

1 MOUNTAIN STRONGHOLDS FOR WOODY ANGIOSPERMS DURING THE LATE
2 PLEISTOCENE IN SE IBERIA

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16 **Abstract**

17 Mediterranean mountains played an essential role during glacial periods as vegetation
18 refugia. The SE Iberia Late Pleistocene woody angiosperm fossil and floristic evidences
19 are reviewed in the context of phylogeographical studies aiming to identify (i) spatial
20 patterns related to woody angiosperms glacial survival, (ii) structural and functional
21 characteristics of montane refugia, and (iii) gaps in knowledge on the woody
22 angiosperm patterns of survival in Mediterranean mountains. The distribution of
23 palaeobotanical data for SE Iberia refugia has been found to be taphonomically biased
24 due to the scarcity of available and/or studied high-altitude Late Pleistocene sites.
25 However, Siles Lake data together with floristic inference provide evidences for woody
26 angiosperms' survival in a high-altitude Mediterranean area. The main features
27 boosting survival at montane contexts are physiographic complexity and water
28 availability. Phylogeography studies have mainly been conducted at a continental scale.
29 Although they cohere with palaeobotanical data to a broad scale, a general lack of
30 sampling of SE Iberian range-edge populations, as well as misconceptions about the
31 origin of the populations sampled, impede to infer the proper location of woody
32 angiosperms' mountain refugia and their importance in the post-glacial European
33 colonisation. We conclude that floristic, geobotanical, palaeobotanical, ethnographical
34 and genetic evidence should be merged to gain a deeper understanding on the role
35 played by Mediterranean mountains as glacial refugia in order to explain the current
36 distribution of many plants and the large biodiversity levels encountered in
37 Mediterranean mountain areas. This is hallmark for effective and efficient conservation
38 and management.

39 **Key-words:** palaeobotany, phylogeography, floristic, mountains, biogeography,
40 Mediterranean

41 **1. Introduction**

42 Most glacial refugia theories in Europe suggest that temperate species survived the
43 cold and dry stages in southern strongholds with little gene flow among them (Tzedakis
44 et al., 2013). Those refuged temperate species colonised northern territories as soon as
45 the glaciers retreated (e.g., Bennett and Provan, 2008; Gavin et al., 2014; Hofreiter and
46 Stewart, 2009; Médail and Diadema, 2009; Tzedakis et al., 2013; Willis, 1996). In this
47 scenario, the role of the Mediterranean peninsulas (Iberian, Italian and Greco-Balkan)
48 seems to have been crucial for the fragmentation and re-distribution of species'
49 ranges. However, these peninsulas are not environmentally homogeneous.
50 Physiographical and climatological diversity mirrors on the past and present plant
51 populations' ranges. This heterogeneity has likely shaped the distribution of refuged
52 flora during cold stages. Smaller-scale refugia, for example, are predicted in these
53 heterogeneous territories during unfavourable environmental conditions (Gómez and
54 Lunt, 2007; Rull, 2009).

55 Médail and Diadema (2009) recognised 52 Mediterranean glacial refugia based
56 on the phylogeographical patterns of 82 plant species, including 41 herb and 41 tree
57 taxa. Yet again, the role of the southern European peninsulas was emphasised with the
58 presence of 25 refugia cohering areas of endemism and hotspots. In line with Médail
59 and Diadema (2009), refugia are classified in three categories: Type 1) moist mid-
60 altitude refugia (400-800 m asl) suited to altitudinal shifts of vegetation belts in
61 response to environmental change, or *in situ* survival; Type 2) deep gorges and closed

62 valleys, with uninterrupted moisture availability, and Type 3) low-altitude sites such as
63 valley bottoms, coastal plains and wetlands, particularly sensitive to changes in aridity.
64 According to this model, more than half of the refugia are located in “submontane
65 [areas] and mountain margins” (Médail and Diadema, 2009 pp. 1338). However, the
66 inclusion of palaeobotanical data points to the occurrence of intramontane refugia
67 (Carrión, 2002b; Pons and Reille, 1988; Tzedakis, 2004). The importance of high-
68 altitude belts as refugia for woody Mediterranean and mesophytic taxa may well have
69 been undervalued. This review aims to fill this gap. South-eastern Iberian mountains
70 are taken as a model owing to the presence of refugia dating from the last glacial (MIS
71 2) (Carrión, 2002b). Aiming to evaluate the Late Pleistocene survival of woody
72 angiosperms (i.e., mesophytes, Mediterranean taxa and Ibero-Maghrebian scrub)
73 considering the likely relevant role of high-altitude Mediterranean mountains,
74 palaeobotanical and phylogeographical data are combined in order to (i) explore spatial
75 patterns related to woody angiosperms glacial survival, (ii) infer high-altitude refugia
76 structural and functional features, and (iii) identify gaps in knowledge hampering the
77 understanding of woody angiosperms survival patterns in Mediterranean mountains.

78 **2. South-eastern Iberia: environmental setting**

79 The Iberian Peninsula is structured around an Inner Plateau crossed and surrounded by
80 mountains. The Pyrenees and Iberian Ranges frame the Ebro valley in the north-east
81 (Fig. 1). The Inner Plateau is surrounded by the Cantabrian Range in the north and the
82 Sierra Morena and the Baetic Ranges in the south, with the Central System dividing the
83 Inner Plateau in two (Fig. 1). These mountain systems and ranges make Iberia a largely
84 heterogeneous land. Altitude gradient overlaps with slope orientation and triggers an

85 uneven distribution of temperatures. Springs and creeks carve sometimes deep gorges
86 and ravines diversifying the geologically complex landscape. Rain-shadow effects also
87 contribute to the landscape heterogeneity and have large importance on plant
88 distribution. Considering the unique mountainous character of Iberia and the fact that
89 these mountains harbour a large portion of the Iberian plant diversity, the role that
90 highlands have played in the current species distributions is obvious (Loidi, 1999).

91 In southern Iberia, the Baetic ranges intercept water-laden winds on western
92 faces, allowing *Quercus suber* development in the thermo- and mesomediterranean
93 belts. In particularly favourable humid locations and gorges, broad-leaved trees (*Q.*
94 *canariensis*, *Q. faginea* ssp. *broteroi*), palaeotropical elements (*Davallia canariensis*,
95 *Laurus nobilis*, *Rhododendron ponticum*) and the endemic *Abies pinsapo* grow in the
96 meso- and supramediterranean (Aparicio Martínez and Silvestre Domingo, 1987; Pérez
97 Latorre et al., 1999). Eastwards, the less water-demanding *Q. ilex* ssp. *ballota* inhabits
98 the meso- and supramediterranean with semi-deciduous oaks (mostly *Q. faginea* ssp.
99 *faginea*, and locally *Q. pyrenaica*). Conifers become more abundant eastwards, with
100 the xerophytic *Pinus halepensis* incorporated into the thermomediterranean scrub, and
101 *P. pinaster* and *P. nigra* sharing the supramediterranean belt with semi-deciduous
102 *Quercus*. Higher altitudes (> 1500-1700 m asl) are inhabited by mountain pinewoods (*P.*
103 *nigra* and, to a lesser extent, *P. sylvestris*), giving way to open pulvinular scrub
104 (*Juniperus communis*, *Erinacea anthyllis*, *Genista versicolor*, *Echinopartum* sp.) and
105 alpine pastureland in the upper oro- and crioromediterranean belts (Blanca, 2002;
106 Lorite, 2001; Valle Tendero et al., 1989; Sánchez Gómez et al., 1997).

107 In SE Iberia, a semi-arid fringe extends beneath the Baetic mountains rain-
108 shadow, hosting a singular Ibero-Maghrebian scrub composed of xerothermic elements
109 (*Periploca laevigata*, *Whitania frutescens*, *Lycium intricatum*, *Osyris quadripartita*,
110 *Chamaerops humilis*, *Maytenus senegalensis* and *Tetraclinis articulata*) (Sainz Ollero et
111 al., 2010; Sánchez Gómez and Alcaraz, 1993; Sánchez Gómez et al., 1997). The
112 intramontane high-altitude depressions (“hoyas”) hold an Irano-Turanian vegetation of
113 perennial xerophytic grasses (e.g., *Stipa* and *Lygeum*), halophilous chenopods (*Suaeda*,
114 *Salsola*, *Halocnemum*, *Arthrocnemum*, *Sarcocornia*), and central European disjunctions
115 such as *Krascheninnikovia ceratoides* (Blanca and Morales, 1991; Sainz Ollero et al.,
116 2010).

