

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

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16

17 **Abstract**

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.

37

38 **Keywords**

39 Pollen analysis; surface samples; vegetation reconstruction; pollen-vegetation relationships; pollen
40 rain; Mediterranean ecosystems.

41

42 **1. Introduction**

43 Pollen-stratigraphic records from sedimentary archives represent one of the most powerful and widely
44 used tools to reconstruct vegetation changes on long (decadal to millennial) timescales (e.g. van Zeist
45 and Wright, 1963; Birks, 1965; Lotter, 1999; Tinner et al., 1999; Sánchez Goñi et al., 2008; Rey et al.,
46 2019). The Iberian Peninsula and its margin is one of the European regions where the amount of
47 palynological investigations has increased most significantly in recent times, stimulated by its diverse
48 landscape, complex land-use history and sensitivity to climate change (Carrión et al., 2010; Sánchez
49 Goñi et al., 2018). Palaeoecology has particularly developed in central Iberia, with the publication of a
50 number of new multi-proxy studies addressing diverse ecological questions like vegetation dynamics,
51 fire history, fire ecology, human impact, or herbivore-vegetation interactions (e.g. Franco Múgica et
52 al., 1998; López-Merino et al., 2010; Abel-Schaad and López-Sáez, 2013; Morales-Molino et al.,
53 2017a, 2019, Luelmo-Lautenschlaeger et al., 2019). Likewise, pollen-based palaeoclimatic research
54 on marine sediments with strong influence of the River Tagus and River Sado plumes has largely
55 moved forward in recent years (e.g. Sánchez Goñi et al., 1999, 2008, 2019; Roucoux et al., 2006;
56 Oliveira et al., 2017).

57 Studies on the modern pollen representation of extant plant communities have long been recognized
58 as playing a central role in assisting the interpretation of fossil palynological records, helping
59 disentangle challenging issues concerning differential pollen production, dispersal and preservation
60 (e.g. Davis and Goodlett, 1960; Wright, 1967; Stevenson, 1985; Bell and Fletcher, 2016). During the
61 last decades, several studies have addressed modern vegetation-pollen relationships all over the
62 Mediterranean region (e.g. Davies and Fall, 2001; Finsinger et al., 2007; Fall, 2012; Bell and Fletcher,
63 2016; López-Sáez et al., 2018), including the Iberian Peninsula (e.g. Stevenson, 1985; Díaz-
64 Fernández, 1994; Andrade Olalla et al., 1994; Aranbarri et al., 2015). The latter research has provided
65 very valuable insights into the pollen representation of Iberian plant communities, but its geographical
66 scope was usually rather narrow, i.e. transects across single mountain ranges (Díaz Fernández, 1994;
67 Andrade Olalla et al., 1994; Sánchez Goñi and Hannon, 1999; Cañellas-Boltà et al., 2009; Aranbarri
68 et al., 2015). In central Iberia, the main focus has been on specific plant communities such as *Pinus*
69 *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 km² 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

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

210 gorges of the Toledo Mountains surrounded by *Quercus pyrenaica* woodlands ($n=2$); (8) 'Beech
211 stands' site was located in one of the three main *Fagus sylvatica* sub-populations of the Iberian
212 Central Range ($n=1$); (9) 'Juniper woodlands' refers to more or less open woodlands dominated by
213 *Juniperus thurifera* with an understory rich in chamaephytes ($n=3$); (10) 'Mountain shrublands' are
214 located above the modern tree line and the dominant species are usually *Cytisus oromediterraneus*
215 and *Juniperus communis* subsp. *alpina* ($n=4$); (11) 'Lowland shrublands' includes communities
216 resulting from the degradation of mid-elevation woodlands where Cistaceae and Lamiaceae are
217 dominant ($n=2$); (12) 'Steppic vegetation' refers to *Macrochloa (Stipa) tenacissima*-dominated
218 communities growing on gypsum in particularly dry settings, where other typical steppic plants such
219 as *Artemisia*, *Ephedra*, *Helianthemum* and Amaranthaceae (Chenopodiaceae) are relevant ($n=2$); and
220 (13) 'Coastal dunes' includes a single site from a dune system on the Portuguese coast ($n=1$).
221 Surface samples mostly consisted of moss polsters but in some cases some litter and/or the topmost
222 soil layer were also collected. At each site we picked up several moss fragments (usually 5) within a
223 plot of *ca.* 20×20 m² following the recommendations in Pardoe et al. (2010). The only exception was
224 at Site no. 1, where we collected the uppermost soil layer. In these plots we recorded vegetation
225 structure and composition, with a particular focus on the woody taxa (i.e. trees, shrubs, dwarf shrubs,
226 and lianas). Local tree cover (%) and, in some cases, shrub cover (%) were also visually estimated in
227 most cases. We also recorded the extra-local vegetation (some hundred metres around the sampling
228 site) when this was different from the local.

