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

Saúl Manzano[1]*, José S. Carrión[1], Lourdes López-Merino[2], Penélope González-Sampériz[3], Manuel Munuera[1], Santiago Fernández[1], Ignacio Martín-Lerma[4], María del Carmen Gómez Ferreras[5]

[1] Department of Plant Biology, Faculty of Biology, University of Murcia, 30100 Murcia (Spain)

[2] Institute of Environment, Health and Societies, Brunel University London, UB8 3PH Uxbridge (UK)

[3] Pyrenean Institute of Ecology-CSIC, Av/ Montañana 1005, 50059 Zaragoza (Spain)
[4] Department of Prehistory, Archaeology, Ancient History, Medieval History and Historiography, University of Murcia, 30071 Murcia (Spain)

[5] Department of Plant Biology I (Botany and Plant Physiology), Complutense University of Madrid, 28040 Madrid (Spain)

* Corresponding author: saul.manzano@um.es, saul.manzano.rodriguez@gmail.com

Abstract

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

Key-words: palaeobotany, phylogeography, floristic, mountains, biogeography, Mediterranean

1. Introduction

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

Médail and Diadema (2009) recognised 52 Mediterranean glacial refugia based on the phylogeographical patterns of 82 plant species, including 41 herb and 41 tree taxa. Yet again, the role of the southern European peninsulas was emphasised with the presence of 25 refugia cohering areas of endemism and hotspots. In line with Medail and Diadema (2009), refugia are classified in three categories: Type 1) moist mid-altitude refugia (400-800 m asl) suited to altitudinal shifts of vegetation belts in response to environmental change, or *in situ* survival; Type 2) deep gorges and closed valleys, with uninterrupted moisture availability, and Type 3) low-altitude sites such as valley bottoms, coastal plains and wetlands, particularly sensitive to changes in aridity. According to this model, more than half of the refugia are located in “submontane [areas] and mountain margins” (Médail and Diadema, 2009 pp. 1338). However, the inclusion of palaeobotanical data points to the occurrence of intramontane refugia (Carrión, 2002b; Pons and Reille, 1988; Tzedakis, 2004). The importance of high-altitude belts as refugia for woody Mediterranean and mesophytic taxa may well have been undervalued. This review aims to fill this gap. South-eastern Iberian mountains are taken as a model owing to the presence of refugia dating from the last glacial (MIS 2) (Carrión, 2002b). Aiming to evaluate the Late Pleistocene survival of woody angiosperms (i.e., mesophytes, Mediterranean taxa and Ibero-Maghrebian scrub) considering the likely relevant role of high-altitude Mediterranean mountains, palaeobotanical and phylogeographical data are combined in order to (i) explore spatial patterns related to woody angiosperms glacial survival, (ii) infer high-altitude refugia structural and functional features, and (iii) identify gaps in knowledge hampering the understanding of woody angiosperms survival patterns in Mediterranean mountains.

2. South-eastern Iberia: environmental setting

The Iberian Peninsula is structured around an Inner Plateau crossed and surrounded by mountains. The Pyrenees and Iberian Ranges frame the Ebro valley in the north-east (Fig. 1). The Inner Plateau is surrounded by the Cantabrian Range in the north and the Sierra Morena and the Baetic Ranges in the south, with the Central System dividing the Inner Plateau in two (Fig. 1). These mountain systems and ranges make Iberia a largely heterogeneous land. Altitude gradient overlaps with slope orientation and triggers an uneven distribution of temperatures. Springs and creeks carve sometimes deep gorges and ravines diversifying the geologically complex landscape. Rain-shadow effects also contribute to the landscape heterogeneity and have large importance on plant distribution. Considering the unique mountainous character of Iberia and the fact that these mountains harbour a large portion of the Iberian plant diversity, the role that highlands have played in the current species distributions is obvious (Loidi, 1999).

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

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

Overall, SE Iberian vegetation landscapes present high mosaicism. Tertiary palaeotropical taxa live together with mesic, Mediterranean and subtropical xerothermic species in a mosaic resulted from a complex palaeogeographical history (Aparicio Martínez and Silvestre Domingo, 1987; Blanca, 2003; Molina-Venegas et al., 2015 a, b, Pérez Latorre et al., 1999). This unique environmental setting is the reason for selecting SE Iberia as a model for studying the role of Mediterranean mountain refugia. In spite of the former, woody angiosperms constitute the most comprehensive assemblage of palaeobotanical remains whose discrimination is achievable, at least, at genus level. Typological taxonomy ruled in palaeobotanical works is followed with reference to fossil remains (Carrión et al., 2015), whereas in reference to extant species and distributions the proposals of Flora Ibérica (www.floraiberica.org) and Anthos project (www.anthos.es) are followed. Ecological characterisation into mesophytes, Mediterranean taxa and Ibero-Maghrebian scrub follows the general consensus adopted by most palaeobotanical papers, and it is supported by Flora Ibérica and floristic and ecological works (Carrión et al*.,* 2001a, 2001b, 2015).