117 Overall, SE Iberian vegetation landscapes present high mosaicism. Tertiary
118 palaeotropical taxa live together with mesic, Mediterranean and subtropical
119 xerothermic species in a mosaic resulted from a complex palaeogeographical history
120 (Aparicio Martínez and Silvestre Domingo, 1987; Blanca, 2003; Molina-Venegas et al.,
121 2015 a, b, Pérez Latorre et al., 1999). This unique environmental setting is the reason
122 for selecting SE Iberia as a model for studying the role of Mediterranean mountain
123 refugia. In spite of the former, woody angiosperms constitute the most comprehensive
124 assemblage of palaeobotanical remains whose discrimination is achievable, at least, at
125 genus level. Typological taxonomy ruled in palaeobotanical works is followed with
126 reference to fossil remains (Carrión et al., 2015), whereas in reference to extant species
127 and distributions the proposals of Flora Ibérica (www.floraiberica.org) and Anthos
128 project (www.anthos.es) are followed. Ecological characterisation into mesophytes,
129 Mediterranean taxa and Ibero-Maghrebian scrub follows the general consensus

130 adopted by most palaeobotanical papers, and it is supported by Flora Ibérica and
131 floristic and ecological works (Carrión et al., 2001a, 2001b, 2015).

132 **3. Late Pleistocene survival in SE Iberian Mountains**

133 Palaeobotanical sites of the Iberian Pleistocene are unevenly distributed (González
134 Sampérez et al., 2010). They are scarce in SE Iberia, i.e. from the 114 sites compiled by
135 González-Sampérez et al. (2010) for Iberia; only 32 are located below 40°. In order to
136 assess the Late Pleniglacial survival of mesophytic, Mediterranean and Ibero-
137 Maghrebian taxa (MIS 2, 24 cal. ka BP, Clark et al., 2009), 26 SE Iberian sites have been
138 selected (Table 1). Due to low taxonomic resolution and weak chronology, Hoyo de la
139 Mina, Salines, River Aguas, Cueva Negra, Ratlla del Bubo and Sima de las Palomas
140 (Badal, 1991; Carrión et al., 2003; Giralt et al., 1999; Schulte et al., 2008; Walker et al.,
141 2006, Uzquiano, unpublished data) were excluded. For the 26 selected sites, 268
142 presences of 41 woody angiosperms (23 mesophytic, 14 Mediterranean thermophytic
143 and 6 xerophytic Ibero-Maghrebian taxa) are recorded at low and high elevations (Fig.
144 2). *Viburnum* and *Rhamnus* comprise both mesophytic and Mediterranean taxa in the
145 study area (Table 2).

146 3.1 Mesophytes

147 Mesophytes include broad-leaved deciduous trees, *Ilex*, *Hedera* and *Vitis*, and appear
148 from coastal areas to high-altitudes. Most remains are deciduous *Quercus* pollen. This
149 pollen type comprises several species (Table 2), including sometimes *Q. suber*, whose
150 palynological discrimination can be challenging (Carrión et al., 2000). Charcoal and

151 pollen of *Alnus*, *Betula*, *Corylus*, *Ulmus* and *Salix* occur in several sedimentary contexts
152 from sea level up to 1320 m asl (Fig. 2).

153 *Acer* occurs mostly at mid-altitude; while *Sambucus*, *Hedera*, *Ilex* and *Juglans* present
154 scattered evidences with no altitudinal pattern. Although woody Rosaceae remains
155 hardly appear in the palaeobotanical record, *Prunus* and *Sorbus/Crataegus* charcoal
156 have been found at 100-1100 m asl. *Carpinus* and *Tilia* are present in four mid-altitude
157 sites, while *Populus* is restricted to two mid-altitude sites (Fig. 2).

158 *Ligustrum* and *Vitis* pollen are only present in Malladetes Cave (500 m asl), while
159 *Frangula* and *Castanea* pollen only in Gorham's Cave (Gibraltar, 5 m asl) (Fig. 2).

160 3.2 *Viburnum*, *Rhamnus* and Mediterranean taxa

161 Although *Viburnum* species are insect-pollinated, their pollen grains are not rare in
162 Mediterranean sites (Carrión et al., 2015). *Viburnum* pollen presence is discontinuous
163 along the altitudinal gradient (Fig. 2). These pollen grains are usually ascribed to *V.*
164 *tinus*, the most widespread species. However, *V. lantana* and *V. opulus* are also present
165 in the area and, plausibly, the three species may have grown together in humid, well-
166 developed humus rich soils (Sánchez Gómez et al., 1997). *Rhamnus* is continuously
167 found along the altitudinal gradient. This genus comprises both deciduous and
168 perennial species, including mesophytes (*Rh. cathartica*, *Rh. alpina*), Mediterranean
169 thermophytes (*Rh. alaternus*, *Rh. lycioides*), and hyperthermophytes (*Rh. velutina*;
170 Rivas-Martínez and Pizarro, 2011).

171 Mediterranean thermophytes, such as evergreen *Quercus* (*Q. ilex* and *Q.*
172 *coccifera*), *Olea*, *Pistacia*, *Phillyrea*, *Buxus*, *Myrtus* and *Arbutus* are well represented at

173 all altitudes in the palaeobotanical record (Fig. 2). *Smilax* appears in a mid-altitude site
174 only, and the punctual presences of *Q. suber*, *Myrica*, *Coriaria* and *Cneorum* are
175 restricted to altitudes below 500 m asl (Fig. 2).

176 3.3 Ibero-Maghrebian scrub

177 Subtropical summer-deciduous thorns, hemi-parasitic *Osyris* and the thorny legume
178 *Calicotome* compose the Ibero-Maghrebian scrub assemblage. Its palaeobotanical
179 record is restricted to pollen at five low-altitude sites (Fig. 2). *Lycium* is the most
180 recurrent pollen type in this assemblage. *Osyris*, *Periploca* and *Whitania* are only found
181 in Perneras Cave (200 m asl), while *Maytenus* and *Calicotome* are exclusive to
182 Gorham's (5 m asl) (Fig. 2). Zoophilous taxa are, although overall underrepresented in
183 the palynological record (Carrión, 2002a), found in Gorham's fossil dung (Carrión et al.,
184 2008).

185 3.4 High-altitude refugia?

186 In order to test Médail and Diadema (2009)'s refugia model, the abundance of
187 palaeobotanical data (Fig. 2) and bioclimatic belts is compared. Bioclimatic belts follow
188 Carrión (2002): thermomediterranean (< 500 m asl), mesomediterranean (500-1000 m
189 asl) and supramediterranean (> 1000 m asl). No oro- and crioromediterranean
190 Pleistocene sites have been studied so far in SE Iberia. Raw analysis of the contingency
191 matrix shows a major concentration of fossil records in the mesomediterranean belt
192 ($\chi^2= 103.11$; $df= 2$, $P > 0.05$), as implied by Type 1 refugia. However, the correction of
193 the data taking into account the number of sites per belt does not show an altitudinal
194 bias ($\chi^2= 3.11$; $df= 2$, $P < 0.05$), indicating that the altitudinal distribution of woody

195 angiosperms Pleistocene refuges is mostly explained by a skew in the fossil record
196 towards lowlands rather than to ecological or geographical features. The widely-
197 recognised Type 1 mid-altitude refugia (400-800 m asl;) are supported by 8 sites (Figs. 1
198 and 2). The more spatially constrained Type 2 refugia existing in sites with continued
199 moisture availability are confirmed by the presence of mesophyte and sclerophyllous
200 taxa in Carihuela, Las Ventanas, Malladetes, Nerja, Cendres, Santa Maira, Tossal de la
201 Roca, d'en Pardo, Bolumini, Ambrosio, Calaveres, Beneito, Padul and Siles (Figs. 1 and
202 2, Table 1). Type 3 refugia appear at a wide range of low-altitude sites with diverse
203 geomorphology: the coastal Mari López and San Rafael marshlands, the Bajondillo,
204 Gorham, Nerja and Les Cendres caves, the perched peat levels of El Asperillo sand cliff,
205 and the warm and moist Les Calaveres, Perneras and Navarrés (Figs. 1 and 2, Table 1).