229

230 3.2 Pollen analysis

231 In the laboratory, we carefully homogenized each sample to prevent overrepresentation of plants
232 growing next to each individual moss polster. Moss sub-samples of *ca.* 5-10 cm³ then underwent
233 physical (wet sieving with a 150 µm mesh, decanting) and chemical (HCl, HF, KOH, acetolysis) to
234 concentrate pollen. We finally mounted slides using glycerol as mounting medium and counted pollen
235 and spores using an optical microscope at 400× magnification. Terrestrial pollen sum (excluding
236 spores and pollen from aquatic plants) was always above 500 pollen grains (Mean ± SE: 531 ± 35)
237 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

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

322 *Quercus pyrenaica/faginea*-t. (Figure 2). Important taxa are Poaceae (ca. 10-20%), Chenopodiaceae
323 (5-20%), *Gypsophila*-t. (>20% in Sample no. 37) and to a lesser extent *Artemisia*, Apiaceae, Cerealia-
324 t. and *Helianthemum* (Figures 2, 3). Finally, Sample no. 1, from the coastal dunes of Portugal, shows
325 relatively low proportion of tree pollen, mostly *Pinus* (ca. 30%; presence of stomata) and *Salix* (ca.
326 10%), and rather high abundances of herbaceous pollen, mostly of Poaceae (10%) and other plants
327 typical of coastal environments such as Chenopodiaceae, *Crithmum maritimum*-t., *Corrigiola*
328 *litoralis*, Cichorioideae, Brassicaceae, and *Aster*-t. (Figures 2, 3).

329

330 4.2 Clustering and ordination

331 The results of the hierarchical clustering on pollen percentage data shows nine major groups (Figure
332 4): (i) Cluster 1 consists of 18 samples where *Pinus* pollen is largely dominant from pine forests and
333 pine-dominated woodlands; (ii) Cluster 2 includes 13 samples with high proportions of *Quercus ilex*-
334 t., from *Quercus ilex* woodlands and ‘dehesas’ as well as mixed thermophilous evergreen forests
335 where *Quercus coccifera* is usually abundant; (iii) Cluster 3 is composed of 12 samples with pollen
336 assemblages dominated by *Quercus pyrenaica/faginea*-t. and moderate abundances of *Quercus ilex*-t.,
337 from plant communities where deciduous *Quercus* (mostly *Quercus faginea* and *Quercus pyrenaica*)
338 are dominant or co-dominant (e.g. riparian forests with *Prunus lusitanica*); (iv) Cluster 4 embraces
339 three samples with a more prominent dominance of deciduous *Quercus* pollen (= *Quercus*
340 *pyrenaica/faginea*-t.); (v) Cluster 5 actually corresponds to Sample no. 13, strongly dominated by
341 *Castanea sativa* pollen and collected in a monospecific chestnut stand; (vi) Cluster 6 encompasses
342 five samples with dominance of herb pollen from mountain shrublands and steppic communities; (vii)
343 Cluster 7 consists of two samples with *Juniperus*-t-dominated assemblages from relatively closed
344 *Juniperus thurifera* stands; (viii) Cluster 8 has only one sample (no. 39) with high percentages of
345 *Fagus sylvatica* and notable representation of other deciduous trees, collected from one of the few
346 beech stands of the Iberian Central Range; and (ix) samples with mixed assemblages without clearly
347 dominant pollen types amalgamate into Cluster 9, which comprises seven samples from several
348 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 thorough 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 *Echinopartum* were dominant in the understory showed much higher percentages of Genisteeae 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