3. Late Pleistocene survival in SE Iberian Mountains

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

3.1 Mesophytes

Mesophytes include broad-leaved deciduous trees, *Ilex, Hedera* and *Vitis*, and appear from coastal areas to high-altitudes. Most remains are deciduous *Quercus* pollen. This pollen type comprises several species (Table 2), including sometimes *Q. suber*, whose palynological discrimination can be challenging (Carrión et al., 2000). Charcoal and pollen of *Alnus*, *Betula*, *Corylus*, *Ulmus* and *Salix* occur in several sedimentary contexts from sea level up to 1320 m asl (Fig. 2).

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

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

3.2 *Viburnum*, *Rhamnus* and Mediterranean taxa

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

Mediterranean thermophytes, such as evergreen *Quercus* (*Q. ilex* and *Q. coccifera*), *Olea, Pistacia, Phillyrea, Buxus, Myrtus* and *Arbutus* are well represented at all altitudes in the palaeobotanical record (Fig. 2). *Smilax* appears in a mid-altitude site only, and the punctual presences of *Q. suber, Myrica, Coriaria* and *Cneorum* are restricted to altitudes below 500 m asl (Fig. 2).

3.3 Ibero-Maghrebian scrub

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

3.4 High-altitude refugia?

In order to test Médail and Diadema (2009)´s refugia model, the abundance of palaeobotanical data (Fig. 2) and bioclimatic belts is compared. Bioclimatic belts follow Carrión (2002): thermomediterranean (< 500 m asl), mesomediterranean (500-1000 m asl) and supramediterranean (> 1000 m asl). No oro- and crioromediterranean Pleistocene sites have been studied so far in SE Iberia. Raw analysis of the contingence matrix shows a major concentration of fossil records in the mesomediterranean belt (χ^2= 103.11; df= 2, P > 0.05), as implied by Type 1 refugia. However, the correction of the data taking into account the number of sites per belt does not show an altitudinal bias (χ^2= 3.11; df= 2, P < 0.05), indicating that the altitudinal distribution of woody angiosperms Pleistocene refuges is mostly explained by a skew in the fossil record towards lowlands rather than to ecological or geographical features. The widely-recognised Type 1 mid-altitude refugia (400-800 m asl;) are supported by 8 sites (Figs. 1 and 2). The more spatially constrained Type 2 refugia existing in sites with continued moisture availability are confirmed by the presence of mesophyte and sclerophyllous taxa in Carihuela, Las Ventanas, Malladetes, Nerja, Cendres, Santa Maira, Tossal de la Roca, d'en Pardo, Bolumini, Ambrosio, Calaveres, Beneito, Padul and Siles (Figs. 1 and 2, Table 1). Type 3 refugia appear at a wide range of low-altitude sites with diverse geomorphology: the coastal Mari López and San Rafael marshlands, the Bajondillo, Gorham, Nerja and Les Cendres caves, the perched peat levels of El Asperillo sand cliff, and the warm and moist Les Calaveres, Perneras and Navarrés (Figs. 1 and 2, Table 1).

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

4. Vegetation dynamics in an altitudinal gradient

4.1 Past vegetation records

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

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

The Late Pleniglacial and Late Glacial record (ca. 20 - 12 cal. ka BP, Fig. 3a) is restricted to the high-altitude Siles (1320 m asl) and the low-altitude Navarrés (225 m asl) records. The landscape was dominated by a steppe composed by Poaceae, *Artemisia* and *Ephedra*, with *Juniperus* and *Pinus* (*P. nigra* and, to a lesser extent, *P. sylvestris,* as inferred from anthracological evidence, Roiron et al., 2013). Junipers and pines would appear scattered throughout the widespread cold and arid landscapes (Carrión, 1992; Carrión et al., 1998; Fernández et al., 2007; Pons and Reille, 1988). Nevertheless, Siles Lake accounts for high-altitude woody angiosperm glacial survival (Fig. 2) with the continuous presence of Mediterranean and mesophytic taxa such as both evergreen and deciduous *Quercus, Betula, Corylus, Fraxinus, Salix, Ulmus, Rhamnus, Olea, Pistacia, Phillyrea, Buxus* and *Arbutus*. Broad-leaved forests must have been discontinuous, and related to the nearby existence of gullies and ravines. Exposed situations with trees are however possible, like it is seen today in the Cantabrian and Sierra Nevada ranges with *Quercus ilex* ssp. *ballota,* which grows punctually above the mesophytic belt (Blanca, 2002; Fernández Prieto, 1981).

