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ORIGINAL ARTICLE

The native status of *Pinus pinaster* on serpentine soils: charcoal analysis and palaeoenvironmental history in Sierra Bermeja (southern Iberian Peninsula, Spain)

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Abstract
Pinus pinaster (maritime pine), a conifer native to the western Mediterranean, has a broad distribution, occupying a wide variety of habitats. On certain substrata such as ultramafic (ultrabasic) rock, the indigenous nature of this conifer has traditionally been questioned by the scientific community, which has regarded it as an introduction. In Sierra Bermeja, mountains forming the largest ultramafic outcrop in western Europe, the dominant woodland formations on serpentine soils are *P. pinaster* and *Abies pinsapo*. However the variable presence, albeit isolated, of various species of arboreal *Quercus* and the frequent forestry plantation of *P. pinaster* in recent centuries have led to broad-leaved woods being generally considered as the dominant natural communities in this mountain range, so marginalizing the role of these conifers. In an attempt to settle this scientific controversy, we have carried out soil charcoal analyses from seven localities in Sierra Bermeja. The palaeoecological data we have gathered show that *P. pinaster* has a natural status and has been present in this mountain range during a large part of the Holocene before the changes to its natural landscape by human activities. These results are of great importance for the management and conservation of rare serpentine ecosystems.

Keywords Conifers · Fire history · Holocene · Serpentine ecosystem · Soil charcoal · Vegetation history

Introduction

Pinus pinaster Aiton (maritime pine) a conifer native to the western Mediterranean region, present in southwest Europe and northwest Africa (Spain, Portugal, France, Italy, Morocco, Algeria and Tunisia) (Vendramin et al. 1998; Alía and Martín 2003; Costa et al. 2005; Alcalde et al. 2006; Farjon and Filer 2013). It has also been widely planted in many areas, especially in France, Spain, Portugal and Morocco, where it has been intensively used for its timber, resin and pulp for the paper industry (Farjon 2008; Rodríguez et al. 2008; Calama et al. 2010; Wahid and Naydenov 2010). Its widespread planting in the second half of the 20th century has been such that today it can be found in all five continents, having been classified as an exotic invasive species in South America and parts of Africa (Charco et al. 2014).

According to several authors (Baradat and Marpeau 1988; Vendramin et al. 1998; Carrión et al. 2000; Burban and Petit 2003; González-Martínez et al. 2007; Fady 2012; Arambarri et al. 2014), its natural area of distribution is the result of events that took place in the last glacial maximum (LGM) and throughout the Holocene. Today it occupies diverse habitats with different substrata (limestone, granite, schist, marly limestone, peridotite), altitudes and mesoclimates, in both coastal areas on dunes and on inland sand dunes, and on medium altitude mountain ranges (Rosúa et al. 2001; Costa et al. 2005; Castroviejo 2010; López-Sáez et al. 2010; Farjon

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and Filer 2013). As *P. pinaster* is sensitive to intense prolonged freezing, it only flourishes in high mountains in the extreme south of its area of distribution, reaching altitudes of 1,500–1,700 m a.s.l. in the Baetic Cordillera in southeast Spain and 2,000–2,200 m in the Atlas mountains in North Africa (Castroviejo 2010; Farjon and Filer 2013; Charco et al. 2014). Its ecological amplitude enables it to occupy dry ecological niches in which it replaces broad-leaved woodlands (Pérez-Raya et al. 1990; Molero et al. 1992). It also forms mixed woods with *Quercus* or other species of *Pinus* (Blanco et al. 1998; Costa et al. 2005) in which it generally plays a secondary role as part of the natural woodland.

However the native status of *P. pinaster* in natural woodlands is a controversial issue in certain areas, in which it has often been regarded as an introduction. In the Iberian Peninsula, where it has its greatest distribution, *P. pinaster* has traditionally been restricted to areas in which it is known to have been present for a long time, according to ethno-botanical and toponymic (place name) information from a variety of historical documentary sources (Gil 1991; Sánchez-Gómez et al. 1995; Rosúa et al. 2001). Nevertheless, it has often been difficult to distinguish natural woodlands from the planted forests resulting from government-backed conifer afforestation plans in Spain and Portugal. These were so important in this region during the second half of the 20th century (Castroviejo 2010; Valbuena-Carabaña et al. 2010) that estimates suggest that of a total of 1.6 million hectares occupied by *P. pinaster* in the Iberian Peninsula, 0.6 million ha are a direct result of afforestation (Gil 1991; Alía et al. 1995; Ministerio de Medio Ambiente 2002). We should also bear in mind the ease with which planted *Pinus* can naturalize in certain cases (Farjon and Filer 2013), and the fact that in recent decades many of these repopulations have not been managed correctly (Madrigal 1998), factors that have traditionally fed the flames of this controversy.

One of the regions in which this issue is most evident is Sierra Bermeja, an ultramafic mountain range in the Baetic Cordillera, southwest Spain, which supports a large population of gymnosperms divided into two communities, woods of *P. pinaster* and of *Abies pinsapo* Boiss. In the case of *P. pinaster*, it develops on serpentine soils (peridotites) as the dominant woodland tree, although the variable, albeit isolated, presence of various *Quercus* species (*Q. rotundifolia* Lam., *Q. suber* L., *Q. pyrenaica* Willd., *Q. faginea* Lam.) and the frequent planting of *P. pinaster* in forestry management in recent centuries (Gómez-Zotano 2004a) has led to a scientific controversy, as to whether coniferous or broad-leaved woods represent the natural ecosystem in this area (Gómez-Zotano 2004b). The predominance of conifers on serpentine substrates also occurs in other Mediterranean mountain systems such as the Rif (Morocco), the Apennines (Italy) and the Troodos (Cyprus). Sierra Bermeja is therefore not an exception in this sense, nor is the presence of *Quercus* woods on this type of ultramafic substrate. One example is the endemic floristic composition on the igneous geological complex of the Troodos mountains, Cyprus, in which *Q. alnifolia, P. brutia, P. nigra* ssp. *pallasiana* and *Cedrus brevifolia* coexist (Barber and Valles 1995; Delipetrou et al. 2008). However in Sierra Bermeja, *P. pinaster* has traditionally been regarded as introduced (Gil 1991; Pérez-Latorre et al. 2001), and only in recent years have new phytosociological theories been emerging in support of the possible claim to natural (autochthonous) status of these pine woods in the massif (Pérez-Latorre et al. 2001; Valle 2003; Rivas-Martínez 2011). This debate is fuelled by the fact that at high altitudes these woods are replaced by the only ultramafic *Abies* (fir) woodland in the world (Cabezudo et al. 1989; Nieto et al. 1991; Blanco et al. 1998), which in this case is considered an exception, given its status as a floristic relict from the Tertiary (Arista 1995; Pérez-Latorre et al. 1999, 2001; Linares et al. 2009).