206 High-altitude mountains are usually ignored in refugia models, as sites lying
207 above *ca.* 800 m asl are usually excluded from the theoretical glacial refugia framework
208 (Bennett and Provan, 2008; Gavin et al., 2014; Hofreiter and Stewart, 2009; Médail and
209 Diadema, 2009; Tzedakis et al., 2013; Willis, 1996). It seems counter intuitive that high-
210 altitude refugia existed during cold periods. Nonetheless, evidence of them has been
211 found during the Late Pleniglacial in the Ambrosio, Las Ventanas and Carihuela caves
212 (Figs. 1 and 2), with the presence of mesophytes and sclerophylls above 950 m asl. Siles
213 Lake is outstanding for the western Mediterranean because its pollen record comprises
214 the uninterrupted occurrence of meso-thermophilous angiosperms from *ca.* 20,300 to
215 500 cal. yr BP in a high plateau context (1320 m asl, Carrión, 2002b). Refuged taxa in
216 these sites account for the conception of a fourth type of refuge (Type 4 or mountain
217 refugia).

218 **4. Vegetation dynamics in an altitudinal gradient**

219 4.1 Past vegetation records

220 The Late Pleistocene to Mid-Holocene SE Iberian vegetation history shows a dynamic
221 picture that can be partially representative of the Last Glacial climate fluctuations. Even
222 if environmental variation during the cold and dry Weichselian occurred at a narrower
223 scale (Carrión, 2003), the effects that changes in moisture availability and temperature
224 had on the expansion and contraction of woody angiosperms in the mid- to high-
225 altitude mountains are likely to be comparable.

226 The Late Pleniglacial Siles and Navarrés palynological records (Carrión, 2002b;
227 Carrión and Van Geel, 1999), together with the Early Holocene Villaverde and Cañada
228 de la Cruz records (Carrión, 2001a, 2001b), were presented in an altitudinal context by
229 Carrión (2002b). This review allowed the reconstruction of the vegetation response to
230 different environmental forcings at a local and regional scale.

231 The Late Pleniglacial and Late Glacial record (ca. 20 - 12 cal. ka BP, Fig. 3a) is
232 restricted to the high-altitude Siles (1320 m asl) and the low-altitude Navarrés (225 m
233 asl) records. The landscape was dominated by a steppe composed by Poaceae,
234 *Artemisia* and *Ephedra*, with *Juniperus* and *Pinus* (*P. nigra* and, to a lesser extent, *P.*
235 *sylvestris*, as inferred from anthracological evidence, Roiron et al., 2013). Junipers and
236 pines would appear scattered throughout the widespread cold and arid landscapes
237 (Carrión, 1992; Carrión et al., 1998; Fernández et al., 2007; Pons and Reille, 1988).
238 Nevertheless, Siles Lake accounts for high-altitude woody angiosperm glacial survival
239 (Fig. 2) with the continuous presence of Mediterranean and mesophytic taxa such as

240 both evergreen and deciduous *Quercus*, *Betula*, *Corylus*, *Fraxinus*, *Salix*, *Ulmus*,
241 *Rhamnus*, *Olea*, *Pistacia*, *Phillyrea*, *Buxus* and *Arbutus*. Broad-leaved forests must have
242 been discontinuous, and related to the nearby existence of gullies and ravines. Exposed
243 situations with trees are however possible, like it is seen today in the Cantabrian and
244 Sierra Nevada ranges with *Quercus ilex* ssp. *ballota*, which grows punctually above the
245 mesophytic belt (Blanca, 2002; Fernández Prieto, 1981).

246 During the period comprised between 12 - 8 cal. ka BP (Fig. 3b) a species-poor
247 understory *Pinus* forest of varying density is inferred as the dominant vegetation.
248 *Pinus* forest expanded through an altitudinal displacement of the timberline over the
249 cryoxerophyllous grassland-scrub composed by *Juniperus*, *Artemisia*, *Ephedra* and
250 Chenopodiaceae/Amaranthaceae. Pine and xerophyte dynamics were likely controlled
251 by aridity and fire disturbance. During this transition, mesophytes attained a minimum.
252 Deciduous *Quercus* are absent from Cañada de la Cruz, and scantily dispersed in
253 Navarrés and Villaverde. However, deciduous *Quercus* curve is continuous in the high-
254 altitude Siles, with the presence of *Betula*, *Corylus*, *Fraxinus*, *Salix*, *Ulmus* and *Hedera*.
255 Although the Holocene onset meant a rise in temperature, the humidity (i.e. water
256 availability) was much lower, likely hampering the development of mesophytes at mid-
257 to low-altitudes and displacing them towards high-altitudes (Carrion 2002b). The
258 aridity characterising this period favoured a rise of Mediterranean taxa. In the low-
259 altitude Villaverde, a continuous curve of evergreen *Quercus* appears together with
260 *Pistacia*, *Olea*, *Cistus* and *Erica*. However, the presence of evergreen *Quercus* in the
261 high-altitude Siles remains punctual with scattered increases, although *Pistacia*,
262 Oleaceae, *Cistus* and *Erica* occur continuously.

263 The more humid conditions reconstructed for the Holocene Mesophytic
264 Optimum (8 - 5 cal. ka BP, Fig. 3c) supposed a woodland altitudinal migration. On the
265 one hand, high-altitude areas experienced a pinewood rise and a grassland-scrub
266 demise. On the other hand, deciduous *Quercus* forests replaced the mid- to high-
267 altitude *Pinus* formations at ca. 7.4 - 5 cal. ka BP. Oaks were accompanied by other
268 mesophytes such as *Acer*, *Betula*, *Corylus*, *Fraxinus*, *Salix*, *Ulmus*, *Juglans*, *Hedera* and
269 *Ilex*. This mesophytic assemblage was replaced by Mediterranean evergreen *Quercus*
270 forests with *Ericaceae*, *Pistacia*, and *Phillyrea* from 5 cal. ka BP onwards, indicating
271 more restricted moisture conditions after the Mesophytic Optimum.

272 The expansion of *Pinus*, xerophytic grassland-scrub and Mediterranean
273 sclerophylls in mid- and high-altitudes characterises the 5 - 3 cal. ka BP vegetation
274 dynamics (Fig. 3d). This fact is likely to be related to a Western Mediterranean
275 aridification trend (Anderson et al., 2011; Jiménez-Espejo et al., 2014; Jiménez-Moreno
276 et al., 2015). On the contrary, mesophytes experienced a decline, restricting their
277 survival to scattered pockets amid mountain pines. Fire events and a series of
278 anthropogenic disturbance-mediated, rapid displacements between mountain *Pinus*
279 and *Pinus pinaster*-evergreen *Quercus* are recorded. The spread of drought-tolerant
280 sclerophylls and high-altitude xerophytic taxa confined pines to a thin belt until fire and
281 anthropogenic disturbance stabilised at 3 cal. ka BP. From this time onwards, humans
282 seem to be the main factor controlling vegetation change (Carrión, 2002b).

283 4.2. Factors controlling taxa survival

284 Siles Lake is deprived of stream connections and fed by precipitation and runoff from a
285 relatively small catchment (3 x 1.5 km). The basin is located in an elevated flat polje

286 surrounded by a series of deeply incised thermic gorges (Carrión, 2002b). Why survival
287 was possible in such a context? The evidence for non-cryophilous taxa in montane
288 contexts during the Late Pleniglacial provides insights to understand it. The Holocene
289 temperature rise might not explain solely refuged vegetation dynamics in the
290 Mediterranean Region, as its climate is characterised by summer drought (Walter,
291 2002) and water is a limiting factor for Mediterranean plants (Galmés et al., 2007), so
292 soil water availability likely played a major role. On the other hand, cold winter
293 temperatures imply shorter vegetative periods, in adaptation to which deciduous
294 species shed their leaves. However, spring refoliation is a water-demanding process
295 hampered when prevailing low temperatures are combined with water availability
296 restrictions during the vegetative period. Under the cold Late Pleniglacial
297 temperatures, the mesophytes and Mediterranean taxa survival at Siles was possible
298 only in places without water availability restrictions, so thermic gorges played a very
299 important role as woody vegetation refuges. Thus, it is plausible that the main factor
300 limiting woody angiosperm presence in Mediterranean mountains was water
301 availability rather than low temperatures (Cowling and Skyes, 1999; Leroy and Arpe,
302 2007). Hence, the survival of small pockets of mesic and thermophytic taxa in
303 mountain areas cannot be regarded as merely anecdotal. This phenomenon is not
304 more often incorporated into models probably because of the scant high-altitude
305 Mediterranean palaeobotanical record.

306 The presence of refugia seems, therefore, related to a number of
307 physiographical features that assure continuous water availability. Narrow and incised
308 gorges at mid- to high-altitude provide protection against wind-induced desiccation,

309 survival in valley bottoms is assured by *in situ* moisture accumulation in deep soils,
310 while coastal enclaves tend to be exposed to moisture loaded winds that reduce water
311 stress. Survival in rock walls and crevices would mean no competition, protection
312 against ecosystem disturbance and in porous rocks, such as limestones, a more or less
313 continuous water reservoir.