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

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

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

4.2. Factors controlling taxa survival

Siles Lake is deprived of stream connections and fed by precipitation and runoff from a relatively small catchment (3 x 1.5 km). The basin is located in an elevated flat polje surrounded by a series of deeply incised thermic gorges (Carrión, 2002b). Why survival was possible in such a context? The evidence for non-cryophilous taxa in montane contexts during the Late Pleniglacial provides insights to understand it. The Holocene temperature rise might not explain solely refuged vegetation dynamics in the Mediterranean Region, as its climate is characterised by summer drought (Walter, 2002) and water is a limiting factor for Mediterranean plants (Galmés et al., 2007), so soil water availability likely played a major role. On the other hand, cold winter temperatures imply shorter vegetative periods, in adaptation to which deciduous species shed their leaves. However, spring refoliation is a water-demanding process hampered when prevailing low temperatures are combined with water availability restrictions during the vegetative period. Under the cold Late Pleniglacial temperatures, the mesophytes and Mediterranean taxa survival at Siles was possible only in places without water availability restrictions, so thermic gorges played a very important role as woody vegetation refuges. Thus, it is plausible that the main factor limiting woody angiosperm presence in Mediterranean mountains was water availability rather than low temperatures (Cowling and Skyes, 1999; Leroy and Arpe, 2007). Hence, the survival of small pockets of mesic and thermophytic taxa in mountain areas cannot be regarded as merely anecdotal. This phenomenon is not more often incorporated into models probably because of the scant high-altitude Mediterranean palaeobotanical record.

The presence of refugia seems, therefore, related to a number of physiographical features that assure continuous water availability. Narrow and incised gorges at mid- to high-altitude provide protection against wind-induced desiccation, survival in valley bottoms is assured by *in situ* moisture accumulation in deep soils, while coastal enclaves tend to be exposed to moisture loaded winds that reduce water stress. Survival in rock walls and crevices would mean no competition, protection against ecosystem disturbance and in porous rocks, such as limestones, a more or less continuous water reservoir.

5. Floristic and phylogeographical evidence for montane refugia

While the palaeobotanical record provides information on past taxa presence, identification to species level is limited. For such reason, floristic and genetic investigations are very helpful, as they provide a larger level of taxonomical detail. Current floristic presence of mesophytes, Mediterranean and Ibero-Magrebian taxa in SE Iberian mountains (Blanca, 2002; Blanca and Morales, 1991; Gómez Mercado, 2011; López Vélez, 1996; Lorite, 2001; Sánchez Gómez and Alcaraz, 1993; Sánchez Gómez et al., 1997; Valle Tendero et al., 1989) has been compared with phylogeographical studies. Table 2 includes those species whose putative survival in mid- and high-altitude settings is supported by palaeobotanical data (Fig. 2). The complete list of the SE Iberian Mediterranean and mesophytic mountain woody angiosperms is provided in Supplementary Information. Widespread Mediterranean taxa (oaks and pines; *P. nigra* ssp*. salzmanii*) form a matrix with mesophytes living in canyons, gorges and soils with constant phreatic level. Some taxa are associated to rock walls and crevices (*Acer granatense, A. monspessulanum, Rh. pumila*), while other to summit scrubs (*Ribes alpinum, Rhamnus saxatilis, Rhamnus alpinus*). The mesophytic assemblage includes biogeographically interesting species, as most of them are in their distribution limits, such as *Betula pendula, Corylus avellana, Ilex aquifolium, Cornus sanguinea, Sorbus* *torminalis, S. aria* and *Ulmus glabra*. Some of them represent disjunctions from the main range (*Q. pyrenaica, Euonymus latifolius, Fraxinus ornus, Salix hastata, S. caprea, S. eleagnos, Viburnum lantana, V. opulus*) or are endemic (*Acer granatense = A. opalus* ssp. *granatense*, *Cotoneaster granatensis, Crataegus granatensis, Prunus ramburii,* see references below).

The coexistence of widely-distributed Central European taxa in the semi-arid SE Iberia has drawn the attention of geobotanists who have hypothesised the existence of mountain refugia (Blanca, 1993, 2002; Blanca and Morales, 1991; Gómez Mercado, 2011; López Vélez, 1996; Lorite, 2001; Valle Tendero et al., 1989; Sánchez Gómez and Alcaraz, 1993; Sánchez Gómez et al., 1997). In general, floristic, palaeobotanical and population genetics information agree to consider SE Iberian mountain flora to have persisted *in situ* the Pleistocene cold stages (Table 2). However, most phylogeographical studies are continental-scale (Table 2). Therefore, persistence and migration inferences are too broad to provide a finer identification of mountain refugia location, nevertheless, molecular evidence provides some insights on refuged species (Gavin et al., 2014; Petit et al., 2003; Rodríguez-Ramírez et al., 2010). Phylogeographical information of *Ilex aquifolium, Hedera helix, H. hibernica, Betula pendula, Corylus avellana, Castanea sativa, Quercus* sp.*, Fraxinus angustifolia, F. ornus, Olea europaea, Frangula alnus, Populus nigra* and *Vitis sylvestris*, confirms the broad importance of S European peninsulas as long-term refugial areas (Table 2). The refuged populations played a significant role in the central European post-glacial recolonisation, and they explain current central European genetic diversity and divergence (Hewitt 2000, Lascoux et al., 2003, Petit et al., 2003). Interestingly, some of the compiled studies remark the importance of N Africa, Anatolia and Caucasus as refugia (Table 2), suggesting more surveys in the Rif-Atlas and Ponto-Caspian regions for a complete understanding of European post-glacial recolonisation (Besnard et al., 2002; Grassi et al., 2008; Heuertz et al., 2006; Lumaret et al., 2002, 2005).