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610

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832 **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 <i>Artemisia campestris</i> subsp. <i>maritima</i> , <i>Elymus farctus</i> , <i>Arundo donax</i> , <i>Ammophila arenaria</i> , <i>Lotus creticus</i> , <i>Cyperus</i> sp., <i>Eryngium maritimum</i> , <i>Otanthus maritimus</i> , <i>Euphorbia paralias</i> , <i>Crithmum maritimum</i> , <i>Pancratium maritimum</i> , <i>Sedum sediforme</i> , <i>Armeria</i> sp., <i>Helichrysum</i> sp., <i>Thymus</i> sp. and <i>Stauracanthus</i> sp.
2	38°29.155'N 009°10.980'W	30	15.7 650 30	Thermo	<u>Mediterranean pinewoods</u> . Open <i>Pinus pinaster</i> stand on dunes with <i>Corema album</i> , <i>Ulex</i> sp., <i>Daphne gnidium</i> , <i>Juniperus phoenicea</i> , <i>Lavandula stoechas</i> and <i>Carpobrotus edulis</i>
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 <i>Pinus pinea</i> , <i>P. pinaster</i> and <i>Quercus suber</i> , with <i>Quercus lusitanica</i> , <i>Cistus crispus</i> , <i>Ulex</i> sp., <i>Calluna vulgaris</i> , <i>Cistus salviifolius</i> , <i>Oxalis pres-caprae</i> , <i>Acacia</i> gr. <i>melanoxydon</i> , <i>Quercus faginea</i> subsp. <i>broteroi</i> and <i>Eucalyptus</i>
4	38°30.611'N 009°08.588'W	20	15.9 650 30	Thermo	<u>Mediterranean pinewoods</u> . <i>Pinus pinea</i> and <i>P. pinaster</i> wood (40% tree cover) on sandy soils with <i>Quercus suber</i> , <i>Cistus crispus</i> , <i>Cistus salviifolius</i> , <i>Lavandula stoechas</i> , <i>Ulex</i> sp., <i>Halimium umbellatum</i> , <i>H. halimifolium</i> and <i>Daphne gnidium</i>
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): <i>Olea europaea</i> , <i>Phillyrea angustifolia</i> , <i>Pistacia lentiscus</i> , <i>Cistus albidus</i> , <i>C. monspeliensis</i> , <i>Arbutus unedo</i> , <i>Quercus coccifera</i> , <i>Juniperus phoenicea</i> , <i>Bupleurum fruticosum</i> , <i>Rhamnus oleoides</i> , <i>Rh. alaternus</i> , <i>Daphne gnidium</i> , <i>Smilax aspera</i> , <i>Erica arborea</i> and <i>Lonicera implexa</i> . Scattered <i>Pinus pinea</i> and <i>Quercus faginea</i> subsp. <i>broteroi</i>