Unlike other Mediterranean serpentine ecosystems that have been very well documented and studied, such as in Italy (Ferrari et al. 1993; Chiarucci and De Dominicis 1997), Albania and Greece (Stevanovic et al. 2003), Morocco (Manthei 2012) and Portugal (Sequeira and Pinto da Silva 1991), there are considerable gaps in the research into the vegetation of Sierra Bermeja as a whole, even though it has aroused great interest amongst botanists. The most important studies took place in the last third of the 20th century, including the botanical studies of serpentine endemic plants and their conservation, and plant physiology studies aimed at finding out more about the effects of the heavy metals in the serpentine soils on the flora in Sierra Bermeja, such as those by Asensi et al. (2004, 2011), Brooks et al. (1995), Gavira and Pérez-Latorre (2003), Gómez-Zotano et al. (2014), Pérez-Latorre et al. (2013), Rivas-Goday (1969) and Rufo et al. (2005). In any case, there have been very few palaeoecological research studies, which may in part be due to the lack of sedimentary fossil records found so far in southern Spain, although these have appeared in other more northerly parts of Iberia (López and López 1994). For Sierra Bermeja as a whole, it is only possible to make theoretical approximations regarding the general Palaeobiogeography of the mountains on the basis of pollen studies carried out in western Mediterranean areas in the south of the Iberian Peninsula near Sierra Bermeja (within a radius of 75 km), such as those by Alba-Sánchez et al. (2010) in the Serranía de Ronda, Gutiérrez et al. (1997) in El Aljibe (Strait of Gibraltar region), Combourieu et al. (2002) and Feddi et al. (2011) in the Alborán Sea region, westernmost Mediterranean, Cortés et al. (2008) in the Cueva de Bajondillo, Rodríguez-Ariza (2004) in the Cueva de Toro on the Mediterranean coast of southern Spain, and Carrión et al. (2008) in Gorham's Cave in Gibraltar. The only studies in Sierra Bermeja itself have been the soil charcoal analyses by Olmedo-Cobo et al. (2017), investigating the ecological roles of various trees.

In this paper we present the results of a soil charcoal (pedoanthracological) analysis of the fossil record in seven sites in the Sierra Bermeja ultramafic mountain range, in order to (1) investigate the natural range of *P. pinaster* in the south of the Iberian Peninsula, (2) provide the first well-dated data on *P. pinaster* on serpentine soils in southern Spain, (3) discuss the origin and history of *P. pinaster* on serpentine soils, (4) study the climatic and human influences on the history of *P. pinaster* in S. Bermeja during the Holocene, and (5) provide a historical background for the fires in the S. Bermeja serpentine ecosystems. This type of palaeoecological information is of particular importance for drawing up strategies for the conservation of genetic resources of the different taxa involved (Vendramin et al. 1998), as well as for forestry management in fire-prone areas. The application of the knowledge obtained from the analysis of soil charcoals can play a key role in the safeguarding and conservation at a local and regional scale of the future Sierra Bermeja National Park (Gómez-Zotano et al. 2014, 2016).

Materials and methods

Study site

Sierra Bermeja is located at the western end of the Baetic Cordillera, not far from Marbella on the coast of southern Spain, Iberian Peninsula (Fig. 1). It is a coastal mountain range of medium altitude (1,508 m, Cerro Abanto) which, with an area of 300 km², is one of the largest peridotite outcrops on the planet (Dickey 1970). The unusual geology of this area influences almost all of its abiotic and biotic characteristics, soils, geomorphology, vegetation and fauna, as well as affecting human uses mainly in the form of forestry and of the landscape. Peridotite is an ultramafic (ultrabasic) igneous rock which is very hard and dense. It is composed of ferromagnetic minerals (90% olivine) which, once altered, have the generic name of serpentines (Gómez-Zotano et al. 2014). The natural geochemical processes at work in the weathering of peridotite give rise to serpentine soils that have exceptional limitations in terms of the nutrients that are essential for plants, such as N, P and K, as well as basic cations. They also provide a low proportion of Ca^{2+}/Mg^{2+} (0.84) and a high content of heavy metals with no known biological function (Cr, Ni, Co, Cu). This causes difficulties for plant and animal life and makes the soils prone to drying out and highly susceptible to erosion (Yusta et al. 1985;

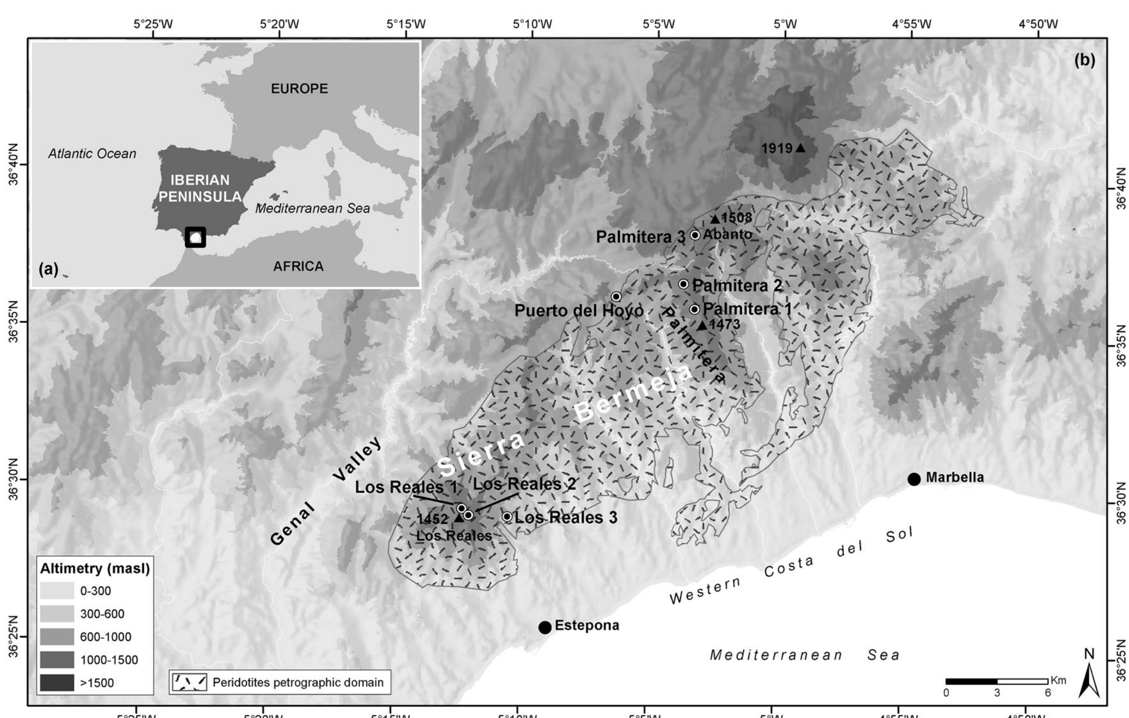

Fig. 1 **a** Location of the study zone in the Iberian Peninsula and in the western Mediterranean; **b** sampling sites on the topographic map of the region