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

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

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

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

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

6. Human impact and mountain plants

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

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

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

7. Concluding remarks

The occurrence of fossil-bearing deposits is especially infrequent in unglaciated mountains and in old land surfaces where sedimentary basins and other low-energy depositional environments are scarce (González-Sampériz et al. 2010). This taphonomical constraint biases the palaeobotanical record towards lowland deposits, which compose the largest source of Pleistocene data for the Mediterranean peninsulas. The absence of palaeobotanical evidence for sites prone to behave as mountain refugia is not evidence of Mediterranean mountain refugia absence.

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

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

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FIGURE CAPTIONS

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

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

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

TABLES

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)	36º56’N 4º07’W	1022	Pollen Charcoal	MIS 3	Lebreton et al.(2006), Vernet and Terral (2006)
5	Carihuela cave (Granada)	37º26’N 3º25’W	1020	Pollen Charcoal	MIS 5 to MIS 2	Carrión (1992a), Carrión et al.(1998, 1999), Fernández et al. (2007)
6	Cova Beneito (Alicante)	38º48’N 0º28’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)	37º04’N 2º88’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)	37º01’N 6º19’W	0	Pollen	Middle-Late Pleistocene	Zazo et al. (1999)
18	Navarrés (Valencia)	39º06’N 0º41’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)	37º32’N 1º25’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)

+ MIS (Marine Isotope Stage).

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					
Acer granatense, A. monspessulanum	-	-	-	-	-
ANACARDIACEAE					
Pistacia lentiscus, P. terebinthus	-	-	-	-	-
AQUIFOLIACEAE					
Ilex aquifolium	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					
Hedera helix	cpDNA: PCR-RFLP, microsatellites	No S and SE **	5/27 ; 2/13	Iberian and Balkans refuge. Putative refugia in Alps/Appenines .	Grivet & Petit (2002)
Hedera hibernica	cpDNA: PCR-RFLP, microsatellites	No SE**	5/27 ; 0/13	Iberian refuge. Post glacial migration from W Iberia Atlantic populations .	Grivet & Petit (2002)
BETULACEAE					
Betula pendula (ssp. *fontqueri*)	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)

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

Juglans regia	-	-	-	-	-
MYRTACEAE					
Myrtus communis	cpDNA: region sequencing	SW and E	4/173 ; 0/14	No glacial refuge inference.	Migliore *et al.* (2012)
OLEACEAE					
Fraxinus angustifolia	cpDNA: microsatellites, cpSSRs	Spread. No SE	5/70 ; 1/18	S Appenines refugia. Hibridisation in glacial refugia (*F. excelsior*).	Heuertz *et al.* (2006)
Fraxinus ornus	cpDNA: microsatellites, cpSSRs	-	0/59 ; 0/4	Italian, Balkanic and N Turkish refugia.	Heuertz *et al.* (2006)
Ligustrum vulgare	-	-	-	-	-
Olea europaea (ssp. *sylvestris*)	cpDNA: SNP	Spread. Incl. S and SE coast.	16/108 ; 0/42	Strait of Gibraltar, Near East and the Aegean refugia.	Besnard *et al.* 2002
Phillyrea angustifolia, P. latifolia	-	-	-	-	-
RHAMNACEAE					
Frangula alnus	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 *et al.* (2003)
Rhamnus alaternus, Rh. alpinus, Rh. catharticus, Rh. infectoria, Rh. lycioides, Rh. myrtifolius, Rh. oleoides, Rh. pumila, Rh. saxatilis	**-**	-	-	-	-