314 **5. Floristic and phylogeographical evidence for montane refugia**

315 While the palaeobotanical record provides information on past taxa presence,
316 identification to species level is limited. For such reason, floristic and genetic
317 investigations are very helpful, as they provide a larger level of taxonomical detail.
318 Current floristic presence of mesophytes, Mediterranean and Ibero-Magrebian taxa in
319 SE Iberian mountains (Blanca, 2002; Blanca and Morales, 1991; Gómez Mercado, 2011;
320 López Vélez, 1996; Lorite, 2001; Sánchez Gómez and Alcaraz, 1993; Sánchez Gómez et
321 al., 1997; Valle Tendero et al., 1989) has been compared with phylogeographical
322 studies. Table 2 includes those species whose putative survival in mid- and high-
323 altitude settings is supported by palaeobotanical data (Fig. 2). The complete list of the
324 SE Iberian Mediterranean and mesophytic mountain woody angiosperms is provided in
325 Supplementary Information. Widespread Mediterranean taxa (oaks and pines; *P. nigra*
326 ssp. *salzmanii*) form a matrix with mesophytes living in canyons, gorges and soils with
327 constant phreatic level. Some taxa are associated to rock walls and crevices (*Acer*
328 *granatense*, *A. monspessulanum*, *Rh. pumila*), while other to summit scrubs (*Ribes*
329 *alpinum*, *Rhamnus saxatilis*, *Rhamnus alpinus*). The mesophytic assemblage includes
330 biogeographically interesting species, as most of them are in their distribution limits,
331 such as *Betula pendula*, *Corylus avellana*, *Ilex aquifolium*, *Cornus sanguinea*, *Sorbus*

332 *torminalis*, *S. aria* and *Ulmus glabra*. Some of them represent disjunctions from the
333 main range (*Q. pyrenaica*, *Euonymus latifolius*, *Fraxinus ornus*, *Salix hastata*, *S. caprea*,
334 *S. eleagnos*, *Viburnum lantana*, *V. opulus*) or are endemic (*Acer granatense* = *A. opalus*
335 ssp. *granatense*, *Cotoneaster granatensis*, *Crataegus granatensis*, *Prunus ramburii*, see
336 references below).

337 The coexistence of widely-distributed Central European taxa in the semi-arid SE
338 Iberia has drawn the attention of geobotanists who have hypothesised the existence of
339 mountain refugia (Blanca, 1993, 2002; Blanca and Morales, 1991; Gómez Mercado,
340 2011; López Vélez, 1996; Lorite, 2001; Valle Tendero et al., 1989; Sánchez Gómez and
341 Alcaraz, 1993; Sánchez Gómez et al., 1997). In general, floristic, palaeobotanical and
342 population genetics information agree to consider SE Iberian mountain flora to have
343 persisted *in situ* the Pleistocene cold stages (Table 2). However, most phylogeographical
344 studies are continental-scale (Table 2). Therefore, persistence and migration inferences
345 are too broad to provide a finer identification of mountain refugia location,
346 nevertheless, molecular evidence provides some insights on refuged species (Gavin et
347 al., 2014; Petit et al., 2003; Rodríguez-Ramírez et al., 2010). Phylogeographical
348 information of *Ilex aquifolium*, *Hedera helix*, *H. hibernica*, *Betula pendula*, *Corylus*
349 *avellana*, *Castanea sativa*, *Quercus* sp., *Fraxinus angustifolia*, *F. ornus*, *Olea europaea*,
350 *Frangula alnus*, *Populus nigra* and *Vitis sylvestris*, confirms the broad importance of S
351 European peninsulas as long-term refugial areas (Table 2). The refuged populations
352 played a significant role in the central European post-glacial recolonisation, and they
353 explain current central European genetic diversity and divergence (Hewitt 2000,
354 Lascoux et al., 2003, Petit et al., 2003). Interestingly, some of the compiled studies

355 remark the importance of N Africa, Anatolia and Caucasus as refugia (Table 2),
356 suggesting more surveys in the Rif-Atlas and Ponto-Caspian regions for a complete
357 understanding of European post-glacial recolonisation (Besnard et al., 2002; Grassi et
358 al., 2008; Heuertz et al., 2006; Lumaret et al., 2002, 2005).

359 The most comprehensive phylogeographical initiative at an European scale, the
360 CYTOFOR RTD program (Petit et al., 2003; Table 2), explored chloroplast variability in 22
361 widespread European trees and shrubs sampled in 25 forests chosen on the premise of
362 high species richness and limited human influence (Lascoux et al., 2003). The most
363 genetically divergent European populations are those from S Italy, Corsica, and the
364 Balkan Peninsula. Surprisingly, central European populations' genetic diversity is higher
365 than expected owing to population admixture from different southern and local refugia
366 (Petit et al., 2003). The role of Iberian Peninsula as a refuge area is very intriguing,
367 since a lower than expected genetic diversity has been previously reported across the
368 region (Petit et al., 2003), challenging the hypothesis of refugial areas as holders of
369 larger genetic diversity (Gómez & Lunt, 2007). Possible explanations are: (i) the
370 Pyrenees as a weaker barrier than the Alps and land connection with western France
371 and the British isles, (ii) more severe Quaternary climatic episodes experienced in
372 Iberia than in the eastern peninsulas, meaning the location of refugia further south
373 than sampled, and (iii) migration of temperate species into Iberia from Italian and
374 Balkan peninsulas (Petit et al., 2003).

375 Although migration routes into Iberia might have existed, the Pyrenees are a
376 strong barrier limiting migration (Cotrell et al., 2005; Hampe et al., 2003; Rodríguez-
377 Sánchez et al., 2010). However, the lack of an exhaustive sampling of the southern

378 Iberian populations is more relevant to explain the unexpected low genetic divergence
379 results obtained (Cotrell et al., 2005; Grivet and Petit, 2002; Fineschi et al., 2000, 2005;
380 Heuertz et al., 2006; Fussi et al., 2010; Lumaret et al., 2005; Mohanty et al., 2002;
381 Palmé et al., 2003a, 2003b; Rendell and Ennos, 2003; Valdré and Vendramin, 2002).
382 The heterogeneity in Iberia plays a major role in the distribution of biodiversity (Sainz
383 Ollero et al., 2010). Classic 20th century geobotanical works recognised the co-
384 occurrence of multiple floristic elements in Iberian landscapes spanning from the
385 Saharo-Sinian to the Artic-Alpine (Blanco et al., 1997). This floristic diversity is the living
386 confirmation of refugial events; hence it is normal that drawing general conclusions
387 using sparse data from easily accessible populations within the species' main
388 distribution ranges provided biased results. A deeper understanding of local flora and
389 vegetation is necessary to make phylogeographical studies more accurate. Relict
390 presences and disjunct populations should be treated as scientific evidence rather than
391 botanical curiosities.

392 In this sense, sampling of S Iberian mountain populations is missing in most
393 studies. These mountains present relict and disjunct range-edge populations essential
394 to understand glacial and post-glacial refugial dynamics. The need of a better sampling
395 of Iberia has been recognised in a few studies, such as for *Populus alba* and *P. nigra*
396 (Cotrell et al., 2005; Fussi et al., 2010). In fact, when a detailed sampling has been
397 performed such as for *Frangula alnus* (Hampe et al., 2003), all but one haplotypes
398 showed to be mountain range-exclusive, revealing that populations persisting in
399 Mediterranean mountains have accumulated a large degree of differentiation.

400 On the available phylogeographical evidence we cannot yet ascertain whether
401 most woody angiosperms today occurring in the SE Iberian mountains survived there
402 during the last cold spell, although palaeobotanical data point to their survival. As we
403 have exposed before, this is due to a general lack of sampling of the southernmost
404 Iberian woody populations, although Species Distribution Modelling and Atmospheric
405 Model Simulations studies infer their persistence (i.e., Leroy and Arpe, 2007; Svenning
406 et al., 2008). The migration routes for many species and the origin of relict and disjunct
407 populations in relation to the species' main range have not yet been surveyed.

