae, *Crithmum maritimum*-t., *Corrigiola*

litoralis, Cichorioideae, Brassicaceae, and *Aster*-t. (Figures 2, 3).

4.2 Clustering and ordination

The results of the hierarchical clustering on pollen percentage data shows nine major groups (Figure

4): (i) Cluster 1 consists of 18 samples where *Pinus* pollen is largely dominant from pine forests and

pine-dominated woodlands; (ii) Cluster 2 includes 13 samples with high proportions of *Quercus ilex*-

t., from *Quercus ilex* woodlands and *'dehesas'* as well as mixed thermophilous evergreen forests

where *Quercus coccifera* is usually abundant; (iii) Cluster 3 is composed of 12 samples with pollen

assemblages dominated by *Quercus pyrenaica/faginea*-t. and moderate abundances of *Quercus ilex*-t.,

from plant communities where deciduous *Quercus* (mostly *Quercus faginea* and *Quercus pyrenaica*)

are dominant or co-dominant (e.g. riparian forests with *Prunus lusitanica*); (iv) Cluster 4 embraces

three samples with a more prominent dominance of deciduous *Quercus* pollen (=*Quercus*

pyrenaica/faginea-t.); (v) Cluster 5 actually corresponds to Sample no. 13, strongly dominated by

Castanea sativa pollen and collected in a monospecific chestnut stand; (vi) Cluster 6 encompasses

five samples with dominance of herb pollen from mountain shrublands and steppic communities; (vii)

Cluster 7 consists of two samples with *Juniperus*-t-dominated assemblages from relatively closed

Juniperus thurifera stands; (viii) Cluster 8 has only one sample (no. 39) with high percentages of

Fagus sylvatica and notable representation of other deciduous trees, collected from one of the few

beech stands of the Iberian Central Range; and (ix) samples with mixed assemblages without clearly

dominant pollen types amalgamate into Cluster 9, which comprises seven samples from several

vegetation types.

349 Axis 1 of the PCA explains 51.5% of the variation in the pollen dataset and mostly discriminates

350 assemblages dominated by *Quercus* (negative values) and *Pinus* (positive values; Figure 5).

351 Meanwhile, Axis 2 explains 25.1% of the variation in the pollen dataset and mainly separates pollen

352 assemblages where *Quercus ilex*-t. is most abundant (negative values) from those where *Quercus*

353 *pyrenaica/faginea*-t. occurs most frequently (positive values; Figure 5). In the ordination bi-plot,

354 samples from pinewoods define a clear cluster but there is no distinction between those dominated by

355 Mediterranean and mountain species. Likewise, pollen assemblages from evergreen oak woods and

356 evergreen mixed thermophilous woodlands largely overlap although are mostly well-separated from

357 the rest. Deciduous oak wood samples form a well-defined group with some samples from other plant

358 communities where deciduous oaks are co-dominant. Finally, the rest of moss polster samples are

359 quite intermingled in the central part of the ordination plot, with a particularly central placement for

360 those from relatively open plant communities, 'Barreiro' and 'MD95-2042'. Interestingly, 'MD95-

361 2042' is closer to the *Pinus*-dominated assemblages than 'Barreiro', which is notably richer in

362 Poaceae.

363

364 **5. Discussion**

365 The results suggest that the moss polsters have mainly collected pollen from the local to extra-local

366 plant communities (up to several hundred metres away), although there was always certain regional

367 representation (Figures 2, 3; Table 1), which is in agreement with previous results from temperate and

368 boreal Europe (Bunting et al., 2005; Broström et al., 2005; Mazier et al., 2008). In this regard, the

369 abundance of *Olea* pollen in all the studied samples should be noted (Figure 2), especially considering

370 that sites on the Iberian Central Range and the Iberian Range are tens of kilometres away from the

371 closest olive orchards. Modern pollen samples from other Mediterranean areas where olive cultivation

372 is regionally widespread also showed regular presence and even moderate abundances of *Olea* far

373 away from the nearest orchards (e.g. Díaz Fernández, 1994; Sánchez Goñi and Hannon, 1999;

374 Finsinger et al., 2007; Fall, 2012; Aranbarri et al., 2015; Bell and Fletcher, 2016) including montane

375 to alpine sites in the Pyrenees (Cañellas-Boltà et al., 2009; Leunda et al., 2017).

376

377   *5.1 Modern pollen signature of widespread forest communities*

378   Major forest communities of the Tagus Basin (i.e. pinewoods and oak woodlands) had rather distinct

379   pollen assemblages according to the results of hierarchical clustering and PCA (Figures 4, 5), which

380   reflected the high percentages of the dominant tree species, i.e. *Pinus*, *Quercus pyrenaica/faginea*-t.

381   and *Quercus ilex*-t. respectively (Figures 2, 3). Nevertheless, the fact that closely related vegetation

382   types clustered together in both the hierarchical clustering and the PCA highlights certain limitations

383   of the taxonomic resolution of pollen analysis (Figures 4, 5).

384   Mediterranean and mountain pinewood samples shared high percentages of *Pinus* pollen as the most

385   distinctive feature, as in most previous studies investigating the pollen rain of these communities

386   elsewhere in the Mediterranean (e.g. Sánchez Goñi and Hannon, 1999; Gerasimidis et al., 2006;

387   López-Sáez et al., 2013). Consequently, they were intermingled in Cluster 1 (Figure 4) and largely

388   overlapped in the PCA bi-plot (Figure 5) despite the very different dominant species and floristic

389   composition of the understory (Table 1). Quantitative morphological analysis of *Pinus* pollen grains

390   might have provided more precise identifications (Desprat et al., 2015) and thus have improved the

391   discrimination of *Pinus*-dominated communities (e.g. Broothaerts et al., 2018), but it is extremely

392   time-consuming and not applied in routine palynological analyses. Further, the high pollen production

393   of *Pinus* may have often hindered the identification of indicator pollen types (Felde et al., 2014)

394   specific to pinewoods dominated by a given pine species (e.g. which pollen types and/or in which

395   abundances are closely related to *Pinus nigra* communities). However, the results still suggest that

396   *Juniperus*-type was particularly frequent in the *Pinus nigra*- and *Pinus sylvestris*-dominated woods of

397   the Iberian Range (Figure 2), in agreement with the abundance of *Juniperus thurifera*, *Juniperus*

398   *communis* and *Juniperus sabina* in the sampling sites (Table 1). Likewise, Ericaceae undiff./*Corema*

399   pollen is remarkably abundant in the sample from a *Pinus pinaster* wood from the coastal dunes of

400   central Portugal where *Corema album* dominates the understory (Sample no. 2; Figure 2 and Table 1).

401   Precising the composition of ancient pinewoods has long been a major research question in

402   Mediterranean palaeoecology and several palynological records identified different typologies of

403   *Pinus* pollen based on quantitative and qualitative features (e.g. Carrión et al., 2000; López-Merino et

404   al., 2009). However, unless throrough quantitative analyses are accomplished (Desprat et al., 2015),

405 macrofossil analysis seems to continue as the most reliable tool to track pine species changes through

406 time if this kind of remains are preserved in the sedimentary sequence (Morales-Molino et al., 2013).