Aguilar et al. 1998; Rufo et al. 2005). The consequences of this special edaphic (soil) environment on the biota can be seen in what is known as "serpentine syndrome", in other words, particular features of the flora on serpentine that are in part exclusively endemic to S. Bermeja (Gómez-Zotano et al. 2014). In addition, the toxicity of the soils excludes most plants from the surrounding Mediterranean vegetation formations, including exotic and/or invasive taxa (Cabezudo et al. 1989; Asensi et al. 2004; Casimiro-Soriguer and Pérez Latorre 2008).

The climate in this coastal mountain range is Mediterranean subhumid to humid (Gómez-Zotano et al. 2016), with an annual average rainfall that varies between 800 mm near the coast and 1,600 mm on the peaks, and probably above 2,000 mm due to hidden precipitation produced by fog, where snow is a frequent sight in winter. The average annual temperature is 12–16 °C and three bio-climatic regions can be distinguished according to altitude: Thermomediterranean up to 800 m, Mesomediterranean (800–1,300 m) and Supramediterranean above 1,300 m (Gómez-Zotano et al. 2016).

The lithological and climatic peculiarities of the area, together with its position on the geographical crossroads between the continents of Europe and Africa, and two large bodies of water, the Atlantic Ocean and the Mediterranean Sea, make it a place of refuge for flora and one of the largest centres of speciation of Mediterranean vegetation in typological, landscape and physiographical terms (Gómez-Zotano 2004a; Alba-Sánchez et al. 2010; Gómez-Zotano et al. 2014). The study area is part of the Baetic Biogeographic Province (Mediterranean Region, Holarctic Kingdom) for plant distribution (chorology) (Rivas-Martínez 1987). Its vegetation is characterized by two main types of woodland, with *P. pinaster* on dry soils on ultramafic rocks, which are replaced at higher altitudes by *Abies pinsapo* (fir) in a unique vegetation type. These woods represent the Querco cocciferae-Pineto acutisquamae S. and Bunio macucae-Abieteto pinsapo S. phytotaxonomic communities (Cabezudo et al. 1989; Nieto et al. 1991; Asensi et al. 2011; Rivas-Martínez 2011).

This area has also seen various phases of human activity which have substantially changed the original plant cover, which is now dominated by commercial forestry for resin. Throughout the 19th and the first half of the 20th century, timber and resin were produced. Since the 1950s, however, these traditional practices have gradually been abandoned, converting S. Bermeja into the hinterland of the highly developed western Costa del Sol (Gómez-Zotano 2004a). Since 2007 there has been a campaign for it to become part of the national parks network of Spain, due to its status as the best example in the country of a serpentine ecosystem (Gómez-Zotano et al. 2014, 2016).

Soil sampling

Seven pedological excavations were carried out at several sites in Sierra Bermeja, all of them in serpentine soils of leptosol type and to a lesser extent regosol type, and of varying development and depth, formed on top of peridotite bedrock (Fig. 1; Table 1). The sampling points were chosen on the basis on ecological guidelines established from the analysis of the current vegetation and species distribution modelling (SDM). The existence of different types of woodland on the summits of the two main mountainous areas of S. Bermeja,

Table 1 Geographical data about the study area and characteristics of the sampling sites

Sites	Geographical coordinates	Altitude (m.a.s.l.)	Geoecological environment	Substrata (soil type)	Depth of the survey (cm)	Sampling levels
Palmitera 1	36°35′53″N 05°03′21″W	1,360	Scrub on the bottom of an endorheic basin	Peridotite (regosol)	80	5
Palmitera 2	36°36′42″N 05°03′48″W	1,202	Pine wood on slope	Peridotite (leptosol)	90	4
Palmitera 3	36°38′03″N 05°03′32″W	1,256	Pine wood with firs on slope	Peridotite (leptosol)	36	2
Los Reales 1	36°29′24″N 05°12′23″W	1,165	Fir wood, pine wood on slope	Peridotite (leptosol)	103	5
Los Reales 2	36°29′13″N 05°12′06″W	1,247	Fir wood on slope	Peridotite (leptosol)	52	4
Los Reales 3	36°29′10″N 05°10′36″W	638	Scrub with pines on slope	Peridotite (leptosol)	29	2
Puerto del Hoyo	36°36′14″N 05°06′28″W	938	Pine wood on slope	Peridotite (leptosol)	137	8

with fir in Los Reales and pine in the Palmitera massif, is complex to understand since the environmental conditions in both areas are identical. For this reason, and taking into account that the soil charcoal analysis offers palaeoecological information, we tried sampling both locations first at Los Reales 1, 2 and 3 and then at Palmitera 1, 2 and 3, to try to find evidence from the past that would help us understand the current vegetation distribution. The comparison of the results obtained is relevant, given the existence of identical ecological conditions of altitude, climate, substrate, soil, slope etc. We also chose the sampling site at Puerto del Hoyo for its interesting intermediate situation as a link between the two nuclei. In each of the samples taken we identified between two and eight sampling levels depending on the soil depth (30 in total), which were partially delimited by the description of the soil horizons; the sampling level ranged between a minimum thickness of 7–10 cm and a maximum of approximately 25 cm. The deepest horizons were subdivided into various sampling levels. The taking of soil samples at each of these levels was done using the usual soil charcoal methods established by Thinon (1992), Carcaillet and Thinon (1996) and Talon et al. (1998). This resulted in the collection of samples of between 2.5 and 8 kg of soil per level, which were processed in the laboratory by water sieving, using mesh sizes of 5, 2 and 0.8 mm.