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

	006°34.745'W		540			and <i>Q. suber</i> (30% tree cover) with <i>Cistus ladanifer</i> , <i>C. salviifolius</i> , <i>C. crispus</i> , <i>Ulex</i> sp., <i>Cytisus scoparius</i> and <i>Crataegus monogyna</i>
			35			
12	39°23.414'N	360	16.2	Meso		<u>Evergreen oak woods.</u> Dehesa of <i>Quercus ilex</i> subsp. <i>ballota</i> (20% tree cover) with <i>Cytisus multiflorus</i> and <i>C. cf. striatus</i>
	006°26.032'W		530			
			40			
13	40°14.775'N	960	11.9	Supra		Monospecific coppiced <u><i>Castanea sativa</i> stand</u> (90-100% tree cover)
	005°53.554'W		800			
			70			
14	40°14.833'N	870	11.8	Supra		<u>Deciduous oak woods.</u> Grazed <i>Quercus pyrenaica</i> stand (70% tree cover) with <i>Pteridium aquilinum</i> , <i>Rosa</i> sp., <i>Rubus</i> gr. <i>ulmifolius</i> , <i>Crataegus monogyna</i> , <i>Clinopodium vulgare</i> and diverse Poaceae
	005°52.811'W		790			
			70			
15	40°15.510'N	770	13.3	Supra		<u>Deciduous oak woods.</u> <i>Quercus pyrenaica</i> - <i>Castanea sativa</i> forest (60-70% tree cover), with <i>Acer monspessulanum</i> , <i>Hedera helix</i> , <i>Cytisus scoparius</i> , <i>Ruscus aculeatus</i> , <i>Lonicera cf. periclymenum</i> , <i>Festuca elegans</i> , <i>Polypodium</i> and <i>Asplenium onopteris</i>
	005°52.508'W		650			
			60			
16	40°13.274'N	1440	9.2	Supra		<u>Mountain shrublands.</u> Rather open <i>Cytisus oromediterraneus</i> shrubland on mountain pass
	005°52.340'W		1100			
			100			
17	40°15.934'N	720	12.8	Supra		<u>Deciduous oak woods.</u> <i>Quercus pyrenaica</i> - <i>Castanea sativa</i> stand (70-80% tree cover) with <i>Daphne gnidium</i> , <i>Ruscus aculeatus</i> , <i>Hedera helix</i> , <i>Rubia peregrina</i> , <i>Teucrium scorodonia</i> , <i>Clinopodium vulgare</i> , <i>Acer monspessulanum</i> , <i>Crataegus monogyna</i> , <i>Cytisus scoparius</i> , <i>Arenaria montana</i> , <i>Luzula cf. forsteri</i> , <i>Brachypodium sylvaticum</i> and <i>Polypodium</i>
	005°51.884'W		690			
			65			
18	40°13.445'N	1370	9.9	Supra		<u>Mountain shrublands.</u> Broom-dominated shrubland (<i>Genista florida</i> , <i>G. cinerascens</i> , <i>Cytisus oromediterraneus</i> , <i>Adenocarpus argyrophyllus</i> , <i>Erica arborea</i> , <i>Lavandula cf.</i>
	005°50.825'W		990			
			90			

					<i>stoechas</i>) not far from the <i>Quercus pyrenaica</i> treeline
19	40°12.854'N 005°47.534'W	810	12.8 670 65	Supra	<u>Deciduous oak woods.</u> <i>Quercus pyrenaica</i> stand (70-80% tree cover) with <i>Cistus psilosepalus</i> , <i>Cytisus scoparius</i> , <i>Pteridium aquilinum</i> , <i>Lavandula pedunculata</i> , <i>Campanula rapunculus</i> and <i>Brachypodium sylvaticum</i>
20	40°22.469'N 005°45.100'W	1030	10.7 770 80	Supra	Small <u><i>Castanea sativa</i> stand</u> (90% tree cover) with <i>Rubus</i> sp., <i>Pteridium aquilinum</i> , <i>Quercus pyrenaica</i> (rare). Some <i>Betula</i> sp. and <i>Frangula alnus</i> closeby
21	40°21.117'N 005°44.713'W	1400	9.4 940 95	Supra	<u>Mountain pinewoods.</u> <i>Pinus sylvestris</i> afforestation (80% tree cover) with <i>Cytisus striatus</i> and <i>Festuca elegans</i> . Shrubland with <i>Erica arborea</i> , <i>Adenocarpus argyrophyllus</i> and <i>Adenocarpus</i> gr. <i>complicatus</i> nearby.
22	40°20.45'N 005°44.250'W	1670	7.6 1180 115	Oro	<u>Mountain shrubland</u> dominated by <i>Cytisus oromediterraneus</i> and <i>Echinopartum ibericum</i> , with <i>Santolina oblongifolia</i> , <i>Avenella hispanica</i> , <i>Nardus stricta</i> and sparse <i>Salix atrocinerea</i> . Extensive <i>Pinus sylvestris</i> afforestation closeby
23	39°28.070'N 005°09.711'W	590	14.9 480 40	Meso	<u>Evergreen oak woods.</u> Coppiced dehesa of <i>Quercus ilex</i> subsp. <i>ballota</i> (20% tree cover) with <i>Arbutus unedo</i> , <i>Viburnum tinus</i> and abundant <i>Cistus ladanifer</i> and <i>Lavandula pedunculata</i> . <i>Eucalyptus</i> and <i>Pinus pinaster</i> afforestations in the surroundings
24	39°28.554'N 005°07.858'W	470	15.2 440 40	Meso	<u>Evergreen oak woods.</u> <i>Quercus ilex</i> subsp. <i>ballota</i> stand (60% tree cover) with <i>Pistacia terebinthus</i> , <i>Acer monspessulanum</i> , <i>Cistus ladanifer</i> , <i>Arbutus unedo</i> , <i>Phillyrea angustifolia</i> , <i>Rosmarinus officinalis</i> , <i>Juniperus oxycedrus</i> , <i>Lavandula stoechas</i> , <i>Thymus mastichina</i> and <i>Rumex</i> cf. <i>induratus</i>
25	39°38.799'N 004°55.456'W	790	13.8 470 50	Meso	<u>Lowland shrublands.</u> <i>Cistus ladanifer</i> shrubland with <i>Phillyrea angustifolia</i> , <i>Lavandula pedunculata</i> , <i>Genista triacanthos</i> , <i>Daphne gnidium</i> , <i>Asparagus acutifolius</i> and scattered and sparse <i>Quercus ilex</i> subsp. <i>ballota</i> trees (5-10% tree cover)