407 Deciduous oak woods showed *Quercus pyrenaica/faginea*-t.-dominated pollen assemblages, in most

408 cases with a significant representation of *Quercus ilex*-t. pollen (Cluster 3 in Figure 4) although the

409 dominance of deciduous *Quercus* pollen (=*Quercus pyrenaica/faginea*-t.) was particularly prominent

410 in certain samples (Cluster 4 in Figure 4). This more conspicuous dominance of deciduous *Quercus*

411 pollen (named *Quercus pyrenaica*-t. there) was more frequent in samples from *Quercus pyrenaica*

412 stands from the Iberian Central Range studied by López-Sáez et al. (2015), probably because some of

413 our samples included in this vegetation type came from sites where the vegetation around was mosaic-

414 like (Table 1). In contrast, lower representation of deciduous *Quercus* and moderate abundance of

415 *Pinus* characterized Sánchez Goñi and Hannon (1999)'s samples from deciduous oak woods, making

416 them more comparable to our samples from the Iberian Range (Figure 2). However, our samples

417 showed in general higher abundances of *Quercus ilex*-t. pollen, probably because of the more

418 Mediterranean setting. Interestingly, Cluster 3 not only embraced samples from deciduous oak woods

419 but also several ones from other plant communities scattered within widespread *Quercus pyrenaica*

420 woods (Figure 4). For instance, *Prunus lusitanica* stands (Samples no. 27, 30) form narrow bands

421 along a stream that is completely surrounded by extensive *Quercus pyrenaica* woodlands on the

422 adjacent slopes, and something similar occurs with one of the studied chestnut stands (Sample no. 20).

423 There is also one sample from a broom-dominated mountain shrubland where deciduous oak pollen is

424 dominant (Sample no. 18), most probably because of the close proximity to the *Quercus pyrenaica*

425 timberline (Table 1). State-of-the-art palynology does not allow separating the different species

426 included in the *Quercus pyrenaica/faginea*-t., but the slight ecological overlap has led some authors to

427 use the names *Q. pyrenaica*-t. and *Q. faginea*-t. in sites where one of these oak species is expected to

428 have been dominant (e.g. López-Merino et al., 2010; Morales-Molino et al., 2017a, b). Recent

429 research on the chemical composition of *Quercus* pollen has revealed promising results for enhanced

430 taxonomic identification (Muthreich et al., 2020), and one should not discard that further refinement

431 of this technique in the near future ends up in the distinction of the different species of white oaks.

432 Western Iberian deciduous oak woods, which develop on acidic soils and under more oceanic

433 conditions (Costa et al., 2005), showed moderate abundances of Ericaceae pollen, in agreement with

434 the relevance of heaths in the understory of the sampled woodlands. The rather intense use of these

435 western deciduous *Quercus* woodlands for free-ranging cattle could account for the consistently

436 moderate percentages of *Plantago lanceolata*-t. observed in their pollen assemblages, in agreement

437 with previous research on the *Quercus pyrenaica* communities of the Iberian Central Range (López-

438 Sáez et al., 2015). Finally, the only sample from deciduous oak woods outside Clusters 3 and 4

439 (Sample no. 41, in Cluster 9) did not show a clear dominance of any tree pollen type, probably as a

440 result of the rather mixed composition of the stand where it was collected and the mosaic-like

441 structure of the regional vegetation.

442 Overall, pollen assemblages from evergreen oak woods were clearly dominated by *Quercus ilex*-t.

443 pollen, although *Quercus pyrenaica/faginea*-t., *Pinus* and to a lesser extent *Juniperus*-t. reached

444 notable representation in the samples from the Iberian Range (Figure 2). As previously explained for

445 deciduous *Quercus* woods of the same area, this pattern may be due to the widespread occurrence of

446 mixed stands and the mosaic-like landscape (Costa et al., 2005; Sainz Ollero et al., 2010).

447 Interestingly, evergreen mixed thermophilous woodlands had pollen assemblages dominated by

448 *Quercus ilex*-t. as well (Figure 2), and this contributes to explain why most of the samples from this

449 vegetation type clustered together with those from evergreen oak woods in Cluster 2 of the

450 hierarchical clustering and the PCA (Figures 4, 5). *Quercus ilex*-t. pollen found abundant and usually

451 dominant in the evergreen mixed thermophilous woodland samples (Figure 2) may actually have been

452 produced mostly by *Quercus coccifera* (Beug, 2004), which is (co-)dominant in several of the

453 sampled evergreen mixed thermophilous woodland sites (Table 1). As indicated above for deciduous

454 oak pollen, ongoing research on pollen chemistry for taxonomical identification of *Quercus*

455 (Muthreich et al., 2020) might bring along relevant implications for palaeoecological research if it

456 eventually allowed distinguishing between *Quercus ilex* and *Quercus coccifera*. In any case, despite

457 that multivariate quantitative analyses showed a significant overlap between the pollen assemblages

458 of these two vegetation types, *Pistacia*, *Phillyrea*, *Ceratonia siliqua*, *Viburnum tinus*-t. and *Smilax*

459 *aspera* seemed to be good indicators to identify these thermophilous woodlands (Figure 2). It is also

460 worth to note here the unexpectedly high tree pollen percentages found in some *'dehesa'* samples

461   despite the rather low tree cover (Figures 2, 3; Table 1), higher than those previously reported from

462   these agro-silvo-pastoral systems (López-Sáez et al., 2010). The traditional management of the

463   *'dehesas'*, which involves tillage, grazing and tree pruning (Olea and San Miguel, 2006), may account

464   for this as it seeks to favour shrub removal and tree blooming while preventing herbaceous plants

465   from flowering. The abundance of Cichorioideae might result from their remarkable tolerance to

466   disturbance but also from differential preservation due to the resistance of this pollen type to

467   degradation (Lebreton et al., 2010), while heavy grazing would explain the abundance of *Plantago*

468   *lanceolata*-t. (Figure 3; López-Sáez et al., 2010). The presence of *Quercus suber*-t. seemed to work in

469   separating western holm oak woods from those typical of the Iberian Range, growing at higher

470   elevation and on limestone (Figure 2). Again, co-dominance of different tree species and mosaic-like

471   landscape could be the underlying reasons why Sample no. 42 was included within Cluster 9 instead

472   of Cluster 2 with the rest of evergreen oak wood samples (Figure 5).

473

474   *5.2 Modern pollen representation of other plant communities of biogeographical interest*

475   As stated in the previous sub-section, the pollen representation of riparian forests with *Prunus*

476   *lusitanica* did not differ significantly from that of the surrounding *Quercus pyrenaica* woods, with the

477   exception of the noticeable representation of *Frangula alnus* and Ericaceae (Figure 2). *Osmunda*

478   *regalis*, a fern typical of riparian environments of western Iberia (Costa et al., 2005), also attained

479   rather high abundances in one of the studied samples. In contrast, *Prunus* pollen was quite rare despite

480   the (co-)dominance of *Prunus lusitanica*, most probably because this tree is insect-pollinated. *Prunus*

481   *lusitanica*-dominated communities have a great biogeographical interest and are seriously threatened

482   (Calleja et al., 2009), so tracking their past occurrence and dynamics using palaeoecological research

483   would be desirable to improve their present and future management. However, our data suggests that

484   an unambiguous palynological footprint for these communities is lacking, and this would in turn

485   hamper addressing this question. In contrast to the sample from a small chestnut stand surrounded by

486   deciduous oak woods where we reported that *Castanea sativa* pollen was rare (Sample no. 20), the

487   closed *Castanea sativa*-dominated stand had a very distinct palynological signature because of the

488   high percentages of *Castanea* pollen, which resulted in a separate cluster (Cluster 5; Figure 4).