When the mineral fraction collected in the mesh after the sieving process had dried, the charcoal content was separated manually with the help of a stereo microscope, after calculating the absolute amount of charcoal in mg of charcoal fragments < 5 mm per kg of mineral residue, for each sampling level. For identification purposes, each fragment of charcoal was split with a scalpel, again with the aid of a stereo microscope, in order to obtain three anatomical sections of the wood (transversal, radial and tangential) in which to observe the detailed characteristics necessary for their taxonomic identification. These sections were studied with great care using an incident light microscope at magnifications 50×, 100×, 200× and 500× with differential interference contrast. In this identification phase, we identified all the samples from each sampling level up to a maximum of 200 fragments from the 5 mm mesh, 200 fragments from the 2 mm mesh and 50 fragments from the 0.8 mm mesh; these limits for charcoal analysis were established due to the large numbers of samples collected at most of the sampling sites. The taxonomic identification of the charcoal was done using wood anatomy keys (Schweingruber 1990a, b; Vernet et al. 2001), and by comparing the pieces with the reference specimens in the charcoal collection at the Physical Geography Laboratory, University of Granada. We then calculated the relative amount in weight (mg charcoal/kg original sample) of the taxa we identified.

As regards *P. pinaster* identifications, in numerous charcoal identification works it is included within the taxonomic group of *P. pinaster, P. pinea* and *P. halepensis*, without reaching the level of species. Nevertheless, *P. pinaster* is well differentiated at this level in most anatomy guides of woods and charcoals (Greguss 1955; Jacquiot 1955; Schweingruber 1990a; Vernet et al. 2001; García et al. 2003) and there are specific publications focusing on its identification and environmental history (Figueiral 1995; Alcalde et al. 2004) which provide criteria for its identification (ESM). As a distinctive element of the transversal section, the large size of the opening of the resin canal of *P. pinaster* is cited by Jacquiot (1955) and Vernet et al. (2001). Of the three species of *Pinus* mentioned, *P. pinaster* has the largest resin canal opening, measuring mostly between 200 and 300 µm, while *P. pinea* and *P. halepensis* have narrower canals, less than 200 µm. Another differentiating characteristic of *P. pinaster* can be observed in radial section, in the appearance of the walls of the transverse tracheids. In most of the referenced sources, *P. pinaster* has wide, clearly dentate (toothed) walls (Jacquiot 1955; Vernet et al. 2001). According to García et al. (2003) and Alcalde et al. (2004) the walls have very pronounced teeth, which in some cases reach the centre of the lumen, as can also be seen in the figures presented by Jacquiot (picture LXII, Ra × 220, 1955). So, based on these two specific characteristics (the size of the opening of the resin canals and the appearance of the walls of the transverse tracheids in radial section), the *Pinus* samples found in the study area can be identified to species level as *P. pinaster*. A third identifying characteristic of *P. pinaster* is that it can have as many as five or six cross-field pits in the radial section, while the other two species have a maximum of four; however, this distinguishing feature was not detected in the *Pinus* samples found in Sierra Bermeja.

Finally, we dated a total of 20 samples of charcoal (19 from *P. pinaster* and 1 from *Quercus* sp.) using ^{14}C AMS (Accelerator Mass Spectrometry) in the Poznań Radiocarbon Laboratory, Poland. The results were calibrated with Oxcal 4.2 (Bronk Ramsay 2009) and the IntCal 09.14c database (Reimer et al. 2013) with a standard deviation of 2σ (95% probability). The chronological data obtained, together with the information previously published by Olmedo-Cobo et al. (2017) referring to dates of five samples of *Quercus* sp. and two of *Abies* sp. from Palmitera 1, were used to contextualize certain issues of the discussion about the ecological role of *P. pinaster* in Sierra Bermeja.

Results

Charcoal concentration analysis

The soil analysis confirmed the existence of charcoal in all the samples we collected. There was a highly variable number of charcoal fragments in 23 of the 30 differentiated sampled levels, and in general those closest to the surface had the highest charcoal values (Table 2). The largest amount was found in the Palmitera 1 material, 137,379.3 mg/kg. The nearby sites of Palmitera 3 and Palmitera 2 totalled 7,831.6 and 7,066.3 mg/kg respectively, while the values in Los Reales 1 and 2 were around 2,000 mg/kg. The lowest absolute levels were found in the Puerto del Hoyo and Los Reales 3 sites, with total values of 413.7 and 197.1 mg/kg respectively. The highest charcoal values by sampling level were found at level II of Palmitera 1 (8–21 cm depth), with a value of 112,086.8 mg/kg (81.5% of the total), and level IV (33–52 cm) from the same site, with 10,825 mg/kg (7.8%). As a way of illustrating the large amount of charcoal in the fossil record in this locality, we should emphasize that even the sampling level with the lowest value (level V, 4,093.5 mg/kg) had a higher value than that of any of the other sampling levels in the other sites, with the exception of levels I of Palmitera 2 (5,997.3 mg/kg) and Palmitera 3 (6,858.8 mg/kg), whose charcoal concentrations represented 85% and 87% respectively of the total values for each site. The maximum values by sampling level in Los Reales 1 and 2 were those from level I (1,219.4 mg/kg, 62%) and level II (993.3 mg/kg, 47%). In Puerto del Hoyo most of the charcoal was found in level I (406.7 mg/kg, 98.3%), while all the charcoal in Los Reales 3 was found in the surface level (197.1 mg/kg). Although one would expect to observe a drop in the values from the deepest levels close to the rocky substrate, the fact that we found four consecutive levels without any charcoal (mesh > 0.8 mm) at the Puerto del Hoyo site is remarkable.

Taxa identifications

We analysed a total of 3,107 charcoal fragments, of which 1,951 turned out to be valid identifications (62.8%), while 1,156 fragments (37.2%) were considered indeterminate (Table 3). Among the identified samples we found two tree taxa, namely *P. pinaster* (720 out of 1,951) and *Abies* sp. (141/1,951), which together represented 44.1% of the total number of positive identifications, and a total of five taxonomic groups identified at family level which were separated into two distinct categories: the first was the

Table 2 Charcoal values in mg/kg soil sample, by sampling level

Levels	Sites						
	Palmitera 1	Palmitera 2	Palmitera 3	Los Reales 1	Los Reales 2	Los Reales 3	Puerto del Hoyo
I	5,717.9	5,997.3	6,858.8	1,219.4	735.9	197.1	406.7
II	112,086.8	898.4	972.8	441	993.3	0	1.6
III	4,656.1	57.1	–	304.6	217.9	–	4.9
IV	10,825	113.5	–	0	168.1	–	0.5
V	4,093.5	–	–	–	–	–	0
VI	–	–	–	–	–	–	0
VII	–	–	–	–	–	–	0
VIII	–	–	–	–	–	–	0
Total	137,379.3	7,066.3	7,831.6	1,965	2,115.2	197.1	413.7

"–" means that the corresponding level does not exist at the sampling point

The sampling points have between 2 and up to a maximum of 8 sampling levels. When "0" appears, the sampling level exists, but no charcoal has been found in it, and therefore the charcoal value is 0