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

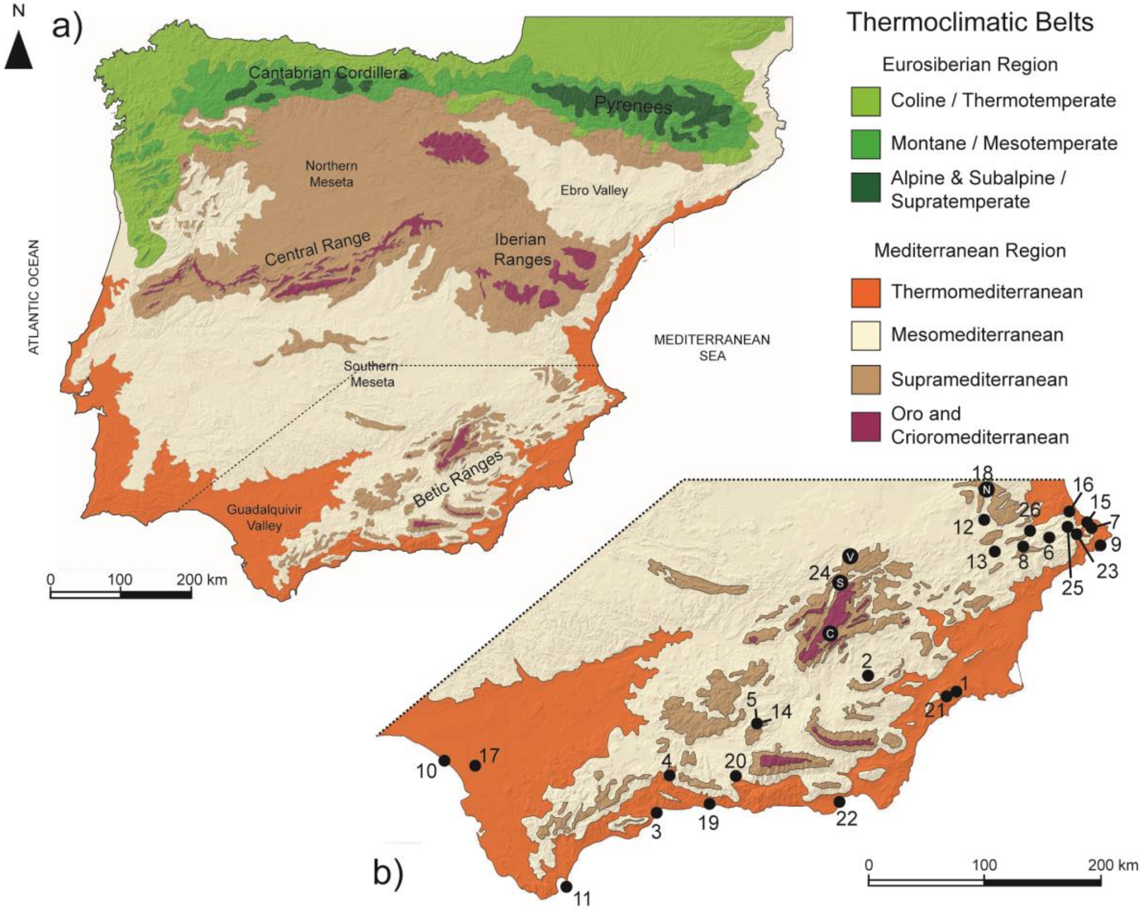
ULMACEAE					
Ulmus glabra	cpDNA: PCR-RFLP	Spread. Incl. S and SE	?/92 (trees) ; 0/31	No glacial refuge inference.	Gil *et al.* (2004)
Ulmus minor	cpDNA: PCR-RFLP, nDNA: microsatellites & AFLP	Spread. Incl. S and SE	?/348 (trees) ; 0/31	No glacial refuge inference. Strong influence of human propagation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

* See text for full references.