489   Pollen assemblages from mountain shrublands above the timberline revealed a notable representation

490   of the regional vegetation, particularly of the forests forming the timberline (Figures 2, 3). Our results

491   also show that local pollen production was rather low, mainly because *Cytisus oromediterraneus*, the

492   dominant shrub in most of our 'Mountain shrubland" sites (Table 1), is insect-pollinated. Neither was

493   *Juniperus*-t. abundant in any of the pollen assemblages of this vegetation type despite its relevance at

494   Site no. 36. In contrast, Poaceae pollen was abundant in good agreement with their abundance in these

495   mountain landscapes (Figures 2, 3; Table 1). Likewise, our data suggest that the pollen representation

496   of Ericaceae accounted better for their true abundance in the surrounding vegetation, not only in

497   mountain shrublands but also in the understory of woodland communities (see Figure 2). Previous

498   research in the Oromediterranean belt of the Iberian Central Range had reported such striking

499   underrepresentation of *Genista*-t. pollen in the extensive *Cytisus oromediterraneus*-dominated

500   shrublands of the Gredos Mountains (Andrade Olalla et al., 1994). In marked contrast, certain pollen

501   spectra of *Pinus sylvestris* stands from the Iberian Central Range where *Cytisus*, *Genista* and

502   *Echinospartum* were dominant in the understory showed much higher percentages of Genisteae pollen

503   (up to 20%; López-Sáez et al., 2013). Less 'controversial' is the modern pollen representation of

504   Ericaceae, as previous research also suggested a good correlation between the abundance of Ericaceae

505   in the extant vegetation and the proportion of pollen found in surface samples (Stevenson, 1985; Díaz

506   Fernández, 1994; López-Sáez et al., 2013, 2015). However, we must note that Ericaceae pollen was

507   underrepresented in samples from *Pinus sylvestris* forests with *Erica australis*-dominated understory

508   (Sánchez Goñi and Hannon, 1999). The palynological signature of steppic vegetation was not only

509   determined by the abundance of grasses and other herbaceous taxa present locally such as

510   Chenopodiaceae, *Artemisia*, *Gypsophila*-t. and Apiaceae, but also by long-distance transported pollen

511   (Figures 2, 3). In similar settings, López-Sáez et al. (2010) found higher abundances of Poaceae and

512   lower input of long-distance transported tree pollen, although the main features of the pollen

513   assemblages were similar.

514   Despite *Juniperus thurifera*-dominated woodlands are currently one of the most characteristic and

515   unique forested communities of the western Mediterranean (Costa et al., 2005), to our knowledge no

516   previous study had addressed their pollen representation. Our data show that the structure of the

517   community, more or less open, had a certain influence in the abundance of *Juniperus*-t. pollen, but

518   this is still largely dominant in the assemblages (Fig. 2). Indeed, *Juniperus*-t. pollen dominated

519   conspicuously in the two samples from relatively closed woodlands (no. 55, 57), which grouped

520   together in a separate cluster (Cluster 7), whereas *Juniperus*-t. was not so dominant in Sample no. 52,

521   which was placed in Cluster 9 (Figure 4). *Juniperus thurifera* is also one of the most relevant trees in

522   the High Atlas (Morocco), but its pollen representation was minimum in surface samples probably

523   because of its rarity at the sampling sites (Bell and Fletcher, 2016). Interestingly, modern pollen

524   representation studies in the ecologically and structurally equivalent juniper communities of the

525   eastern Mediterranean and south-western Asia (dominated by *Juniperus excelsa*, *Juniperus*

526   *foetidissima*, and to a lesser extent *Juniperus phoenicea*) have reported a range of *Juniperus*-t. pollen

527   percentages similar to the samples from the Iberian Range (Davies and Fall, 2001; Hajar et al., 2008;

528   Djamali et al., 2009; Fall, 2012). Last but not least, it is worth to note the abundance of *Helianthemum*

529   and Lamiaceae pollen in the pollen assemblage from the open juniper stand (Figure 2), in agreement

530   with their relevance in the extant plant community.

531   *Fagus* pollen dominated in the sample from the beech-dominated stand of the Hayedo de la Pedrosa

532   but high percentages of *Pinus*, deciduous *Quercus* and Ericaceae pollen were also found (Figure 2).

533   This can be explained considering two features of the site: (i) the rather open structure of this beech

534   wood, coppiced and with a dense understory where several *Erica* species, *Arctostaphylos uva-ursi* and

535   *Vaccinium myrtillus* were abundant (see Table 1); and (ii) the spatial distribution of forest

536   communities at the extra-local scale (several kilometres radius), with widespread *Quercus pyrenaica*

537   (and *Quercus petraea*) woods and *Pinus sylvestris* afforestations. Despite the local abundance (even

538   co-dominance) of *Ilex aquifolium* and *Sorbus* spp., the pollen of these insect-pollinated trees was quite

539   rare. Similar abundances have been reported for *Ilex aquifolium* in *Pinus sylvestris-Ilex aquifolium*

540   stands of the northern Iberian Range (Sánchez Goñi and Hannon, 1999) and in *Quercus pyrenaica-*

541   *Fagus sylvatica* forests of the Ayllón Mountains (López-Sáez et al., 2015).

542   Finally, our results showed rather high percentages of *Cistus* in extensive shrublands dominated by

543   *Cistus ladanifer* (Figure 2), despite rockroses are insect-pollinated. Stevenson (1985) obtained similar

544   results in the rather similar *Halimium*-dominated shrublands of the Doñana National Park (south-

545   western Spain). Nevertheless, high regional tree pollen representation was quite high and led this

546   sample to be placed within the undifferentiated Cluster 9 (Figure 4). In any case, more samples from

547   this vegetation type would be needed to properly assess the abundances of *Cistus* pollen that define

548   these shrublands.

549

550   *5.3 Some implications for the interpretation of fossil records*

551   Our moss samples reflected mostly the composition of the local to extra-local plant communities (up

552   to several hundred metres away from the sampling site), particularly when the surrounding vegetation

553   was relatively closed and the dominant plant species were wind-pollinated. Consequently, they

554   certainly provide relevant insights into the interpretation of fossil pollen records from forest hollows

555   and small mires/bogs/lakes, which have a similar source area of pollen (Bradshaw, 2013) and are

556   probably the most widely used archive for vegetation reconstruction (e.g. López-Merino et al., 2010;

557   Abel-Schaad and López-Sáez, 2013; Ramos-Román et al., 2016; Morales-Molino et al., 2017a, 2019).

558   Additionally, moss samples accumulate pollen rain during several years, time-averaging pollen

559   deposition in a similar way to mires (Pardoe et al., 2010). On the contrary, comparison of pollen

560   assemblages from larger lakes with the moss surface samples can be done but must be necessarily

561   cautious because previous research has pointed out significant differences in their pollen catchments

562   (Lisitsyna et al., 2012).

563   The comparison between pollen assemblages from moss polsters and estuarine/deep-sea sediments

564   deserves even more attention, but there are some aspects worth to highlight. First, the closer location

565   of 'MD95-2042' to samples from pinewoods in the PCA plot compared to 'Barreiro' suggests

566   overrepresentation of *Pinus* pollen in the marine realm, supporting previous research on pollen

567   representation in deep-sea sediments (e.g. Heusser and Balsam, 1977) and the common practice in

568   marine palynology of excluding *Pinus* from the main sum used to calculate percentages (e.g. Sánchez

569   Goñi et al., 1999). Second, the quite central position of both 'Barreiro' and 'MD95-2042' in the PCA

570   plot could be pointing towards a relatively balanced representation of the main forested communities

571   inhabiting the Tagus Basin today. Moreover, marine/estuarine samples grouped together with pollen

572   assemblages from rather open environments (Figure 5). This brings further support to marine

573 sediments averaging the pollen representation of the entire basin as anthropogenic open vegetation

574 (e.g. crops, pasturelands) is dominant in the study area (Cordovil et al., 2018), but its pollen

575 representation largely under-investigated here as we focused on (semi-)natural plant communities.

576 Our results are therefore in line with previous results suggesting that pollen assemblages from deep-

577 sea sedimentary sequences of the European margin integrate the pollen signal from the vegetation of

578 the adjacent hydrographic basins (e.g. Sánchez Goñi et al., 1999; Roucoux et al., 2005; Naughton et

579 al., 2007). Nevertheless, only *ad hoc* studies based on a sampling design of high spatial resolution and

580 stratified according to vegetation types and latter weighting of the pollen representation taking into

581 account the surface covered by each vegetation type will contribute to elucidate this question in a

582 robust manner. Last but not least, the different timespan potentially covered by marine surface

583 samples (several centuries; Naughton et al., 2007) and moss polsters (several years; Lisitsyna et al.,

584 2012) adds further complexity to the picture.