Table 3 Number of samples, *n*, corresponding to the different taxa and groups identified

Sites	Identified samples, *n*							Total
	P. pinaster	*Abies* sp.	Gymnosperms	*Quercus* sp.	Angiosperms	Shrubs group	Indeterm.	
Palmitera 1	118	23	26	525	14	17	411	1,134
Palmitera 2	182	0	28	41	31	70	188	540
Palmitera 3	130	0	22	4	19	34	103	312
Los Reales 1	153	20	57	0	24	3	129	386
Los Reales 2	52	98	6	0	65	15	154	390
Los Reales 3	6	0	1	0	24	15	86	132
Puerto del Hoyo	79	0	26	7	16	0	85	213
Total	720	141	166	577	193	154	1,156	3,107

group of *Quercus* sp. (Fagaceae) samples, whose significance reached 29.5% of the identifications (577/1,951), but it was not possible to distinguish between shrubby taxa (*Q. coccifera* type) and trees (*Q. rotundifolia, Q. suber, Q. pyrenaica, Q. faginea* type). The second category groups together various shrubby taxa belonging to the Cistaceae, Fabaceae, Ericaceae and Berberidaceae, which only represent 7.9% (154/1,951). We also partially identified other charcoal which could be grouped together in Gymnosperm and Angiosperm categories, although higher levels of identification could not be achieved. These categories made up 8.5% and 9.9% respectively of the total number of identified samples (166/1,951 and 193/1,951).

The greatest taxonomic diversity was found in the Palmitera 1 material in which we found both arboreal elements, *P. pinaster* and *Abies* sp., and also all the taxonomic groups under consideration, indeterminate gymnosperm, *Quercus* sp., indeterminate angiosperm and shrubs group. By contrast, the samples that produced the least taxonomic diversity were Los Reales 3 (*P. pinaster*, indeterminate gymnosperm, indeterminate angiosperm and shrubs group) and Puerto del Hoyo (*P. pinaster*, indeterminate gymnosperm, *Quercus* sp. and indeterminate angiosperm).

As regards the taxonomic values, *P. pinaster* is dominant in 12 of the 23 sampling levels in which we found charcoal, with specific values of over 100 mg/kg in levels I of Palmitera 2 and Palmitera 3, and an exceptionally high score of 1,708.3 mg/kg in level II of Palmitera 1 (Fig. 2). *Abies* sp. only shows one specific outstanding value in level II of Palmitera 1 (226.6 mg/kg). Together with these trees, the other large differentiated group, *Quercus* sp., only showed outstanding values in Palmitera 1 as a whole, with values ranging between 83.6 and 163.6 mg/kg in the different sampling levels, although once again level II stood out above the others, reaching a value of 520 mg/kg. The taxa grouped as shrubs were usually less important in the material. The only noteworthy charcoal value was in sampling level I of Palmitera 2, with 41.4 mg/kg. As regards the indeterminate samples of Gymnosperms and Angiosperms, they had maximum values of 123.3 mg/kg and 60.8 mg/kg respectively, once again in level II of Palmitera 1.

Finally, in all the samples we found a considerable number of charcoals which proved indeterminate. Most of these were vitrified samples in which it was impossible to recognise any anatomical characteristics. These fragments were the most numerous both in number and in charcoal content in sampling levels I of Palmitera 1, II and IV of Palmitera 2, I of Los Reales 1, II, III and IV of Los Reales 2, I of Los Reales 3 and I, II, III and IV of Puerto del Hoyo. The greatest amount of indeterminate charcoal per sampling level was found in level II of Palmitera 1, with 514.1 mg/kg.

Dating the charcoal

Nineteen samples of *P. pinaster* were dated from a total of 16 out of 23 samples in which charcoal was found. These produced ages ranging between 8,180 years cal BP and the present (Table 4). Ten of the samples proved to be thousands of years old (> 1,800 years cal BP), and these were found in three of the seven sampled sites. The earliest dates were from Palmitera 1, with two samples that cover a large part of the first half of the Holocene, 8,180–5,604 years cal BP. Four of the fragments dated from Los Reales 1 were also of considerable age, although they fall within a much smaller time period, 7,244–6,793 years cal BP. The next four dates are more recent and belong to a wider time span than the previous ones, from the Los Reales 2 material, 3,156–1,827 years cal BP. The remaining nine samples were fairly recent, less than 300 years old, and were present in six of the seven sites (all except Los Reales 2), as well as the only sample of *Quercus* sp. dated from Palmitera 2.

Discussion

The fossil charcoal record shows that *P. pinaster* is native on ultramafic substrata

The results of this research clearly demonstrate, and for the first time, that *P. pinaster* is native on the ultramafic substrata of Sierra Bermeja. This finding is in line with other archaeobotanical studies that have shown the presence and importance of conifers in the natural landscape of the Iberian Peninsula during the Quaternary, in both the Mediterranean and the Atlantic watersheds (Mateus 1989; Carrión et al. 2000; Franco-Múgica et al. 2005). In the specific case of *P. pinaster*, there are numerous fossil charcoal and pollen records which support its status as growing naturally within its current distribution area in the Iberian Peninsula. *Pinus* pollen that can be attributed to *P. pinaster* from the recent Quaternary and the Holocene (the last 115,000 years) has been found in various parts of Spain and Portugal by Aira et al. (1989), Carrión et al. (2000), Díaz et al. (1990), Dupré (1988), Figueiral (1993, 1995) Figueiral and Terral (2002), Gómez-Orellana (2002), Janssen and Woldringh (1981), López-Saéz et al. et al. (2010), Ramil-Rego (1992), Teixeira (1945) and Teixeira and Pais (1976).