408 **6. Human impact and mountain plants**

409 Are climate and physiographic heterogeneity the only factors explaining the current
410 plant distribution in Mediterranean mountains? Both palaeobotanical and
411 archaeological research have reconstructed an intense history of grazing, trampling and
412 fire that opened landscapes and drove vegetation altitudinal shifts in SE Iberian
413 mountain areas during the last millennia (Carrión, 2002b). However, the assumption of
414 some formations to be human-induced could, sometimes, be erroneous. For example,
415 *Juniperus thurifera* populations were assumed to be favoured by recent anthropogenic
416 action (Carrión et al., 2004), while palaeobotanical work has demonstrated that they
417 have experienced a Late Holocene expansion related to an aridification trend (Carrión
418 et al., 2004).

419 The mesophytes currently inhabiting SE Iberian mountains are time
420 transgressive relict populations that survived in sites that buffered climatic extremes
421 and assured water availability. However, their presence has not only a relict origin, but
422 also a strong anthropogenic imprint (Carrión, 2002b, Carrión et al., 2004; López

423 Santalla et al., 2003). Many mesophyte populations are scattered in areas where
424 anthropogenic action has not cleared them out completely (Abel Schaad et al., 2014;
425 Blanca, 2002; Gómez Mercado, 2011; Sánchez Gómez et al., 1997; Valle Tendero et al.,
426 1989). However, the human-induced character of some landscapes with relict taxa has
427 not impeded high diversity. On the contrary, anthropogenic imprint may well favour
428 rich communities, and cultural landscapes are an example of this (Blondel, 2006). For
429 instance, the emblematic Montejo beech wood (Montejo de la Sierra, Central Iberia)
430 has mistakenly been considered as barely human-influenced beech forest on the basis
431 of its high diversity (Lascoux et al., 2003), while six decades ago it was a key
432 smallholding for local cattle husbandry seasonal dynamics (López Santalla et al., 2003).
433 Included as one of CYTOFOR's sampling points, it challenges one of its sampling
434 assumptions blurring the interpretations in Petit et al. (2003). On the contrary, human-
435 afforested thought-to-be Lillo pinewood (Cantabrian Ranges, N Iberia) has been
436 demonstrated to be of natural origin after the palynological study performed by García
437 Antón et al. (1997). This reinforces the idea that not only floristic and geobotanical
438 research, but also palaeobotanical and ethnographical studies are crucial for the
439 sampling design in phylogeographical studies.

440 **7. Concluding remarks**

441 The occurrence of fossil-bearing deposits is especially infrequent in unglaciated
442 mountains and in old land surfaces where sedimentary basins and other low-energy
443 depositional environments are scarce (González-Sampériz et al. 2010). This
444 taphonomical constraint biases the palaeobotanical record towards lowland deposits,
445 which compose the largest source of Pleistocene data for the Mediterranean

446 peninsulas. The absence of palaeobotanical evidence for sites prone to behave as
447 mountain refugia is not evidence of Mediterranean mountain refugia absence.

448 However, although the palaeobotanical evidence for refugia in SE Iberia is
449 taphonomically biased, the outstanding high-altitude Siles Lake palynological record
450 demonstrates the survival of woody angiosperms through the last glacial (Carrión,
451 2002b). It is likely that not only steep altitudinal gradients allowing quick altitudinal
452 shifts (Willis, 1994) were important for the long-term persistence of woody
453 populations, but also the existence of stable water availability. Phylogeographic studies
454 have given insight into patterns of survival and post-glacial migration for some of the
455 taxa whose Late Pleistocene presence in SE Iberia is palaeobotanically supported.
456 However, these studies are mainly conducted at a broad, continental scale. Searching
457 for the genetic imprint of refuges and linking them to defined geographical settings
458 could only be achieved if phylogeographical works include the range-edge southern
459 Mediterranean populations, otherwise results are biased. Southern Iberian relict
460 populations are recognised by floristic and geobotanical works. These relict
461 populations are usually scattered, small and quartered in places of difficult access, and
462 this is likely the reason for none of the extant individuals being included in
463 phylogeographical analyses (Table 2).

464 The combination of palaeobotanical, ethnographical, floristic and
465 phylogeographical information is of hallmark importance to conservation practices in
466 Mediterranean mountain areas. No real and effective management could be expected
467 without a deep understanding of structural and functional aspects of the spaces and
468 species we want to preserve.

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816 **FIGURE CAPTIONS**

817 FIGURE 1. (a) Iberian thermoclimatic belts, and (b) palaeobotanical records
818 considered in this study. Blank dots refer to Pleistocene sites (Table 1). Lettered dots
819 refer to N) Navarrés (Carrión and Van Geel, 1999), V) Villaverde (Carrión, 2001a), S)
820 Siles Lake (Carrión, 2002b), and C) Cañada de la Cruz (Carrión, 2001b).

821 FIGURE 2. Mesophytic, Mediterranean and Ibero-Maghrebian woody
822 angiosperm taxa presences in Late Pleniglacial sites from SE Iberia. Site numbers as in
823 Table 1 and Figure 1b.

824 FIGURE 3. Altitudinal vegetation dynamics in the Segura Mountains (SE Iberia)
825 for the last 20,000 years ago: (a) Late Pleniglacial and Late Glacial, (b) Late Pleistocene
826 and Early Holocene, (c) Holocene Mesophytic Optimum, and (d) Mid-Holocene. Based
827 on Carrión (2002b).

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832 TABLES

833 TABLE 1. List of SE Iberian Pleistocene palaeobotanical sites considered in this work.

Site Number	Site	Coordinates	Altitude (m asl)	Material	Chronology (only Pleistocene)	References
1	Algarrobo cave (Murcia)	37°38'N 1°17'W	290	Pollen	MIS* 2	Munuera and Carrión (1991)
2	Ambrosio cave (Almería)	37°49'N 2°5'W	950	Charcoal	MIS 2	Rodríguez-Ariza (2005)
3	Bajondillo (Málaga)	36°38'N 4°29'W	0	Pollen	MIS 3 – MIS 2	López -Saez et al. (2007)
4	Boquete de Zafarraya (Málaga)	36°56'N 4°07'W	1022	Pollen Charcoal	MIS 3	Lebreton et al.(2006), Vernet and Terral (2006)
5	Carihuela cave (Granada)	37°26'N 3°25'W	1020	Pollen Charcoal	MIS 5 to MIS 2	Carrión (1992a), Carrión et al.(1998, 1999), Fernández et al. (2007)
6	Cova Beneito (Alicante)	38°48'N 0°28'W	680	Pollen Charcoal	MIS 3 - MIS 2	Carrión (1992b), Carrión and Munuera (1997)
7	Cova Bolumini (Alicante)	38°50'N 0°00'W	170	Charcoal	MIS 2	Badal (1991)
8	Cova d'en Pardo (Alicante)	38°44'N 0°26'W	500	Pollen	MIS 2	Soler et al. (1999)

9	Cova de Les Cendres (Alicante)	38°41'N 0°09'E	45	Charcoal	MIS 3 - MIS 2	Badal (1991), Vernet (1997), Badal and Carrión (2001)
10	EL Asperillo (Huelva)	37°04'N 2°88'W	50	Pollen	MIS 2	Stevenson (1984)
11	Gorham's cave (Gibraltar)	36°07'N 5°20'W	5	Pollen Charcoal	MIS 3 - MIS 2	Carrión et al. (2008)
12	Laguna de San Benito (Valencia)	38°56'N 1°06'W	671	Pollen	MIS 3 - MIS 2	Dupré et al. (1996)
13	Laguna de Villena (Alicante)	38°37'N 0°55'W	502	Pollen	MIS 4 to MIS 2	Yll et al. (2003)
14	Las Ventanas cave (Granada)	37°26'N 3°26'W	1056	Pollen	MIS 2	Carrión et al. (2001c)
15	Les Calaveres cave (Alicante)	38°47'N 0°01'W	180	Pollen	MIS 3 - MIS 2	Dupré (1988)
16	Malladetes cave (Valencia)	39°00'N 0°17'W	500	Pollen	MIS 3 - MIS 2	Dupré (1988)
17	Mari López (Huelva)	37°01'N 6°19'W	0	Pollen	Middle-Late Pleistocene	Zazo et al. (1999)
18	Navarrés (Valencia)	39°06'N 0°41'W	225	Pollen	MIS 3 – MIS 2	Carrión and Dupré (1996), Carrión and Van Geel (1999)
19	Nerja cave (Málaga)	36°45'N 3°50'W	110	Charcoal	MIS 2	Badal (1991), Vernet (1997), Aura et al. (2002)

20	Padul (Granada)	37°00'N 3°36'W	723	Pollen	MIS 11 to MIS 2	Florschütz et al. (1971), Pons and Reille (1988), Ortiz et al. (2004)
21	Perneras cave (Murcia)	37°32'N 1°25'W	100	Pollen	MIS 3 – MIS 2	Carrión et al. (1995)
22	San Rafael (Almería)	36°46'N 2°37'W	8	Pollen	MIS 2	Pantaleón-Cano et al. (2003)
23	Santa Maira (Alicante)	38°43'N 0°13'W	650	Charcoal	MIS 2	Aura et al. (2005)
24	Siles lake (Jaén)	38°23'N 2°30'W	1320	Pollen	MIS 2	Carrión (2002b)
25	Tossal de La Roca (Alicante)	38°47'N 0°15'W	650	Pollen	MIS 2	López-Sá Charcoal ez and López-García (1999), Uzquiano (1988)
26	Túnel dels Sumidors (Valencia)	38°53'N 0°41'W	500	Pollen	MIS 2	Dupré (1988)

834 + MIS (Marine Isotope Stage).