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

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

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


N
a)
Cantabrian Cordillera
Pyrenees
Northern Meseta
Ebro Valley
Central Range
Iberian Ranges
ATLANTIC OCEAN
MEDITERRANEAN SEA
Southern Meseta
Betic Ranges
Guadalquivir Valley
0
100
200 km
Thermoclimatic Belts
Eurosiberian Region
Coline / Thermotemperate
Montane / Mesotemperate
Alpine & Subalpine / Supratemperate
Mediterranean Region
Thermomediterranean
Mesomediterranean
Supramediterranean
Oro and Crioromediterranean
b)
18
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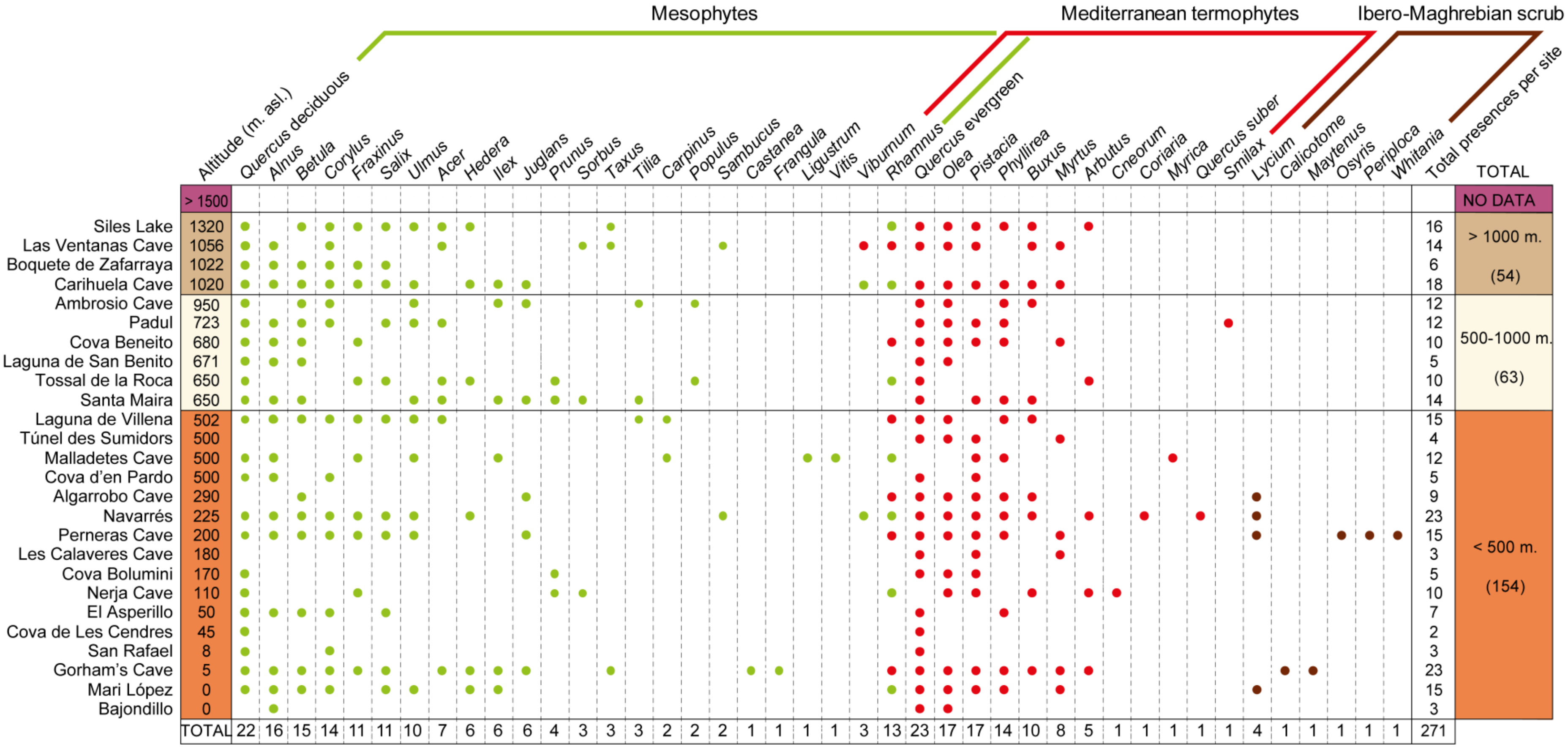
200 km

Figure 1



		Mesophytes																						Mediterranean termophytes														Ibero-Maghrebian scrub							
	Altitude (m. asl.)	*Quercus* deciduous	*Alnus*	*Betula*	*Corylus*	*Fraxinus*	*Salix*	*Ulmus*	*Acer*	*Hedera*	*Ilex*	*Juglans*	*Prunus*	*Sorbus*	*Taxus*	*Tilia*	*Carpinus*	*Populus*	*Sambucus*	*Castanea*	*Frangula*	*Ligustrum*	*Vitis*	*Viburnum*	*Rhamnus*	*Quercus* evergreen	*Olea*	*Pistacia*	*Phyllirea*	*Buxus*	*Myrtus*	*Arbutus*	*Cneorum*	*Coriaria*	*Myrica*	*Quercus suber*	*Smilax*	*Lycium*	*Calicotome*	*Maytenus*	*Osyris*	*Periploca*	*Whitania*	Total presences per site	TOTAL
	> 1500																																												NO DATA
Siles Lake	1320	●		●	●	●	●	●	●	●					●										●	●	●	●	●	●		●												16	> 1000 m. (54)
Las Ventanas Cave	1056	●	●		●				●					●	●				●					●	●	●	●	●		●	●													14	
Boquete de Zafarraya	1022	●	●	●	●	●	●																																					6	
Carihuela Cave	1020	●	●	●	●	●	●	●		●	●	●												●	●	●	●	●	●	●	●													18	
Ambrosio Cave	950	●		●	●			●			●	●				●		●								●	●		●	●														12	500-1000 m. (63)
Padul	723	●	●	●	●		●	●	●																	●	●	●	●								●							12	
Cova Beneito	680	●	●	●		●																			●	●	●	●	●		●													10	
Laguna de San Benito	671	●	●	●																						●	●																	5	
Tossal de la Roca	650	●				●	●		●	●			●					●							●	●						●												10	
Santa Maira	650	●	●	●				●	●		●	●	●	●		●										●		●	●	●														14	
Laguna de Villena	502	●	●	●	●	●	●	●	●							●	●								●	●	●		●	●														15	< 500 m. (154)
Túnel des Sumidors	500																									●	●	●			●													4	
Malladetes Cave	500	●	●			●		●			●						●					●	●		●			●	●						●									12	
Cova d'en Pardo	500	●	●		●																					●		●																5	
Algarrobo Cave	290			●								●													●	●	●	●	●	●								●						9	
Navarrés	225	●	●	●	●	●	●	●		●									●					●	●	●	●	●	●	●		●		●		●		●						23	
Perneras Cave	200	●	●	●	●	●	●	●				●													●	●	●	●	●		●							●			●	●	●	15	
Les Calaveres Cave	180																									●		●			●													3	
Cova Bolumini	170	●											●													●	●	●																5	
Nerja Cave	110	●				●							●	●											●		●	●		●		●	●											10	
El Asperillo	50	●	●	●	●		●																			●			●															7	
Cova de Les Cendres	45	●																								●																		2	
San Rafael	8	●			●																					●																		3	
Gorham's Cave	5	●	●	●	●	●	●		●	●	●	●			●					●	●				●	●	●	●	●	●	●	●							●	●				23	
Mari López	0	●	●	●	●		●	●		●	●														●	●	●	●	●		●							●						15	
Bajondillo	0		●																							●	●																	3	
	TOTAL	22	16	15	14	11	11	10	7	6	6	6	4	3	3	3	2	2	2	1	1	1	1	3	13	23	17	17	14	10	8	5	1	1	1	1	1	4	1	1	1	1	1	271	