However, pollen identification does not always reach the level of species and sometimes it is even difficult to differentiate between several genera within the same family (Carrión 2002). In the case of *P. pinaster*, failures occur in the identification criteria for some pollen grains, making it necessary to do statistical analyses of the pollen dimensions. However, these analyses do not ensure that all grains correspond to the predominant taxon resulting from the mathematical

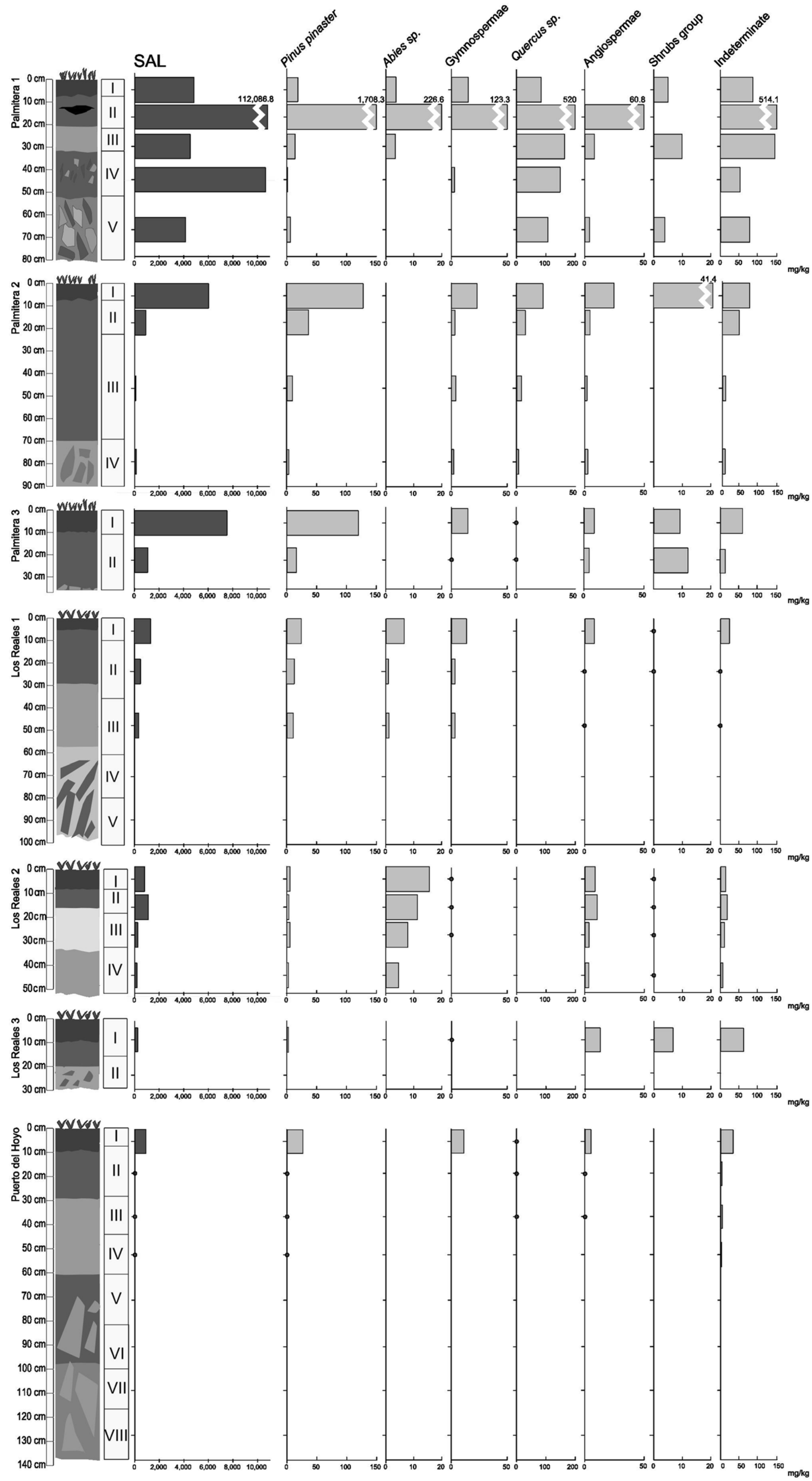

Fig. 2 Charcoal content, in mg charcoal/kg soil sample, for the taxa identified in the levels analysed. SAL is sum of charcoal values (content) by level

Table 4 ^{14}C-datings of *P. pinaster* by sampling level

Sites	Layer (depth in cm)	Radio-carbon dating of *P. pinaster*		
		^{14}C-age (years BP)	Calibrated age (years BP, 95%)	Lab.code
Palmitera 1	I (0–7)	70 ± 30	260–226	Poz-78849
	IV (33–52)	4,965 ± 35	5,854–5,604	Poz-78854
	V (53–80)	7,300 ± 40	8,180–8,020	Poz-78857
Palmitera 2	I (0–8)	162.26 ± 0.44 pMC modern	–	Poz-78887
	II (9–23)	120 ± 30	272–211	Poz-78867
	III (24–68)	154.35 ± 0.38 pMC modern	–	Poz-78868
Palmitera 3	I (0–11)	148.11 ± 0.41 pMC modern	–	Poz-78882
	II (12–36)	155.84 ± 0.43 pMC modern	–	Poz-78883
Los Reales 1	I (0–9)	110 ± 30	270–212	Poz-78860
	II (10–36)	6,200 ± 40	7,244–6,994	Poz-78861
	III (37–61)	6,170 ± 40	7,170–6,949	Poz-78862
		6,070 ± 40	7,151–6,793	Poz-78886
		6,140 ± 40	7,164–6,930	Poz-83916
Los Reales 2	I (0–7)	2,895 ± 30	3,156–2,947	Poz-83915
	III (18–33)	2,405 ± 30	2,682–2,349	Poz-82528
	IV (34–52)	1,955 ± 30	1,987–1,827	Poz-82524
		2,005 ± 30	2,038–1,883	Poz-82526
Los Reales 3	I (0–16)	210 ± 30	305–present	Poz-78863
Puerto del Hoyo	I (0–8)	101.42 ± 0.34 pMC modern	–	Poz-78864

procedure (Carrión et al. 2000). Another frequent problem of pollen analyses is that the geographical evidence obtained is generally on a regional scale and not predominantly local, making it difficult to establish the catchment area of a pollen spectrum (Fuentes et al. 2007; Oxman 2011). This means that the pollen sequences probably do not accurately reflect the spatial distribution of the vegetation in the Quaternary (López-Sáez et al. 2010). The charcoal evidence, by contrast, guarantees the presence of the taxon at a particular place and, unlike the pollen analyses, allows us to reconstruct the history of the burnt woody vegetation with great spatial precision (Talon et al. 1998; Cunill et al. 2012, 2015). This means that the charcoal records show the presence of *P. pinaster* in the Iberian Peninsula with chronologies of 33,000 years BP in Portugal (Figueiral 1995), while in Spain, ages of 4,360 ± 40 BP were detected in the Duero basin (Franco-Múgica et al. 2005; Hernández et al. 2011; Morales-Molino et al. 2011), 2,387 ± 32 BP on the southern slopes of Sierra de Gredos (López-Sáez et al. 2010), 2,235 ± 40 BP at the archaeological site of Los Castillejos (Rubiales et al. 2009) and between the Copper Age and 725 ± 40 BP at several sites in southeastern Spain (Rodríguez-Ariza 2000; Alcalde et al. 2004). Outside the Iberian Peninsula, Baradat and Marpeau (1988) and Paquereau (1964) reported the existence of *P. pinaster*-type pollen in the Medoc (France) and in the Rif region of Morocco, with respective ages of 7,000 and 8,000 BP, while Carcaillet et al. (1997) dated *P. pinaster* charcoal in Corsica to 915 ± 40 BP.