585

586 **6. Conclusions**

587 The main forested ecosystems of central Iberia show rather distinct pollen assemblages with high

588 proportions of the pollen equivalents to the dominant tree species (basically pines and oaks).

589 Nevertheless, taxonomical refinement within major pollen types such as *Quercus ilex*-t. and *Pinus*

590 would notably improve the discrimination of ecologically relevant plant communities such as: (i)

591 *Quercus ilex*-dominated woodlands and forests versus *Quercus coccifera*-dominated maquis and

592 mixed evergreen thermophilous woodlands, and (ii) Mediterranean pinewoods versus mountain

593 pinewoods. In contrast, rare narrowly distributed communities dominated by *Prunus lusitanica* does

594 not have any distinctive pollen signature from the surrounding vegetation, probably because of the

595 low pollen production and/or poor dispersal of this insect-pollinated species. Shrubland and steppic

596 communities have less differentiated pollen spectra because regional pollen is dominant, which is in

597 turn probably related to lower local pollen production and/or to the dominance of insect-pollinated

598 species (e.g. mountain shrublands dominated by *Cytisus oromediterraneus*). An outstanding exception

599 concerns *Cistus*, as *Cistus ladanifer*-dominated shrubland showed high percentages of pollen from

600 this insect-pollinated plant. Pollen assemblages from moss polsters collected in central Iberia provide

601   relevant information to improve the interpretation of fossil pollen data from mires and bogs. These

602   results can also be useful for lake and marine records but must be taken with caution, and the need for

603   carefully designed studies to assess the relationships between vegetation cover and the pollen

604   representation of continental and marine samples must be highlighted.

605

606   **Acknowledgements**

610

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FIGURE CAPTIONS

833 **Fig. 1.** Location of the Tagus Basin in central Iberia and the sampling sites considered in this study

834 (1-62), coloured according to their thermoclimatic belt. The location of the estuarine ('Barreiro') and

835 marine ('MD95-2042') surface samples used for comparison is indicated by black dots.

836

837 **Fig. 2.** Percentage pollen diagram of the surface samples from the Tagus Basin: selected trees and

838 shrubs. Samples are arranged according to the dominant extant vegetation around the sampling sites.

839 *Pinus* stomata: dots denote 'presence'.

840

841 **Fig. 3.** Percentage pollen diagram of the surface samples from the Tagus Basin: selected upland herbs,

842 and fern spores and dung fungal spores. Samples are arranged according to the dominant extant

843 vegetation around the sampling sites.

844

845 **Fig. 4.** Dendrogram showing the results of Ward's hierarchical clustering applied to the percentage

846 pollen data from the surface samples collected in the Tagus Basin. The dataset has been split into nine

847 clusters, which are represented in different colours. The 'vegetation type' column shows the dominant

848 extant vegetation around each of the sampling sites, while a brief description of each of the nine

849 clusters is provided to the right of the figure.

850

851 **Fig. 5.** Ordination biplot of the principal component analysis (PCA) on untransformed pollen

852 percentage data of the surface samples collected in the Tagus Basin. Axes 1 and 2 explain 51.5 and

853 25.1% of the variation in this dataset, respectively. Blue arrows denote species scores of the main

854 pollen types. Coloured symbols represent the composition of the dominant local to extra-local extant

855 vegetation at the sampling sites (see legend). Two core-top samples from the River Tagus estuary

856 ('Barreiro') and a deep-sea core off the Portuguese margin ('MD95-2042') were passively added to

857 the ordination to assess the modern pollen representation of the sediments coming from the Tagus

858 Basin ('Marine samples', represented by red diamonds).

859

860   **Table 1.** Main features of the sampling sites in the Tagus Basin.

Site No.	Geographical coordinates	Altitude (m asl)	T (°C)[a] P (mm)[a] P$_{summer}$ (mm)[a]	Vegetation belt	Vegetation type and description
1	38°29.247'N 009°10.988'W	10	15.7 650 30	Thermo	<u>Coastal dunes</u> with *Artemisia campestris* subsp. *maritima*, *Elymus farctus*, *Arundo donax*, *Ammophila arenaria* , *Lotus creticus*, *Cyperus* sp., *Eryngium maritimum*, *Otanthus maritimus*, *Euphorbia paralias*, *Crithmum maritimum*, *Pancratium maritimum*, *Sedum sediforme*, *Armeria* sp., *Helichrysum* sp., *Thymus* sp. and *Stauracanthus* sp.
2	38°29.155'N 009°10.980'W	30	15.7 650 30	Thermo	<u>Mediterranean pinewoods.</u> Open *Pinus pinaster* stand on dunes with *Corema album*, *Ulex* sp., *Daphne gnidium*, *Juniperus phoenicea*, *Lavandula stoechas* and *Carpobrotus edulis*
3	38°27.715'N 009°09.752'W	90	15.6 680 30	Thermo	<u>Mediterranean pinewoods.</u> Disturbed woodland (40% tree cover) dominated by *Pinus pinea*, *P. pinaster* and *Quercus suber*, with *Quercus lusitanica*, *Cistus crispus*, *Ulex* sp., *Calluna vulgaris*, *Cistus salviifolius*, *Oxalis pres-caprae*, *Acacia* gr. *melanoxylon*, *Quercus faginea* subsp. *broteroi* and *Eucalyptus*
4	38°30.611'N 009°08.588'W	20	15.9 650 30	Thermo	<u>Mediterranean pinewoods.</u> *Pinus pinea* and *P. pinaster* wood (40% tree cover) on sandy soils with *Quercus suber*, *Cistus crispus*, *Cistus salviifolius*, *Lavandula stoechas*, *Ulex* sp., *Halimium umbellatum*, *H. halimifolium* and *Daphne gnidium*
5	38°27.524'N 009°00.631'W	250	15.2 760 35	Thermo	<u>Evergreen thermophilous woodlands.</u> Maquis (1-3 m tall; 100% canopy cover): *Olea europaea*, *Phillyrea angustifolia*, *Pistacia lentiscus*, *Cistus albidus*, *C. monspeliensis*, *Arbutus unedo*, *Quercus coccifera*, *Juniperus phoenicea*, *Bupleurum fruticosum*, *Rhamnus oleoides*, *Rh. alaternus*, *Daphne gnidium*, *Smilax aspera*, *Erica arborea* and *Lonicera implexa*. Scattered *Pinus pinea* and *Quercus faginea* subsp. *broteroi*