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838 TABLE 2. Extant floristic and phylogeographic evidence for mesophytic and Mediterranean taxa occurring during MIS 2 in SE Iberian mountains.

FLORISTIC EVIDENCE*	MATERIAL AND METHODS			MAIN CONCLUSIONS	REFERENCES
	Molecular Marker: Method	Iberian Sampling	Iberian/ Total populations; Iberian / Total haplotypes.		
ACERACEAE					
<i>Acer granatense</i> , <i>A. monspessulanum</i>	-	-	-	-	-
ANACARDIACEAE					
<i>Pistacia lentiscus</i> , <i>P. terebinthus</i>	-	-	-	-	-
AQUIFOLIACEAE					
<i>Ilex aquifolium</i>	cpDNA: PCR-RFLP, nDNA: microsatellites	No S**	3/16 ; 0/8	Iberian and Italian refugia. Possible balkanic. Recolonisation through Atlantic coast from southern refugia.	Rendell & Ennos (2003)
ARALIACEAE					
<i>Hedera helix</i>	cpDNA: PCR-RFLP, microsatellites	No S and SE **	5/27 ; 2/13	Iberian and Balkans refuge. Putative refugia in Alps/Appenines .	Grivet & Petit (2002)
<i>Hedera hibernica</i>	cpDNA: PCR-RFLP, microsatellites	No SE**	5/27 ; 0/13	Iberian refuge. Post glacial migration from W Iberia Atlantic populations .	Grivet & Petit (2002)
BETULACEAE					
<i>Betula pendula</i> (ssp. <i>fontqueri</i>)	cpDNA: PCR-RFLP	No S**	3/47 ; 0/13	Iberian and Italian refugia (but not into recolonisation of Europe). Mid latitude (E &W) refugia origin of recolonisation.	Palmé et al (2003a)

<i>Corylus avellana</i>	cpDNA: PCR-RFLP, microsatellites	No S**	3/26 ; 0/10	Western refugia origin of recolonisation. Range-edge highest variability (Italian & Balkan peninsulas).	Palmé & Vendramin (2002)
BUXACEAE					
<i>Buxus sempervirens</i>	-	-	-	-	-
CAPRIFOLIACEAE					
<i>Sambucus ebulus</i> , <i>S. nigra</i>	-	-	-	-	-
<i>Viburnum lantana</i> , <i>V. opulus</i> , <i>V. tinus</i>	-	-	-	-	-
ERICACEAE					
<i>Arbutus unedo</i>	-	-	-	-	-
FAGACEAE					
<i>Castanea sativa</i>	cpDNA, mtDNA: PCR-RFLP	No SE. Only W	14/38 ; 0/11	Iberian refugia (possible) All Ib. populations polymorphic.	Fineschi <i>et al.</i> (2000)
<i>Quercus faginea</i> (ssp. <i>faginea</i>)	cpDNA: PCR-RFLP	Spread. No relict	200/200 ; 14/14	Iberian W/E/S coastal refugia inland and uphill recolonisation.	Olalde et al (2002)**
<i>Quercus pyrenaica</i>	cpDNA: PCR-RFLP	Spread. No relict E/SE	200/200 ; 14/14	Iberian W/E/S coastal refugia inland and uphill recolonisation.	Olalde et al (2002)**
<i>Quercus ilex</i> ssp. <i>ballota</i>	cpDNA: PCR-RFLP	Spread. No SE	42/174 ; 9/24	Iberian, S Italian, Balkanic, N African refugia	Lumaret <i>et al.</i> (2002)
<i>Quercus suber</i>	cpDNA: PCR-RFLP	SW and NE. No SE	34/91 ; ?/9	S Iberian, S Italian, S Balkanic and N African refugia.	Lumaret <i>et al.</i> (2005)
<i>Quercus alpestris</i> , <i>Q. coccifera</i> ****, <i>Q. lusitanica</i> .	-	-	-	-	-
JUGLANDACEAE					

<i>Juglans regia</i>	-	-	-	-	-
MYRTACEAE					
<i>Myrtus communis</i>	cpDNA: region sequencing	SW and E	4/173 ; 0/14	No glacial refuge inference.	Migliore <i>et al.</i> (2012)
OLEACEAE					
<i>Fraxinus angustifolia</i>	cpDNA: microsatellites, cpSSRs	Spread. No SE	5/70 ; 1/18	S Appenines refugia. Hibridisation in glacial refugia (<i>F. excelsior</i>).	Heuertz <i>et al.</i> (2006)
<i>Fraxinus ornus</i>	cpDNA: microsatellites, cpSSRs	-	0/59 ; 0/4	Italian, Balkanic and N Turkish refugia.	Heuertz <i>et al.</i> (2006)
<i>Ligustrum vulgare</i>	-	-	-	-	-
<i>Olea europaea</i> (ssp. <i>sylvestris</i>)	cpDNA: SNP	Spread. Incl. S and SE coast.	16/108 ; 0/42	Strait of Gibraltar, Near East and the Aegean refugia.	Besnard <i>et al.</i> 2002
<i>Phillyrea angustifolia</i> , <i>P. latifolia</i>	-	-	-	-	-
RHAMNACEAE					
<i>Frangula alnus</i>	cpDNA: PCR-RFLP	E and W Baetics	10/78 ; 7/21	Recolonisation of Europe from Balkans solely. Only 1 Iberian haplotype in more than mountain range.	Hampe <i>et al.</i> (2003)
<i>Rhamnus alaternus</i> , <i>Rh. alpinus</i> , <i>Rh. catharticus</i> , <i>Rh. infectoria</i> , <i>Rh. lycioides</i> , <i>Rh. myrtifolius</i> , <i>Rh. oleoides</i> , <i>Rh. pumila</i> , <i>Rh. saxatilis</i>	-	-	-	-	-

ROSACEAE					
<i>Crataegus monogyna</i>	cpDNA: PCR-RFLP	No S**	3/21 ; 0/4	Weak phylogeographical structure.	Fineschi <i>et al.</i> (2005)
<i>C. granatensis</i>	-	-	-	-	-
<i>Prunus spinosa</i>	cpDNA: PCR-RFLP	No S**	3/25 ; 2/32	S European refugia (inferred).	Mohanty <i>et al.</i> (2002)
<i>Prunus avium</i> , <i>P. insititia</i> , <i>P. mahaleb</i> , <i>P. postrata</i> , <i>P. ramburii</i> .	-	-	-	-	-
<i>Sorbus aria</i> , <i>S. domestica</i> , <i>S. hybrida</i> , <i>S. torminalis</i>	-	-	-	-	-
SALICACEAE					
<i>Populus alba</i>	cpDNA: PCR-RFLP	?	1/26 ; 0/57	Further samples in S Iberia needed to stablish conclusions	Fussi <i>et al.</i> (2010)
<i>Populus nigra</i>	cpDNA: PCR-RFLP	NE. No S	100/671 (trees) ; 38/81	Central-NE Iberian, Italian and N Balkans refugia. Need of more structured sampling in Iberia.	Cotrell <i>et al.</i> (2005)
<i>Populus x canescens</i>	cpDNA: PCR-RFLP	-	0/26 ; -	-	Fussi <i>et al.</i> (2010)
<i>Salix atrocinerea</i>	cpDNA: PCR-RFLP	No S**	1/2 ; -	Hibridisation with <i>S. caprea</i> . Haplotypes are not traceable to original sp.	Palmé <i>et al.</i> (2003)
<i>Salix caprea</i>	cpDNA: PCR-RFLP	No S**	2/24 ; 0/32	High latitude refugia. More variation in Central-N Europe.	Palmé <i>et al.</i> (2003)
<i>Salix alba</i> , <i>S. eleagnos</i> , <i>S. fragilis</i> , <i>S. hastata</i> , <i>S. neotricha</i> , <i>S. purpurea</i> , <i>S. triandra</i>	-	-	-	-	-
SANTALACEAE					
<i>Osyris quadripartita</i>	-	-	-	-	-

ULMACEAE					
<i>Ulmus glabra</i>	cpDNA: PCR-RFLP	Spread. Incl. S and SE	?/92 (trees) ; 0/31	No glacial refuge inference.	Gil <i>et al.</i> (2004)
<i>Ulmus minor</i>	cpDNA: PCR-RFLP, nDNA: microsatellites & AFLP	Spread. Incl. S and SE	?/348 (trees) ; 0/31	No glacial refuge inference. Strong influence of human propagation on genetic structure.	Gil <i>et al.</i> (2004)
VITACEAE					
<i>Vitis sylvestris</i>	nDNA: microsatellites	SW and N	9/32 ; -	Iberian, Italian and Caucasus refugia. No recolonisation from Iberian populations.	Grassi <i>et al.</i> (2008)

839 * See text for full references.