This soil charcoal evidence together with the pollen data allows us to view the Iberian Peninsula as a vast territory in which, since at least the last phase of the Quaternary and throughout the Holocene up to the present, *P. pinaster* has demonstrated great tenacity and a capacity to occupy various habitats, from woodland to serial vegetation stages, based on its theoretical glacial refugia from which it spread. In the case of Sierra Bermeja, we had so far only been able to estimate the native status of the species on the basis of the pollen records from Cueva de Bajondillo on the Mediterranean coast of southern Spain (Cortés et al. 2008) and Gorham´s Cave, Gibraltar (Carrión et al. 2008), sites situated respectively 70 and 40 km away from S. Bermeja. These records suggest that *P. pinaster* has been naturally present in the area for at least 100,000 years, with a first period of discontinuity up to 20,000 years ago, and a second phase of continuous presence right through until today. In both cases the environmental conditions, notably different from those in this area today for reasons connected with local soils and regional climate, would have permitted, as shown in the corresponding pollen diagrams, phases of alternation between vegetation with arboreal *Quercus* and with *Pinus*. Such a dynamic seems unlikely to have been possible in this mountain range, due to the limitations imposed on *Quercus* by the soil derived from peridotite. This hypothesis coincides with the data obtained from other pollen analyses in the Baetic Cordillera, which suggest that *P.*

pinaster played an important role in the Holocene landscapes there (Carrión 2002; Carrión et al. 2004, 2007).

With the radiocarbon dates for *P. pinaster* obtained in our research we can undoubtedly broaden the area of its natural distribution in the Iberian Peninsula to include the whole of the ultramafic mountain range of Sierra Bermeja. The location of the sampled sites covers the whole of the S. Bermeja peridotite area from the western end at Los Reales to the east at Palmitera, which includes sites at different altitudes (interval 638-1,360 m), different topographical conditions and natural environments, above all woods and scrub, vegetation types which are dominant in this massif.

This is the first contribution of this kind for *P. pinaster* in S. Bermeja, and also corroborates the fact that this mountain range is the southernmost location in Europe in which the native status of maritime pine has been confirmed, at least at medium and high altitudes, over 600 m. This takes on greater significance when we consider, based on the dating results obtained, that *P. pinaster* has existed there continuously throughout practically all the Holocene from 8,180–1,827 years cal BP until the present, as demonstrated by the recent dates, the historical documentary sources (Gómez-Zotano 2004a) and its presence there today. We can therefore rule out an origin of *P. pinaster* by human introduction in S. Bermeja, as the chronology of the fossil charcoal record predates any afforestation work carried out in this area. These results also confirm that this conifer belongs to a select group of plants that grow on the rather toxic serpentine soils that have developed on top of ultramafic substrata (Liétor et al. 2002).

Another possible explanation for the dates which we obtained is that S. Bermeja might have been a refuge for *P. pinaster* during the last glacial maximum. This ecological role has already previously been established for other areas of the Baetic and Iberian mountain systems, which have been considered explicit glacial refugia for *P. pinaster* and therefore as the sources for its postglacial spread (Alía 1989; González-Martínez et al. 2007). In these types of unconnected southerly refugia, the genomes diverged without large geographical displacement due to colder and less cold episodes in the Ice Age (Hewitt 2001). In fact, several analyses of isoenzymatic markers of *P. pinaster* from nuclei considered relicts in the south of the Iberian Peninsula and North Africa have shown the existence of high genetic differentiation of the species between these regions (Salvador et al. 2000; Gómez et al. 2001, 2005; González-Martínez et al. 2001, 2007; Vieira et al. 2009; Wahid and Naydenov 2010). Therefore, there is great genetic similarity between separate populations in the Baetic Cordillera (González-Martínez et al. 2007), which, in turn, are genetically distant from their other Iberian populations, such as the *P. pinaster* of S. Bermeja, which have the highest known genetic variability (Salvador et al. 1997). Finally, Burban and Petit (2003), using the analysis of maternally inherited and paternally inherited markers from mitochondrial DNA and chloroplast DNA, pointed out that there could also have been dispersion of *P. pinaster* across the Strait of Gibraltar from Morocco to the Iberian Peninsula, something which in any case does not inhibit the possibility of southern Iberian refugia.

The role of *P. pinaster* in Sierra Bermeja during the Holocene

The analysis of the fossil charcoals allows us to argue that *Pinus* was been part of the natural woodland in Sierra Bermeja throughout the Holocene together with the Tertiary relict fir *A. pinsapo*, based on the number of *P. pinaster* samples found and their chronology. We can therefore discard the long-standing phytosociological theory, according to which the natural (potential) vegetation on ultramafic soils only included Fagaceae with *Q. rotundifolia, Q. pyrenaica, Q. suber* and *Q. faginea*. The theory rejected the possibility that *P. pinaster* could have been part of the dominant vegetation during the Holocene in this area, or at most assigned it to an ecological role as a substitute for these broad-leaved woods after the original environmental conditions had changed (Rivas-Martínez 1987). In fact, the data we have collected could corroborate the phytosociological hypotheses that argue that coniferous woods both of *P. pinaster* and *A. pinsapo* are mature and natural parts of the vegetation on the Baetic peridotite region and do not only represent regressive phases with secondary pine woods following loss of oak woods (Ceballos and Vicioso 1933; Cabezudo et al. 1989; Nieto et al. 1991; Blanco et al. 1998; Pérez-Latorre et al. 1999, 2001; Valle 2003). In this theoretical context, *A. pinsapo* would be an exception, given its generally accepted status as a relict from the Tertiary (Arista 1995; Pérez-Latorre et al. 1999, 2001; Linares et al. 2009). It grows in woods which had managed to survive the post-glacial decline suffered by the rest of the southernmost Mediterranean fir, surviving in damper mountain areas at medium altitude (García and de Palacios 2007; Linares 2011; Guzmán et al. 2012), such as Sierra Bermeja.