trees

6	38°27.704'N 009°00.294'W	190	15.5 730 30	Thermo	Evergreen thermophilous woodlands. Mixed forest (100% tree cover) with tree *Quercus coccifera*, *Q. faginea* subsp. *broteroi*, *Pistacia lentiscus*, *Phillyrea latifolia*, *Arbutus unedo*, *Viburnum tinus*, *Ceratonia siliqua*, *Juniperus phoenicea*, *Erica arborea*, *Rhamnus alaternus* and *Myrtus communis*. Abundant lianas (*Smilax aspera*, *Lonicera implexa*) and epiphytic ferns (*Polypodium*, *Davallia*)
7	38°27.702'N 009°00.185'W	160	15.5 730 30	Thermo	Evergreen thermophilous woodlands. Mixed forest (100% tree cover) with tree *Quercus coccifera*, *Q. faginea* subsp. *broteroi*, *Pistacia lentiscus*, *Phillyrea latifolia*, *Arbutus unedo*, *Viburnum tinus*, *Ceratonia siliqua*, *Juniperus phoenicea*, *Erica arborea*, *Rhamnus alaternus* and *Myrtus communis*. Abundant lianas (*Smilax aspera*, *Lonicera implexa*) and epiphytic ferns (*Polypodium*, *Davallia*)
8	38°27.989'N 008°59.825'W	120	15.9 680 30	Thermo	Evergreen thermophilous woodlands. Maquis (3 m tall; 80% canopy cover): *Quercus coccifera*, *Phillyrea latifolia*, *Ph. angustifolia*, *Pistacia lentiscus*, *Juniperus phoenicea*, *Erica arborea*, *Arbutus unedo*, *Viburnum tinus*, *Coronilla* sp., *Lonicera implexa*, *Osyris lanceolata*, *Rosmarinus officinalis*, *Smilax aspera*, *Daphne gnidium* and *Cistus* spp.
9	38°29.051'N 008°58.657'W	90	15.4 750 35	Thermo	Evergreen thermophilous woodlands. Maquis (6-10 m tall; 80% canopy cover): *Pistacia lentiscus*, *Ceratonia siliqua*, *Juniperus phoenicea*, *Phillyrea latifolia*, *Olea europaea*, *Myrtus communis*, *Jasminum fruticans*, *Viburnum tinus* and *Smilax aspera*
10	39°15.197'N 006°34.864'W	360	16.0 550 35	Meso	Evergreen thermophilous woodlands. Dehesa of *Quercus ilex* subsp. *ballota* (30-40% tree cover), with *Cistus crispu*s, *C. ladanifer*, *C. salviifolius*, Apiaceae and *Celtica gigantea*
11	39°15.514'N	330	16.1	Meso	Evergreen oak woods. Dehesa of *Quercus ilex* subsp. *ballota*

No.	Coordinates			Belt	Vegetation description
	006°34.745'W	540 35			and *Q. suber* (30% tree cover) with *Cistus ladanifer, C. salviifolius, C. crispus, Ulex* sp., *Cytisus scoparius* and *Crataegus monogyna*
12	39°23.414'N 006°26.032'W	360 530 40	16.2	Meso	<u>Evergreen oak woods.</u> Dehesa of *Quercus ilex* subsp. *ballota* (20% tree cover) with *Cytisus multiflorus* and *C.* cf. *striatus*
13	40°14.775'N 005°53.554'W	960 800 70	11.9	Supra	Monospecific coppiced <u>*Castanea sativa* stand</u> (90-100% tree cover)
14	40°14.833'N 005°52.811'W	870 790 70	11.8	Supra	<u>Deciduous oak woods.</u> Grazed *Quercus pyrenaica* stand (70% tree cover) with *Pteridium aquilinum, Rosa* sp., *Rubus* gr. *ulmifolius, Crataegus monogyna, Clinopodium vulgare* and diverse Poaceae
15	40°15.510'N 005°52.508'W	770 650 60	13.3	Supra	<u>Deciduous oak woods.</u> *Quercus pyrenaica-Castanea sativa* forest (60-70% tree cover), with *Acer monspessulanum, Hedera helix, Cytisus scoparius, Ruscus aculeatus, Lonicera* cf. *periclymenum, Festuca elegans, Polypodium* and *Asplenium onopteris*
16	40°13.274'N 005°52.340'W	1440 1100 100	9.2	Supra	<u>Mountain shrublands.</u> Rather open *Cytisus oromediterraneus* shrubland on mountain pass
17	40°15.934'N 005°51.884'W	720 690 65	12.8	Supra	<u>Deciduous oak woods.</u> *Quercus pyrenaica-Castanea sativa* stand (70-80% tree cover) with *Daphne gnidium, Ruscus aculeatus, Hedera helix, Rubia peregrina, Teucrium scorodonia, Clinopodium vulgare, Acer monspessulanum, Crataegus monogyna, Cytisus scoparius, Arenaria montana, Luzula* cf. *forsteri, Brachypodium sylvaticum* and *Polypodium*
18	40°13.445'N 005°50.825'W	1370 990 90	9.9	Supra	<u>Mountain shrublands.</u> Broom-dominated shrubland (*Genista florida, G. cinerascens, Cytisus oromediterraneus, Adenocarpus argyrophyllus, Erica arborea, Lavandula* cf.

stoechas) not far from the *Quercus pyrenaica* treeline

19	40°12.854'N 005°47.534'W	810 670 65	12.8	Supra	Deciduous oak woods. *Quercus pyrenaica* stand (70-80% tree cover) with *Cistus psilosepalus, Cytisus scoparius, Pteridium aquilinum, Lavandula pedunculata, Campanula rapunculus* and *Brachypodium sylvaticum*
20	40°22.469'N 005°45.100'W	1030 770 80	10.7	Supra	Small <u>*Castanea sativa* </u>stand (90% tree cover) with *Rubus* sp., *Pteridium aquilinum, Quercus pyrenaica* (rare). Some *Betula* sp. and *Frangula alnus* closeby
21	40°21.117'N 005°44.713'W	1400 940 95	9.4	Supra	<u>Mountain pinewoods.</u> *Pinus sylvestris* afforestation (80% tree cover) with *Cytisus striatus* and *Festuca elegans*. Shrubland with *Erica arborea, Adenocarpus argyrophyllus* and *Adenocarpus* gr. *complicatus* nearby.
22	40°20.45'N 005°44.250'W	1670 1180 115	7.6	Oro	<u>Mountain shrubland</u> dominated by *Cytisus oromediterraneus* and *Echinospartum ibericum*, with *Santolina oblongifolia, Avenella hispanica, Nardus stricta* and sparse *Salix atrocinerea*. Extensive *Pinus sylvestris* afforestation closeby
23	39°28.070'N 005°09.711'W	590 480 40	14.9	Meso	<u>Evergreen oak woods.</u> Coppiced dehesa of *Quercus ilex* subsp. *ballota* (20% tree cover) with *Arbutus unedo, Viburnum tinus* and abundant *Cistus ladanifer* and *Lavandula pedunculata*. *Eucalyptus* and *Pinus pinaster* afforestations in the surroundings
24	39°28.554'N 005°07.858'W	470 440 40	15.2	Meso	<u>Evergreen oak woods.</u> *Quercus ilex* subsp. *ballota* stand (60% tree cover) with *Pistacia terebinthus, Acer monspessulanum, Cistus ladanifer, Arbutus unedo, Phillyrea angustifolia, Rosmarinus officinalis, Juniperus oxycedrus, Lavandula stoechas, Thymus mastichina* and *Rumex* cf. *induratus*
25	39°38.799'N 004°55.456'W	790 470 50	13.8	Meso	<u>Lowland shrublands.</u> *Cistus ladanifer* shrubland with *Phillyrea angustifolia, Lavandula pedunculata, Genista triacanthos, Daphne gnidium, Asparagus acutifolius* and scattered and sparse *Quercus ilex* subsp. *ballota* trees (5-10% tree cover)