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

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

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

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

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

	002°00.126'W		520			cover) with <i>Quercus faginea</i> , <i>Q. pirenaica</i> , <i>Q. ilex</i> subsp.
			80			<i>ballota</i> , <i>Arctostaphylos uva-ursi</i> , <i>Cistus laurifolius</i> , <i>Lavandula pedunculata</i> and <i>Crataegus monogyna</i>
59	40°49.753'N	1000	10.8	Supra		<u>Mediterranean pinewoods</u> . <i>Pinus pinaster</i> forest (70-80% tree
	001°59.811'W		520			cover) with <i>Acer monspessulanum</i> , <i>Corylus avellana</i> , <i>Lonicera</i>
			80			<i>etrusca</i> , <i>Prunus mahaleb</i> , <i>Sambucus nigra</i> , <i>Ulmus minor</i> ,
						<i>Ligustrum vulgare</i> , <i>Cistus laurifolius</i> and <i>Berberis vulgaris</i>
						subsp. <i>seroi</i>)
60	40°37.583'N	1440	9.2	Supra		<u>Mountain pinewoods</u> . Mixed woodland (50% tree cover)
	001°49.814'W		600			dominated by <i>Pinus nigra</i> , with <i>P. sylvestris</i> , <i>Quercus faginea</i> ,
			110			<i>Q. ilex</i> subsp. <i>ballota</i> , <i>Buxus sempervirens</i> , <i>Juniperus sabina</i> ,
						<i>J. thurifera</i> , <i>Juniperus communis</i> , <i>Berberis vulgaris</i> subsp.
						<i>seroi</i> , <i>Artemisia pedemontana</i> , <i>Rosa</i> sp., <i>Thymus vulgaris</i> and
						<i>Lavandula latifolia</i>
61	40°33.017'N	1560	8.4	Oro		<u>Mountain pinewoods</u> . Open <i>Pinus sylvestris</i> woodland with
	001°48.112'W		650			<i>Juniperus sabina</i> , <i>J. communis</i> , <i>Buxus sempervirens</i> , <i>Rosa</i>
			120			sp. and <i>Berberis vulgaris</i> subsp. <i>seroi</i>
62	40°36.106'N	1350	9.3	Supra		<u>Mountain pinewoods</u> . <i>Pinus sylvestris</i> forest with <i>Quercus</i>
	001°46.774'W		590			<i>pyrenaica</i> , <i>Rosa pimpinellifolia</i> , <i>Prunus spinosa</i> and <i>Cistus</i>
			110			<i>laurifolius</i>

861

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).