This proven ecological role of conifers in S. Bermeja does not mean that there were no *Quercus* woods there in the early and mid Holocene despite the fact that the available *Quercus* chronological data collected by Olmedo-Cobo et al. (2017) (5 fragments from Palmitera 1) and the only sample of *Quercus* sp. dated in this research (Palmitera 2) are all fairly recent. Although any assertions in this direction must be made with great caution, due to the large number of undated *Quercus* sp. samples found in certain locations, is possible that the role of *Quercus* sp. in the woodlands of S. Bermeja among the dominant presence of *P. pinaster* must be reconsidered, as Olmedo-Cobo et al. (2017) have already pointed out from data obtained in Palmitera 1. In addition, the large number of unidentified charcoal fragments means that we must be careful before making any assertions that go beyond what the dating results have allowed us to establish.

The importance of fire in the natural landscape of Sierra Bermeja

The high charcoal values from some of the sampled sites in S. Bermeja, for example > 7,000 mg/kg in Palmitera 2 and 3 and > 137,000 mg/kg in Palmitera 1, demonstrate the importance of fires in the configuration of the natural landscape during practically all of the Holocene. This remains true today, as it has been estimated that fires recur every 14.5 years in this mountain range (Vega-Hidalgo 1999). This is a common factor in the development of vegetation in Mediterranean environmental conditions, as shown by research in various Mediterranean regions (Ajbilou et al. 2006; Gil-Romera et al. 2008; Mouillot et al. 2003; Tinner at al. 2016). Fire is also a determining factor in the creation of mountain landscapes in the north and centre of the Iberian Peninsula (Ejarque et al. 2010; Bal et al. 2011; Cunill et al. 2013; Pérez-Sanz et al. 2013; Pérez-Obiol et al. 2016; Álvarez et al. 2017), where the climate is much less favourable to it. In the case of Palmitera 1 for example, in topographic terms this site is at the bottom of a small closed (endorheic) basin with an unusually deep soil due to the accumulation of sediments there, which may explain the large volume of charcoal that we found. The charcoal accumulation zone in level II of this site may also be related to the frequency of fires in recent years, since all the dating results obtained for *Quercus* sp., the dominant taxon at this level, were less than 150 years old, pMC (percent modern carbon). In any case, the high charcoal values for level II and for the site as a whole have never been seen anywhere else. In mountain or mid-mountain environments in the Pyrenees, the Alps or in central Europe, where most of these kinds of soil charcoal analyses have been done, the specific charcoal concentration by level rarely exceeds 2,000 mg/kg (Touflan and Talon 2008; Bal et al. 2010; Cunill et al. 2015; Novák et al. 2017). Higher values have only been found in northern Germany, around 9,000 mg/kg per level (Robin et al. 2013) and in the centre of the Iberian Peninsula, around 23,000 mg/kg (Álvarez et al. 2017). In Sierra Bermeja as a whole, fire is even more important as a modeller of the landscape due to the toxicity of the serpentine soils and their limited development, which together with the frequent steep slopes, complicates post-fire recolonisation and regeneration of both the tree cover, the woody shrub layer and to a lesser extent grasslands.

The dates of the *P. pinaster* samples show that there were fires between 8,120 and 6,793 years cal BP. Although earlier fires are not known, it is possible that fires since 8,120 years cal BP could be associated with an increase of the prehistoric population in the coastal area at the foot of Sierra Bermeja during the Neolithic and Chalcolithic (Posac 1973; Ferrando de la Lama 1988; Navarro et al. 1993; Fernández et al. 2007). Although there are almost no data about earlier Palaeolithic settlements (Fernández et al. 2000), palaeoenvironmental research suggests that hunter-gatherer societies had little impact on natural vegetational cycles, including fires, especially given that the environmental conditions at that time were less favourable to fire than at present. The signs of fires from 8,120 years cal BP may also have been influenced by the increasingly drier and warmer climate in the western Mediterranean over the period 12,000–10,000 years cal BP, which culminated in a period of maximum high temperatures, which was probably also very dry, around 10,000–9,000 years cal BP in the Alborán Sea area, as reported by Cacho et al. (2001). Other signs of fires detected throughout the mid to late Holocene occurred around 5,854–5,604 years cal BP (one date from the Palmitera 1 samples) and in the period between 3,156 and 1,827 years cal BP, in five samples collected from Los Reales 2. Finally, according to various documentary sources (Gómez-Zotano 2004a, b; Vega-Hidalgo 1999), in recent centuries, in particular since the 18th c., there have been frequent fires, as also confirmed by the fairly recent dates of *P. pinaster* (nine samples less than 300 years old) obtained at all the sites except for Los Reales 2.

Conclusions

Soil charcoal analysis has once more proved to be a useful tool for obtaining information on local ecology, particularly when it involves a reconstruction of vegetation history. From the analysis of the soil charcoal found at seven sites in Sierra Bermeja we have obtained valuable new data about the palaeoecological history of *P. pinaster* in southwest Europe. In particular, our results demonstrate its natural status in the western Baetic Cordillera, and what is more important, its natural presence in the peridotite massif of Sierra Bermeja, an area where it has traditionally been regarded as an introduced taxon.

We also corroborated the ancient presence of *P. pinaster* in this area, the oldest charcoal sample of *P. pinaster* having a calibrated age of 8,180-8,020 years, so allowing us to solve the scientific controversy regarding its ecological role on soils derived from peridotite. Based on the undeniably native character of *P. pinaster* in Sierra Bermeja, and accepting that *A. pinsapo* is a Tertiary relict there, our results confirm that conifers were part of the natural vegetation on the ultramafic rocks in this area throughout the Holocene. This allows us first to validate the phytosociological hypotheses that defended the natural status of the conifers *P. pinaster* and *A. pinsapo* as the most evolved vegetation phases on the Baetic peridotite substrata, and secondly to discard the long-standing phytosociological theory according to which the natural vegetation on ultramafic soils consisted of members of the Fagaceae. Our hypothesis is reinforced by the absence of ancient soil charcoal evidence of *Quercus* sp. in the massif in previous analyses and in our own research. However, there are still many uncertainties about the role of *Quercus* sp. in the past, given that the only mature *Quercus* sp. woods there today are in very local enclaves with particular soil conditions, where they represent relict communities. The chronologies we obtained also suggest that Sierra Bermeja may have acted as an isolated refugium for *P. pinaster* during the last glacial maximum, from which it could have migrated north and east after the glacial maximum, in the Late Glacial period and Holocene.

Finally, the high charcoal values found in some of the sites in Sierra Bermeja demonstrate the important role of fire in the landscape dynamics of this area during the Holocene. Fire still has an important role there today as can be seen from various documentary sources, and must therefore be regarded as a very important ecological factor. The evidence from these documentary sources must be combined with the palaeoecological information available about fire cycles when drawing up strategies for the conservation of genetic resources of the trees in these mountains, and for good management in terms of the decisions that must be taken to ensure the restoration of rare serpentine ecosystems.

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