26	39°37.865'N 004°55.184'W	890 530 55	12.9	Meso	Evergreen oak woods. Mixed *Quercus ilex* and *Q. faginea* stand on scree, with *Pistacia terebinthus* (abundant), *Phillyrea angustifolia, Cistus ladanifer, C. populifolius, Viburnum tinus* and *Rubus* gr. *ulmifolius. Lonicera implexa, Cytisus scoparius, Viburnum tinus, Arbutus unedo, Erica arborea* and *Genista florida* in the understory. Pine afforestations and olive groves closeby.
27	39°34.784'N 004°53.693'W	820 530 55	12.8	Supra	Riparian forest with *Prunus lusitanica*, *Frangula alnus, Prunus lusitanica, Erica arborea* and *Hedera helix* particularly rich in ferns (e.g. *Polystichum, Dryopteris, Osmunda*). *Quercus pyrenaica* stands upslope
28	39°34.709'N 004°53.655'W	860 530 55	12.8	Supra	Deciduous oak woods. *Quercus pyrenaica* coppice (70% tree cover) with *Erica arborea* (abundant), *Cistus ladanifer* (rare) and *Daphne gnidium. Quercus ilex* stand on the opposite slope
29	39°34.567'N 004°53.541'W	900 530 55	12.8	Supra	Deciduous oak woods. Closed *Quercus pyrenaica* coppiced stand
30	39°34.462'N 004°53.357'W	900 580 60	12.1	Supra	Riparian forest with *Prunus lusitanica* (dominant), *Ilex aquifolium, Taxus baccata, Frangula alnus* and *Osmunda regalis*, surrounded by *Quercus pyrenaica* stands
31	40°41.077'N 004°01.130'W	1030 450 70	11.4	Supra	Evergreen oak woods. *Quercus ilex* subsp. *ballota* woodland (30% tree cover) with *Juniperus oxycedrus, Cistus ladanifer, C. laurifolius, Celtica gigantea* and *Lavandula pedunculata. Pinus pinaster* stands nearby.
32	40°45.108'N 004°00.971'W	1500 890 105	7.9	Supra	Mountain pinewoods. *Pinus sylvestris* forest (80-90% tree cover) with *Cytisus scoparius, Cistus laurifolius, Juniperus communis, Pteridium aquilinum* and *Rosa* sp.
33	40°53.501'N 004°00.933'W	1190 540 85	10.2	Supra	Deciduous oak woods. Dense *Quercus pyrenaica* stand (90% tree cover) with *Cistus laurifolius* and *Rubus* gr. *ulmifolius* (rare)

34	40°53.493'N 004°00.844'W	1180	10.1 550 85	Supra	Deciduous oak woods. *Quercus pyrenaica* stand (70% tree cover) with abundant *Cistus laurifolius*
35	40°46.536'N 004°00.298'W	1770	7.0 1130 120	Oro	Mountain pinewoods. *Pinus sylvestris* woodland (60-70%) with *Cytisus oromediterraneus*, *Genista cinerascens* and *Juniperus communis* subsp. *alpina*
36	40°47.339'N 003°59.938'W	1920	6.0 1330 135	Oro	Mountain shrubland dominated by *Cytisus oromediterraneus* and *Juniperus communis* subsp. *alpina*
37	40°01.176'N 003°35.995'W	560	14.8 390 45	Meso	Steppic vegetation dominated by *Macrocholoa (Stipa) tenacissima* with *Salsola vermiculata, Atriplex halimus), Tamarix* sp. and *Lycium europaeum. Phragmites australis* communities nearby
38	40°01.142'N 003°35.789'W	580	14.8 390 45	Meso	Steppic vegetation dominated by *Macrochloa (Stipa) tenacissima* with *Ephedra* sp., *Helianthemum squamatum, Lepidium subulatum, Reseda suffruticosa, Frankenia thymifolia, Retama sphaerocarpa, Artemisia campestris* and *Artemisia herba-alba*
39	41°12.957'N 003°24.788'W	1700	7.1 840 115	Oro	*Fagus sylvatica* stand with *Ilex aquifolium, Sorbus aucuparia, S. aria, Erica arborea, Arctostaphylos uva-ursi, Vaccinium myrtillus* and *Cytisus scoparius. Quercus pyrenaica* and *Betula pendula* stands and pine afforestations nearby
40	40°24.721'N 003°09.214'W	710	13.5 430 45	Meso	Lowland shrublands. Garrigue on gypsum with *Quercus coccifera* and sparse *Quercus ilex* subsp. *ballota* and *Quercus faginea* (10% tree cover). *Ephedra* sp., *Genista scorpius, Macrochloa (Stipa) tenacissima, Salvia lavandulifolia, Euphorbia nicaeensis, Ononis tridentata, Thymus* sp., *Helianthemum squamatum, Lithodora fruticosa, Rosmarinus officinalis, Bupleurum fruticescens, Rosmarinus officinalis* and *Lepidium subulatum. Pinus halepensis* afforestation, *Quercus*

faginea stands and cereal fields closeby

41	40°37.087'N	800	13.1	Meso	Deciduous oak woods. *Quercus faginea-Pinus halepensis*
	002°40.957'W	430			stands recolonizing old fields (60% tree cover) with *Quercus*
		55			*ilex* subsp. *ballota, Juniperus oxycedrus, Genista scorpius,*
					Arctostaphylos uva-ursi (abundant), *Ononis fruticosa,*
					Dorycnium pentaphyllum, Bupleurum rigidum, Olea europaea,
					Crataegus monogyna, Lonicera etrusca, Lavandula latifolia,
					Thymus vulgaris, Lithodora fruticosa, Jasminum fruticans and
					Cornus sanguinea
42	40°39.247'N	900	12.4	Meso	Evergreen oak woods. Open *Quercus ilex* subsp. *ballota*
	002°33.970'W	470			woodland (30% tree cover) with *Juniperus oxycedrus,*
		55			*Juniperus phoenicea, Rosmarinus officinalis, Rosa* sp., *Genista*
					pumila, Crataegus monogyna, Genista scorpius, Jasminum
					fruticans, Rubia peregrina, Arctostaphylos uva-ursi, Galium
					fruticescens, Lavandula latifolia, Thymus vulgaris, Satureja
					intrincata and scattered *Pinus halepensis*
43	41°00.376'N	1150	10.6	Supra	Mediterranean pinewoods. Open *Pinus pinaster* woodland
	002°27.381'W	520			(60% tree cover) with *Quercus faginea, Calluna vulgaris,*
		75			*Erica scoparia, Cistus laurifolius, Crataegus monogyna* and
					Arctostaphylos uva-ursi
44	40°59.479'N	1120	10.8	Supra	Mediterranean pinewoods. Mixed *Pinus pinaster-Quercus*
	002°27.348'W	520			*faginea* stand (70-80% tree cover) with *Calluna vulgaris,*
		75			*Cistus laurifolius, Crataegus monogyna, Juniperus communis*
					and *Prunus spinosa. Erica scoparia*-dominated heathland
					nearby
45	40°58.417'N	1100	10.8	Supra	Mediterranean pinewoods. *Pinus pinaster* woodland (70% tree
	002°25.388'W	520			cover) with *Quercus faginea, Juniperus communis, Cistus*
		75			*laurifolius* and *Lavandula pedunculata*
46	40°42.509'N	890	12.3	Meso	Mediterranean pinewoods. Open *Pinus nigra-Quercus ilex*
	002°24.524'W	470			subsp. *ballota* woodland (40% tree cover) with abundant

			55		*Rosmarinus officinalis, Juniperus phoenicea, Juniperus oxycedrus, Arctostaphylos uva-ursi, Salvia lavandulifolia, Brachypodium retusum, Lavandula latifolia, Thymus vulgaris, Genista scorpius, Lithodora fruticosa, Helianthemum* sp. And sparse *Pinus halepensis*
47	40°44.672'N 002°23.904'W	810	12.4 460 55	Meso	<u>Mediterranean pinewoods.</u> *Pinus nigra-P. halepensis* forest (90% tree cover), with a dense understory of *Arctostaphylos uva-ursi, Rosmarinus officinalis, Juniperus phoenicea* and *Juniperus oxycedrus*
48	41°02.905'N 002°22.179'W	1220	10.4 540 80	Supra	<u>Deciduous oak woods.</u> Small stand of *Quercus faginea* (70-80% tree cover) with *Cistus laurifolius, Quercus ilex* subsp. *ballota, Genista scorpius, G. pumila* subsp. *pumila, Juniperus communis* and *Euphorbia nicaeensis*. Pine afforestation closeby
49	41°02.704'N 002°22.084'W	1200	10.4 540 80	Supra	<u>Evergreen oak woods.</u> Open *Quercus ilex* subsp. *ballota* woodland (40% tree cover) with *Quercus faginea, Thymus vulgaris, Juniperus communis, Helianthemum cinereum, Crataegus monogyna, Genista scorpius, Cistus laurifolius* and *Euphorbia nicaeensis*
50	40°53.091'N 002°21.835'W	1180	11.1 540 70	Supra	<u>Evergreen oak woods.</u> *Quercus ilex* subsp. *ballota* woodland with *Juniperus thurifera, Quercus faginea, Genista scorpius, Lavandula latifolia, Thymus vulgaris, Satureja intrincata, Amelanchier ovalis* and *Santolina chamaecyparissus*
51	40°55.535'N 002°21.092'W	1060	11.2 530 70	Supra	<u>Deciduous oak woods.</u> *Quercus faginea* woodland (60% tree cover) with *Juniperus communis, Amelanchier ovalis, Genista scorpius, Crataegus monogyna, Euphorbia nicaeensis, Lavandula latifolia, Salvia lavandulifolia, Thymus* sp. and *Rosa* sp.
52	41°03.506'N 002°10.726'W	1340	9.6 590	Supra	<u>Juniper woodlands.</u> Open *Juniperus thurifera* woodland with *Juniperus communis, Genista scorpius, Rosa* sp.*, Thymus*