846

847 Figure 2

848

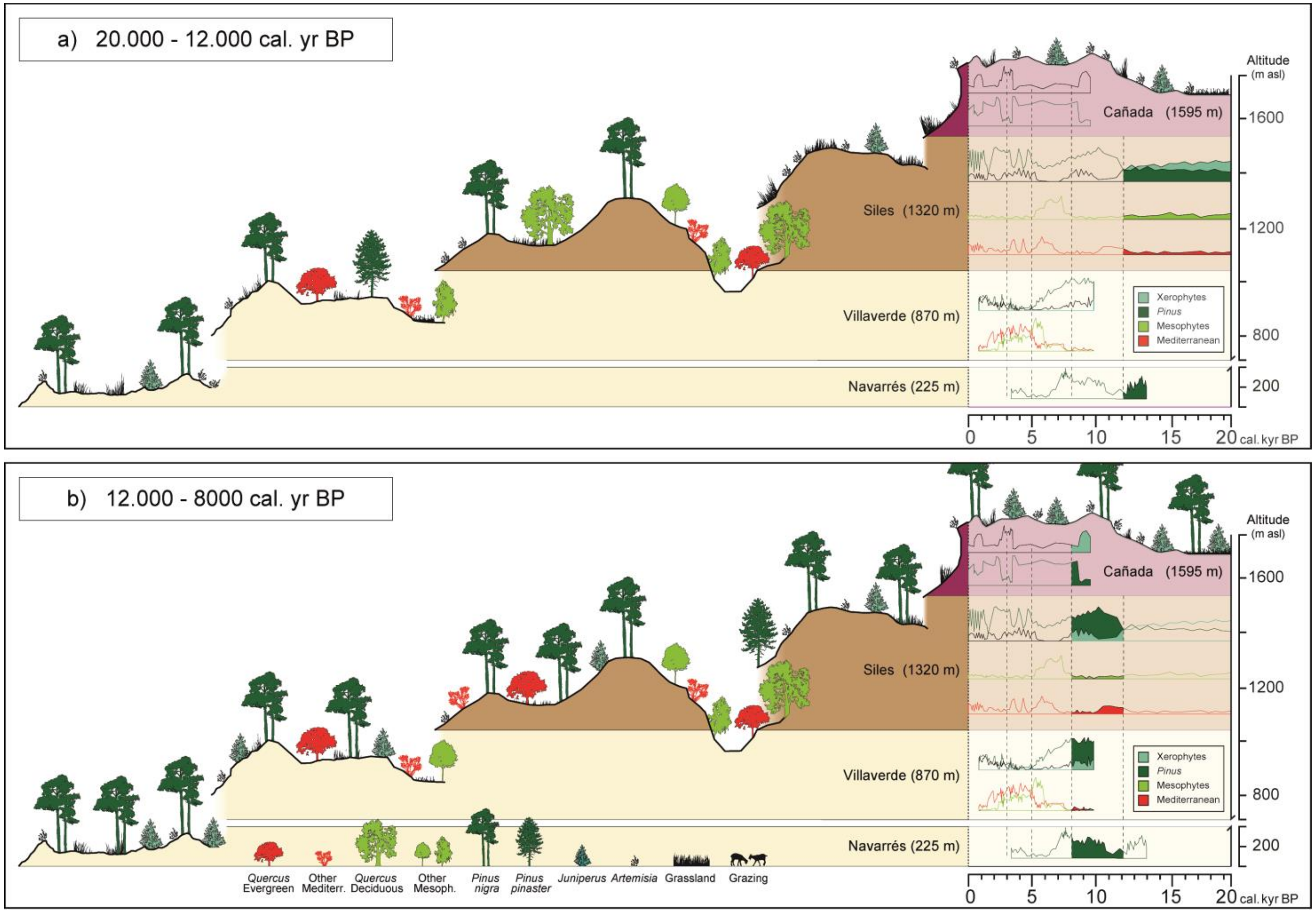

a) 20.000 - 12.000 cal. yr BP
b) 12.000 - 8000 cal. yr BP
Cañada (1595 m)
Siles (1320 m)
Villaverde (870 m)
Navarrés (225 m)
Altitude (m asl)
1600
1200
800
200
Xerophytes
Pinus