840 ** Papers derived from CYTOFOR PROJECT. Samples in Iberia only from Pyrenees, Galicia (NW) and Central Range.

841 *** Olalde *et al.* (2002) is centred in the Iberian Peninsula .

842 **** Although included in López de Heredia *et al.* (2007), no works on this species is comprehensive enough as to draw conclusions.

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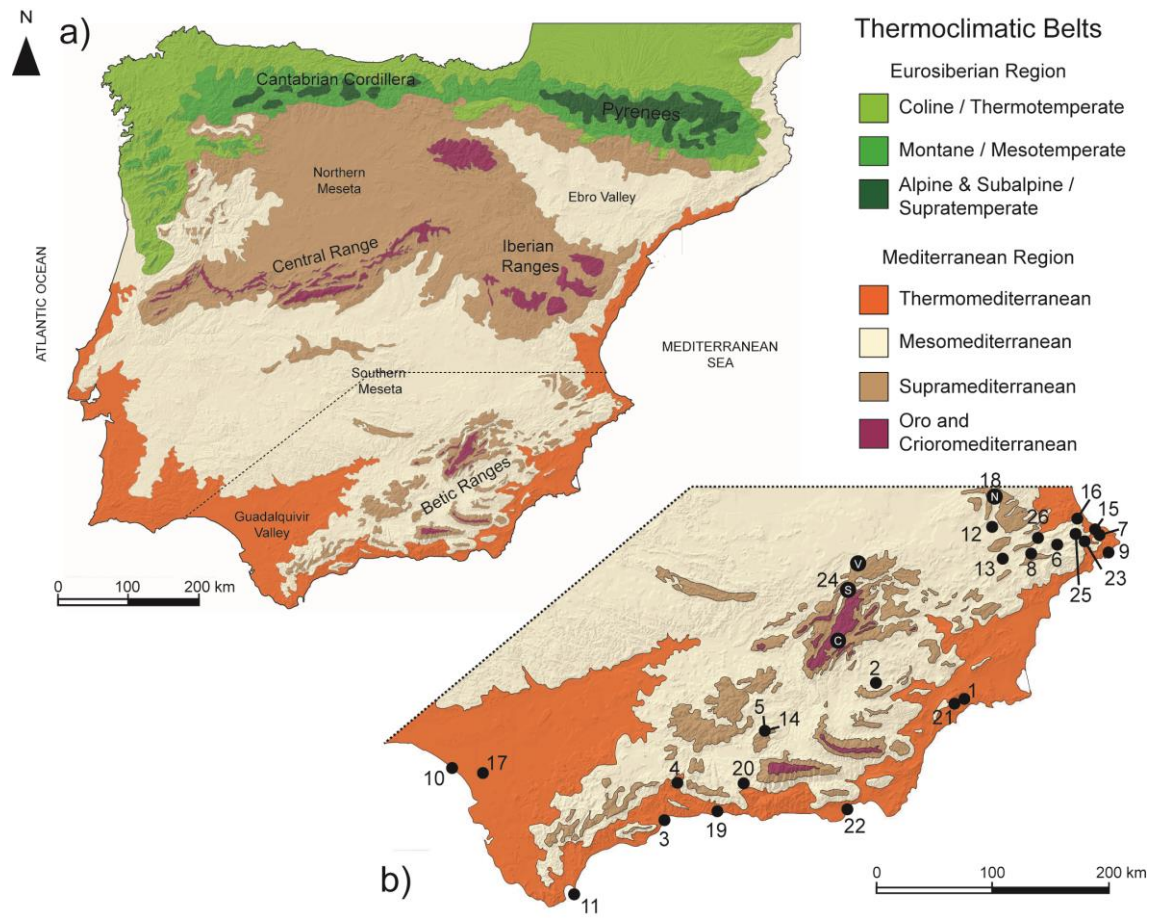
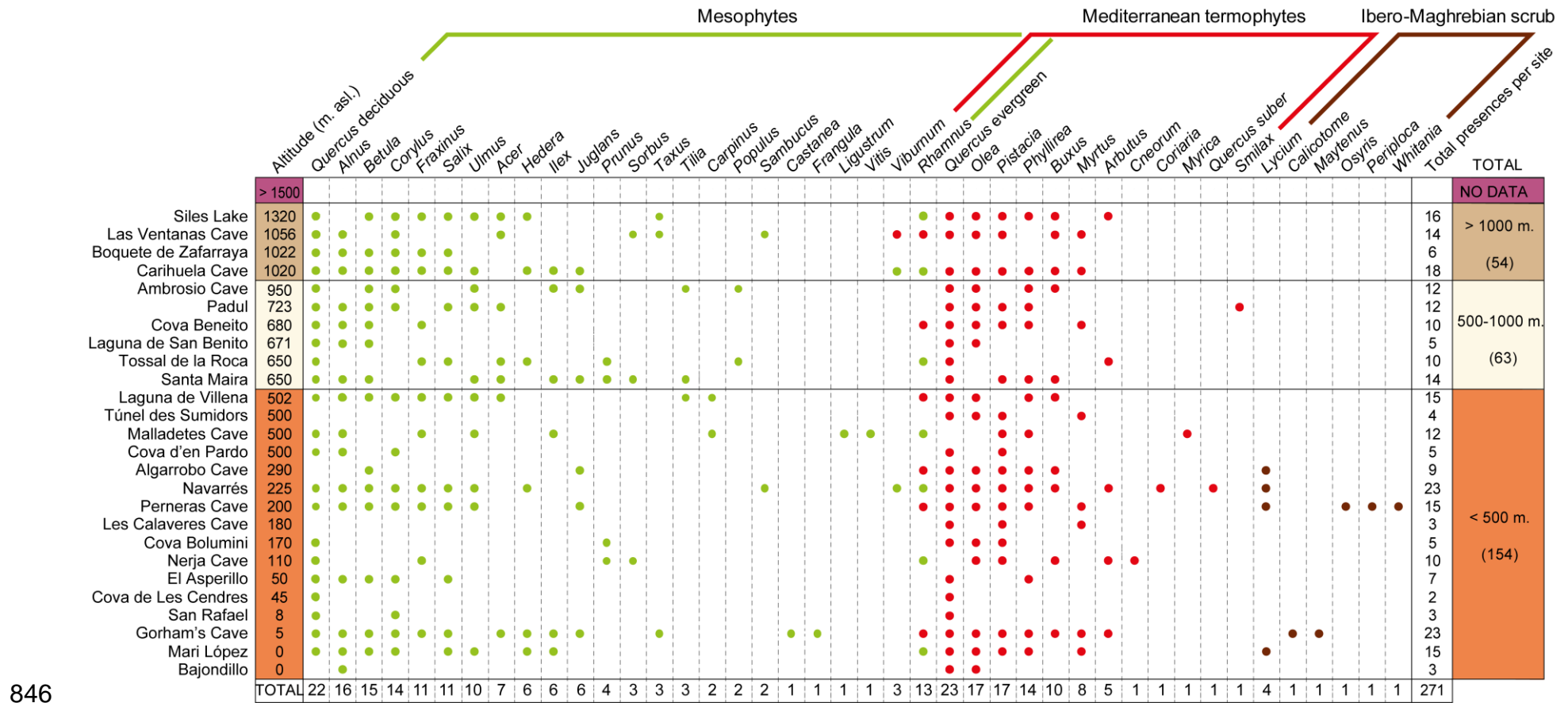