		95			*vulgaris, Helianthemum* sp., *Genista pumila* subsp. *pumila* and sparse *Quercus faginea* and *Q. ilex* subsp. *ballota*
53	40°58.478'N 002°07.596'W	1210 550 85	10.4	Supra	Deduous oak woods. Mixed *Quercus pyrenaica-Q. faginea* stand (70% tree cover) with *Viburnum lantana, Juniperus communis, Lonicera xylosteum, Crataegus monogyna, Prunus mahaleb, Lonicera periclymenum, Cistus laurifolius, Prunus spinosa* and *Ligustrum vulgare*
54	40°48.655'N 002°03.194'W	1040 510 75	11.2	Supra	Mountain pinewoods. Closed *Pinus nigra* forest (90% tree cover) with *Amelanchier ovalis, Rosa* sp., *Prunus mahaleb, Juniperus thurifera, Juniperus communis, Quercus faginea, Euphorbia* sp. and shrubby Lamiaceae (*Satureja, Thermoymus, Salvia, Lavandula*)
55	40°55.328'N 002°02.834'W	1280 570 90	9.9	Supra	Juniper woodlands. Rather dense *Juniperus thurifera* woodland (40% tree cover) with *Juniperus communis, Genista scorpius, Lavandula latifolia, Satureja intricata, Thymus vulgaris, Helianthemum cinereum, H. apenninum, H. oelandicum* subsp. *incanum* and *Artemisia pedemontana*
56	40°48.671'N 002°02.785'W	990 500 75	11.3	Supra	Mountain pinewoods. *Pinus nigra* woodland with *Juniperus thurifera* (60-70% tree cover) with *Genista scorpius, Rosa* sp., *Juniperus communis, Ligustrum vulgare, Digitalis obscura, Satureja intricata, Berberis vulgaris* subsp. *seroi, Lavandula latifolia, Salvia lavandulifolia, Euphorbia nicaeensis* and *Clematis vitalba*
57	40°54.192'N 002°02.624'W	1320 580 95	9.6	Supra	Juniper woodlands. Rather dense *Juniperus thurifera* woodland (40% tree cover) with sparse *Quercus faginea* and *Q. ilex* subsp. *ballota, Juniperus communis, Genista scorpius, Lavandula latifolia, Satureja intricata, Thymus vulgaris, Helianthemum cinereum, H. apenninum, H. oelandicum* subsp. *incanum* and *Artemisia pedemontana*
58	40°49.826'N	1120	10.8	Supra	Mediterranean pinewoods. *Pinus pinaster* woodland (50% tree

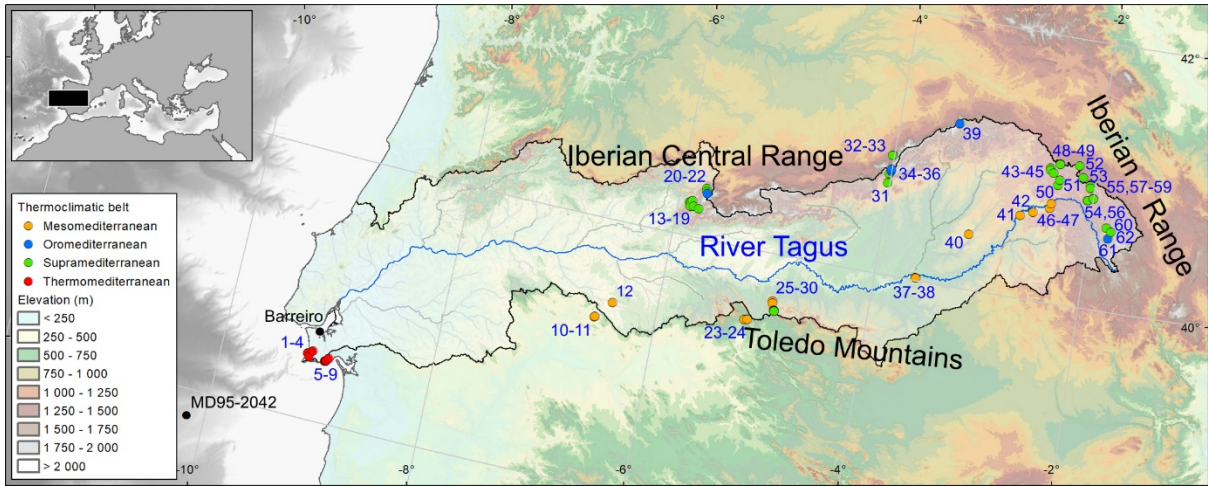|						
			520			cover) with *Quercus faginea, Q. pirenaica, Q. ilex* subsp. *ballota, Arctostaphylos uva-ursi, Cistus laurifolius, Lavandula pedunculata* and *Crataegus monogyna*
			80			
59	40°49.753'N 001°59.811'W	1000	10.8 520 80		Supra	Mediterranean pinewoods. *Pinus pinaster* forest (70-80% tree cover) with *Acer monspessulanum, Corylus avellana, Lonicera etrusca, Prunus mahaleb, Sambucus nigra, Ulmus minor, Ligustrum vulgare, Cistus laurifolius* and *Berberis vulgaris* subsp. *seroi)*
60	40°37.583'N 001°49.814'W	1440	9.2 600 110		Supra	Mountain pinewoods. Mixed woodland (50% tree cover) dominated by *Pinus nigra*, with *P. sylvestris, Quercus faginea, Q. ilex* subsp. *ballota, Buxus sempervirens, Juniperus sabina, J. thurifera, Juniperus communis, Berberis vulgaris* subsp. *seroi, Artemisia pedemontana, Rosa* sp., *Thymus vulgaris* and *Lavandula latifolia*
61	40°33.017'N 001°48.112'W	1560	8.4 650 120		Oro	Mountain pinewoods. Open *Pinus sylvestris* woodland with *Juniperus sabina, J. communis, Buxus sempervirens, Rosa* sp.and *Berberis vulgaris* subsp. *seroi*
62	40°36.106'N 001°46.774'W	1350	9.3 590 110		Supra	Mountain pinewoods. *Pinus sylvestris* forest with *Quercus pyrenaica, Rosa pimpinellifolia, Prunus spinosa* and *Cistus laurifolius*

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862 Abbreviations: T = Mean annual temperature, P = mean annual precipitation, P_{summer} = mean summer

863 precipitation (June-August), Thermo = Thermomediterranean, Meso = Mesomediterranean, Supra =

