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Mountain strongholds for woody angiosperms during the Late Pleistocene in SE Iberia

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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.

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).

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 Médail 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

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Reille, 1988; Tzedakis et al., 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 Ariza, 1993; Sánchez Gómez et al., 1997).

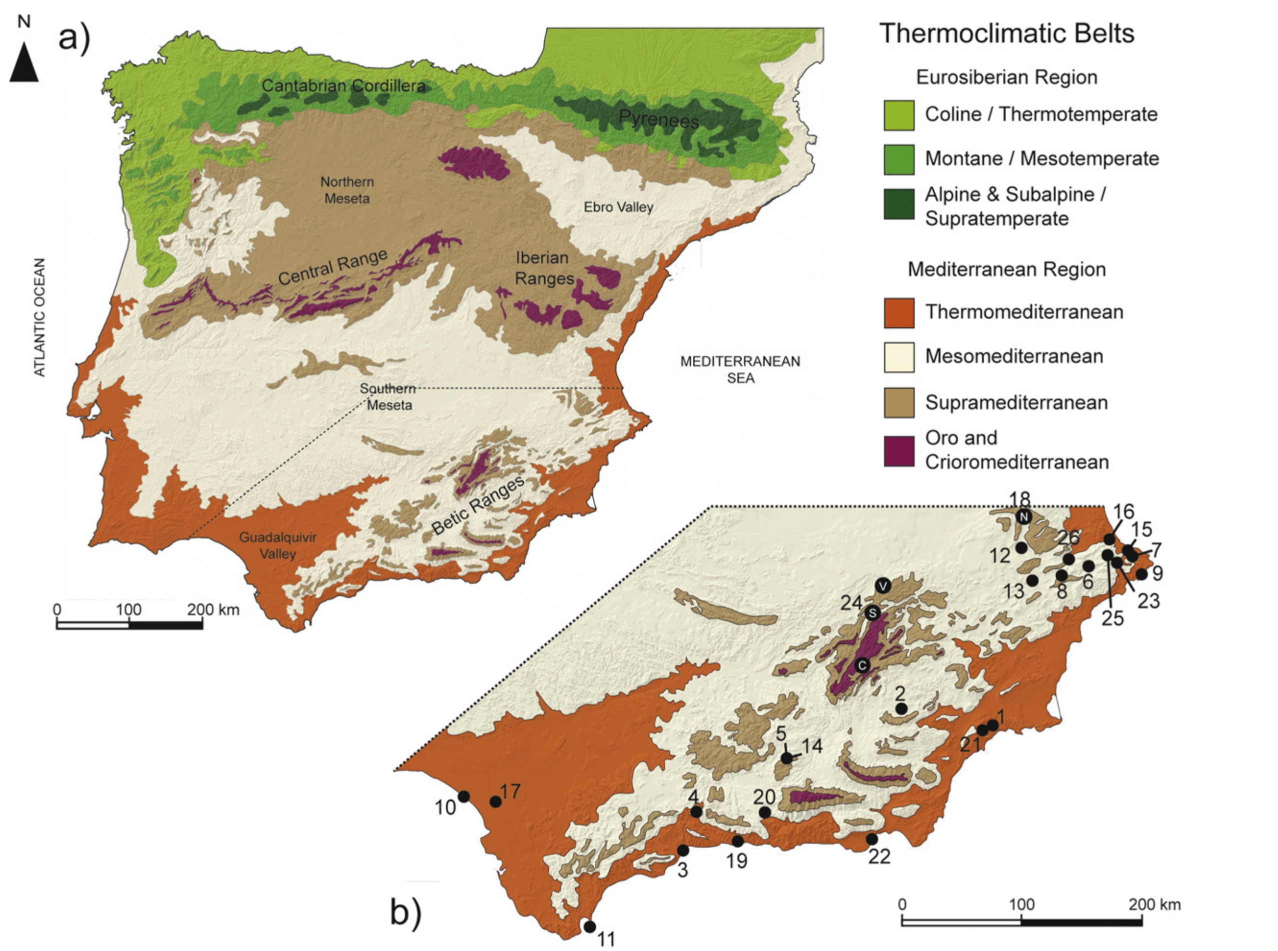

Fig. 1. (a) Iberian thermoclimatic belts, and (b) palaeobotanical records considered in this study. Blank dots refer to Pleistocene sites (Table 1). Lettered dots refer to N) Navarrés (Carrión and Van Geel, 1999), V) Villaverde (Carrión et al., 2001a), S) Siles Lake (Carrión, 2002b), and C) Cañada de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