Figure 1

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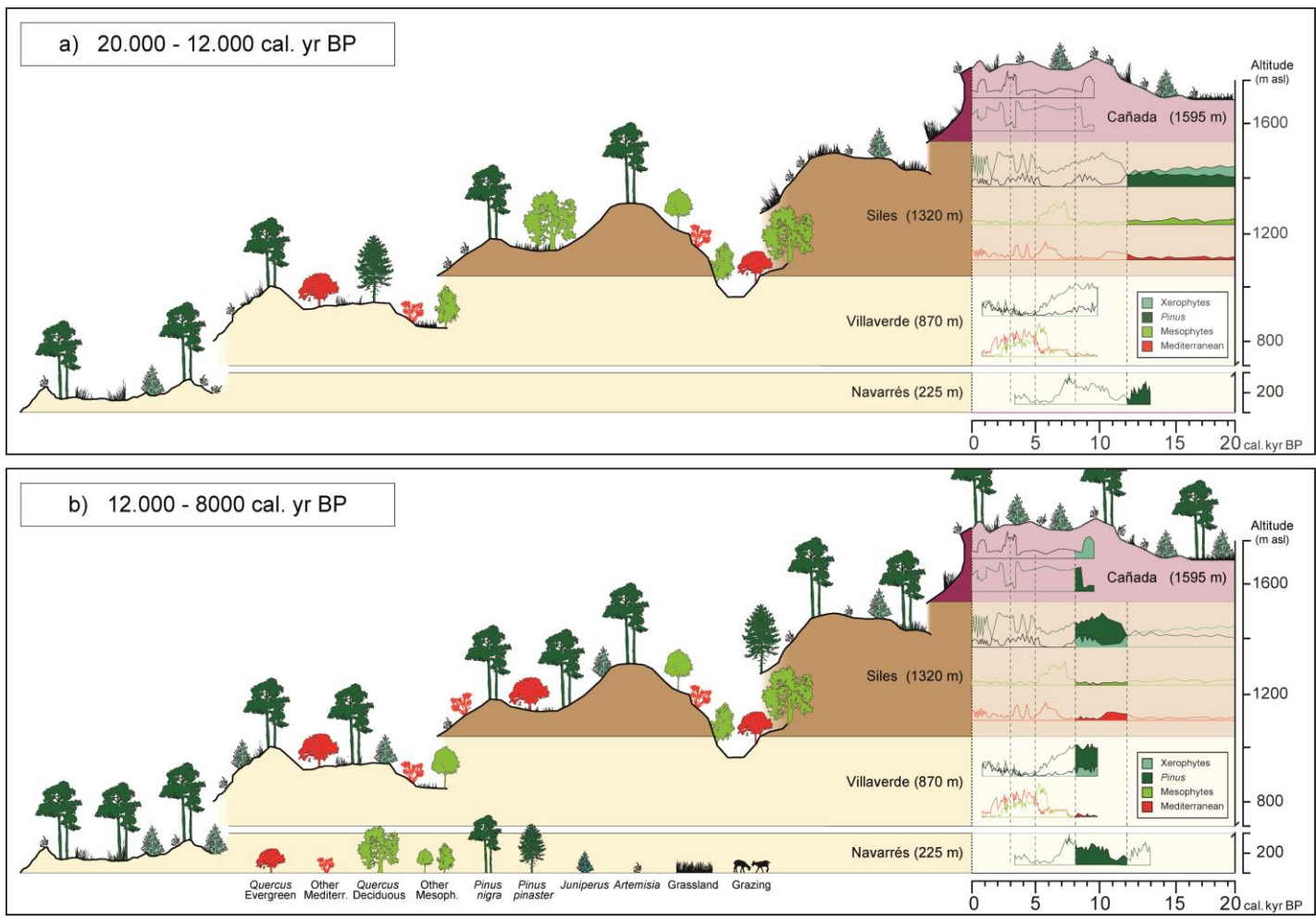


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Figure 2

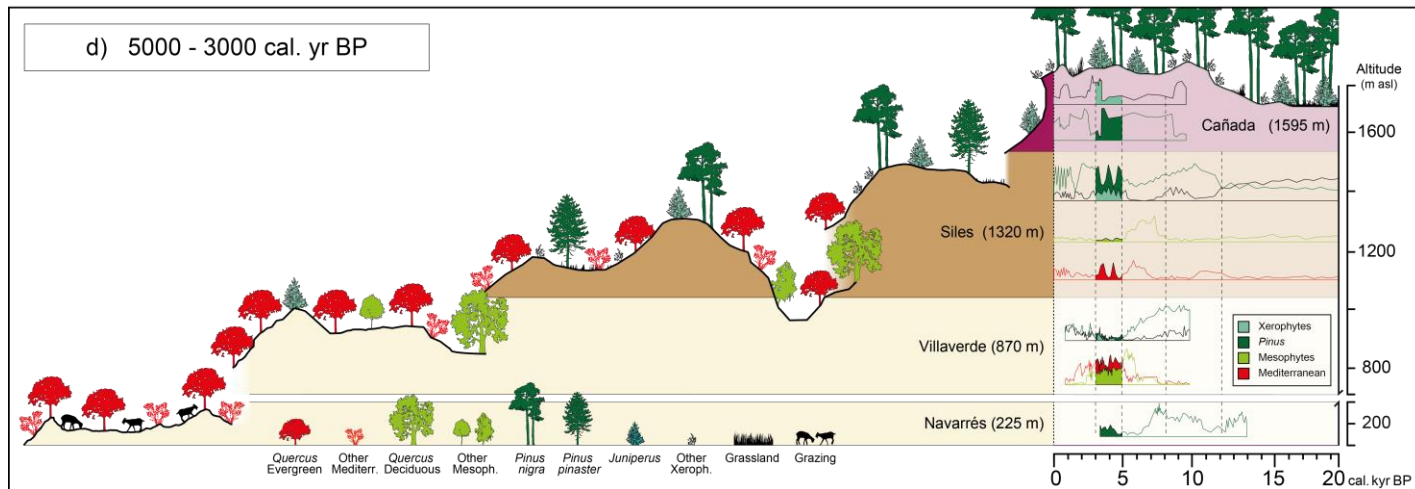
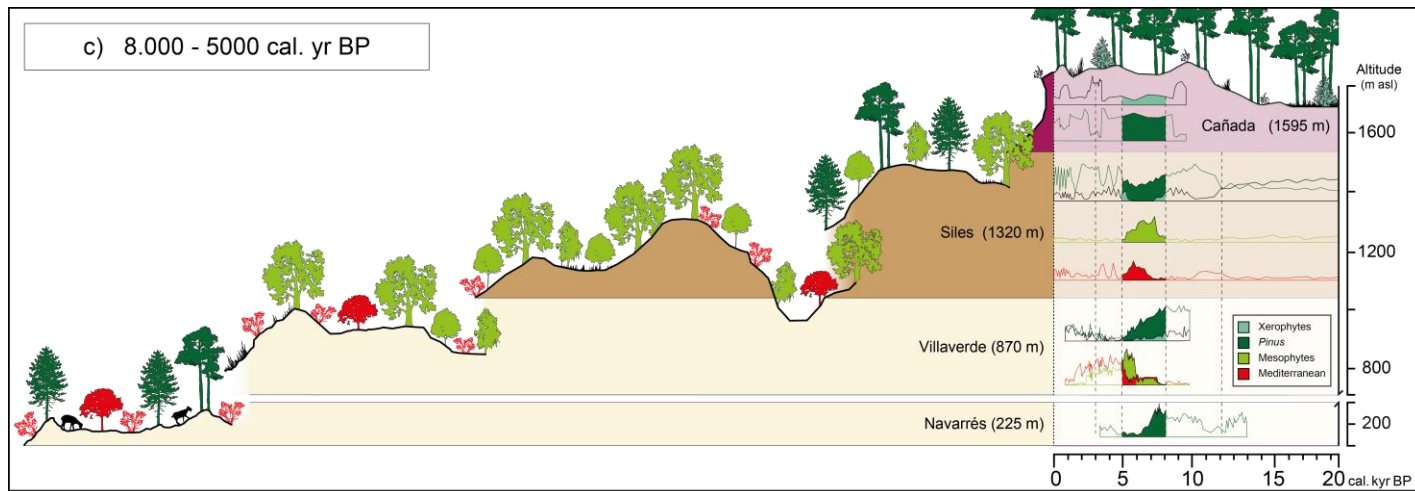
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Figure 3



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Figure 3 (cont.)