864 Supramediterranean, Oro = Oromediterranean

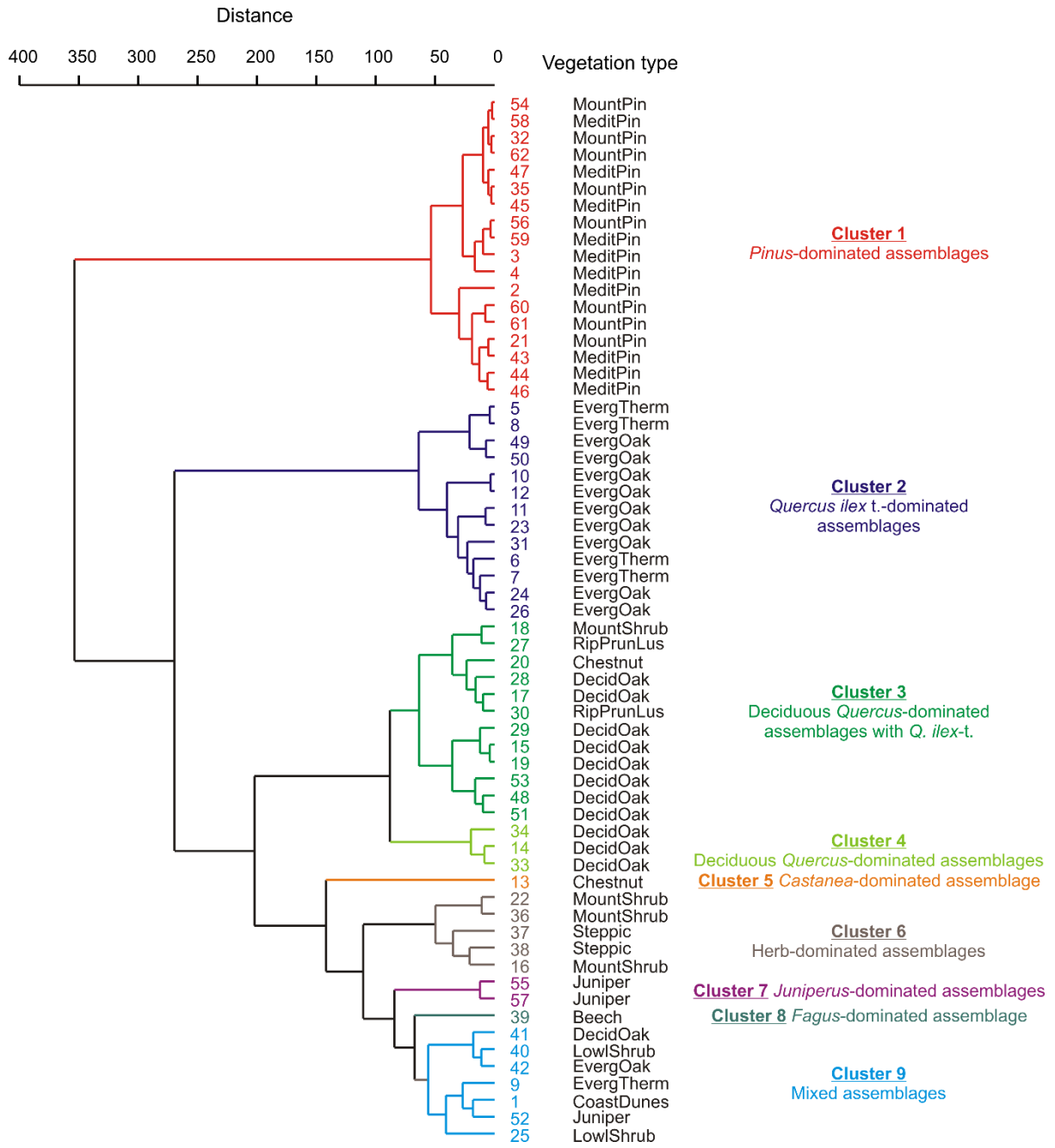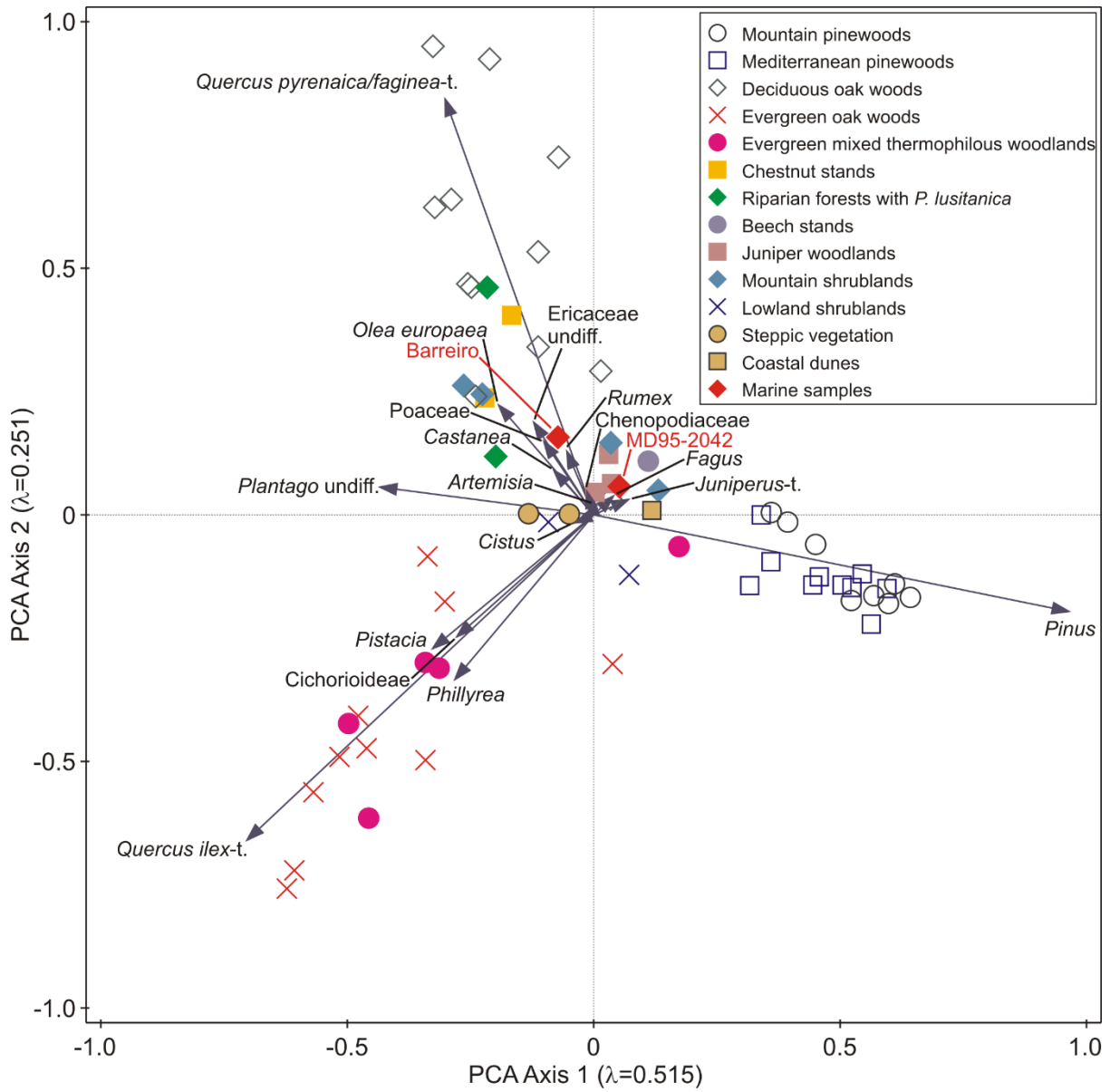865 [a] Values obtained from WorldClim 2 (Fick and Hijmans, 2017).

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Figure 1.

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Figure 2.

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874 **Figure 3.**

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Figure 4.

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880 **Figure 5.**