Mesophytes
Mediterranean
0
5
10
15
20
cal. kyr BP
Quercus Evergreen
Other Mediterr.
Quercus Deciduous
Other Mesoph.
Pinus nigra
Pinus pinaster
Juniperus
Artemisia
Grassland
Grazing

Figure 3

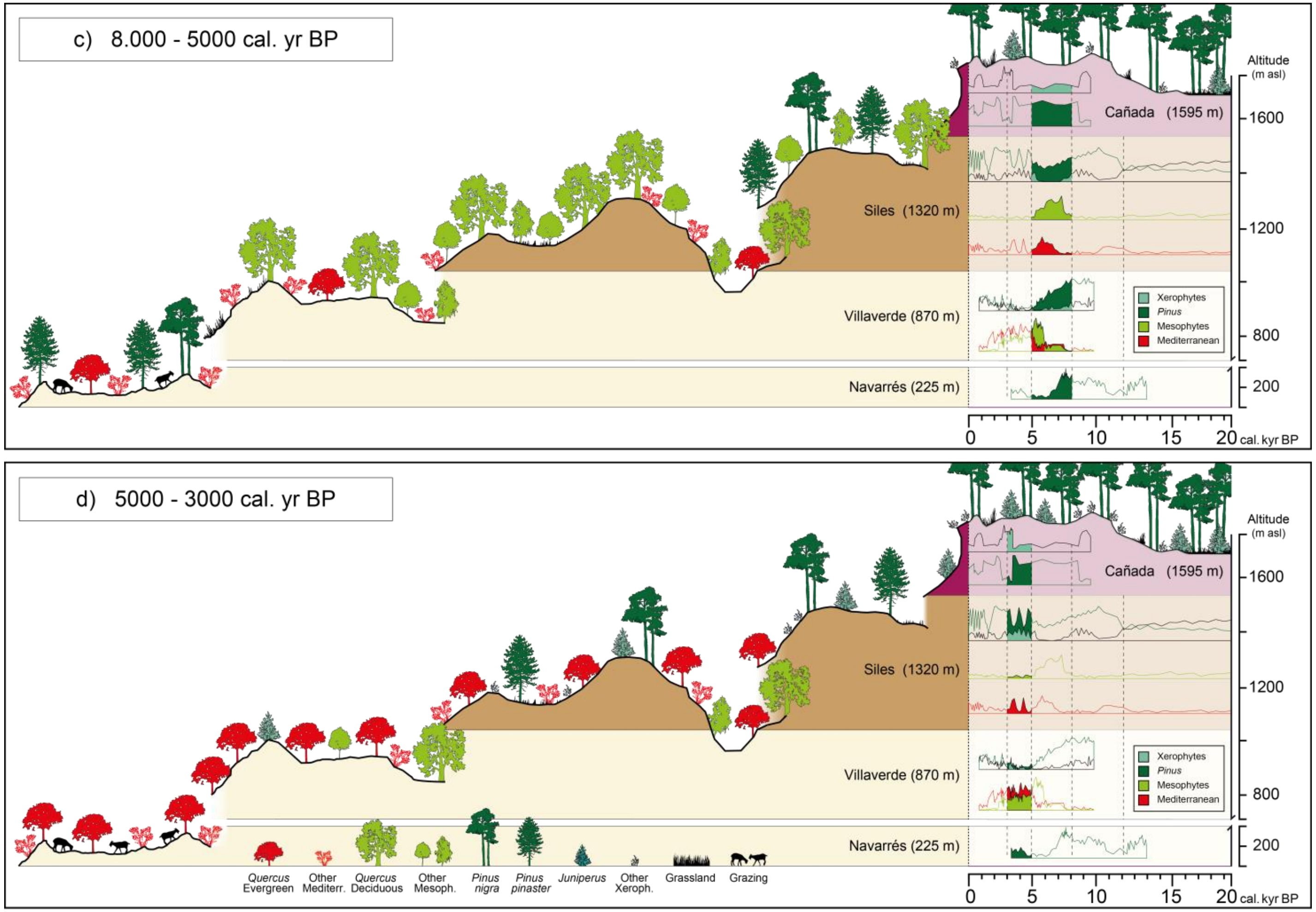


Figure 3 (cont.)