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The history of *Abies pinsapo* during the Holocene in southern Spain, based on pedoanthracological analysis

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Abstract
The aim of this research is to reconstruct the ancient distribution area of *Abies pinsapo* Boiss. (Spanish fir) in the Serranía de Ronda region, southern Spain, during the Holocene. The main method was pedoanthracological analysis, the study of non-archaeological charcoal found in natural soils. In this research a total of 37 soil excavations were done in several mountain ranges with potentially favourable places for firs to have grown in the past. Specific sites and places such as hillsides, endorheic basins (with no outflow), sinkholes, summits and mountain passes were selected on the basis of evidence from a range of different sources including ancient documents, pollen studies and species distribution models. The soil samples collected from these sites were prepared in the laboratory and the charcoal was identified and radiocarbon dated. Statistical and cartographic analyses were also done. The study revealed evidence of past populations of *Abies* sp. in places where it is no longer found today. A total of 47 different chronologies were obtained from these sites with ages ranging between 9,931 cal BP and 78 cal BP. In addition, the wide variations in the charcoal values enabled us to make an initial estimate of the importance of ancient forest fires in different places in the Serranía de Ronda. When this information has been considered with all the other available data sources, it will be an essential resource for the efficient management of relict fir woods in southern Spain.

Keywords Palaeoecology · Soil charcoal · Abies · Distribution area · Holocene · Iberian Peninsula

Introduction

Understanding how and why biological organisms are distributed in space is a central principle of biogeographical research (Miller 2010), and the analysis of relations between taxa and their environment is a priority issue in any ecological discipline (Guisan and Zimmermann 2000). Precise information about the distribution of existing taxa is therefore fundamental when it comes to assessing regional biodiversity. However, in many cases the existing data are insufficient (Choe et al. 2016) and as a result the real state of many endangered plants is far from certain because the locations and the state of conservation of all the existing populations are unknown (McCune 2016).

One example is *Abies pinsapo* Boiss. (Spanish fir), one of the most unusual tree species in Spain, with enormous ecological value, and the only strictly Mediterranean fir that grows naturally in our study area (Linares et al. 2010a,b). From a palaeobiogeographical point of view, the most widely accepted theories state that it originated in a common ancestor that formed extensive fir forests in the western Mediterranean during the Cenozoic, as is demonstrated by fossil evidence (Linares 2011). Its wide extension across southern Europe during the Pleistocene was greatly influenced by the recurrent oscillations in the climate, which caused continuous advances and retreats of the glaciers, which then led to the contraction and fragmentation of the distribution areas of the taxa which were best adapted to temperate climates (van der Veken et al. 2007; Alba-Sánchez and López-Sáez 2013). For much of this period, the north and centre of the Iberian Peninsula was covered by ice and snow, but this did not prevent the massive expansion of firs and other mountain conifers in forests south of the ice line that occupied a large part of the mountain ranges in the south

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of the peninsula and also in the highest, coldest and wettest peaks in north Africa. When the last glacial period came to an end about 15,000 years ago and temperatures began to rise, these isolated *Abies* forests began to move to higher and damper mountain areas such as the Serranía de Ronda in southern Spain (Taberlet and Cheddadi 2002; Carrión et al. 2003).

Today *A. pinsapo* is only found in Andalucia as an endemic in the Rondeño, western, part of the Cordillera Bética mountain chain, in the Serranía de Ronda and more specifically in the Sierra de las Nieves and Sierra Bermeja mountains in the province of Málaga, and in the Sierra del Pinar and the Sierra del Endrinal in the province of Cádiz (Navarro-Cerrillo et al. 2006a). These limestone-peridotite areas in medium to high mountains (1,000–2,000 m) retain similar ecological characteristics to those which existed during the Würm glacial period lower down in the southernmost part of the Iberian Peninsula, which has enabled them to become biogeographical refuge areas for *A. pinsapo*. This has facilitated its survival there to the present day, while ensuring its genetic isolation and independent evolution from other European and North African firs in the Mediterranean basin (Jaramillo-Correa et al. 2010; Alba-Sánchez et al. 2018).

The classification of *A. pinsapo* as an endangered relict species that is especially vulnerable to any alterations in its habitat has led to a great deal of academic interest in recent decades as to its current situation and future prospects. The result is that its conservation has been well covered in a range of different scientific fields. Various studies have been published by the Junta de Andalucía (regional government) (Junta de Andalucía 1996–1999, 2003, 2008, 2012, 2013) and there have also been a number of recent scientific publications (Liétor 2002; Gómez-Zotano 2004; Navarro-Cerrillo et al. 2006b; Soto 2006; Linares et al. 2009, 2010a, b, 2011a, b, 2013; de Vita et al. 2010; Esteban et al. 2010; Sánchez-Robles et al. 2012; Blanes et al. 2013; López-Tirado and Hidalgo 2014; Navarro-Cerrillo et al. 2014). All of these have studied this species today or in the recent past (since the 18th century), and have mainly concentrated on subjects such as the conservation, restoration and regeneration of the *Abies* woods, the protection of its habitats and the fight against the real threats to which it is exposed today.

As regards this last issue, the main risk factors threatening *A. pinsapo* today are forest fires, the isolation of the populations and their monostructural characteristics, the alteration of its habitats due to erosion and loss of soil, diseases associated with fungi and insects, and to a lesser extent hybridization and atmospheric pollution (López-Quintanilla 2013). These factors have slowed the recovery of this fir since the mid 20th century, once human pressure on its ecological niches from tree felling, charcoal making and overgrazing had subsided. There are even some localities from which *A. pinsapo* has disappeared as a result of catastrophes such as deliberately started fires or clearance by tree felling; Gómez-Zotano (2004) and Soto (2006) identified examples of this kind in various mountain ranges, the Sierras de Alcaparaín, Palmitera, Real, de las Apretaderas in the province of Málaga and Sierra de los Pinos in Cádiz. In addition, in the mountains where *A. pinsapo* survives today, there were other areas of firs there in the past which were lost for the same reasons and have never recovered.

The Junta de Andalucía (regional government) has carried out various management programmes and projects to encourage the conservation, recovery and sustainability of the Spanish fir (2003, 2008, 2013) within the framework of the Estrategia Andaluza de Gestión Integrada de la Biodiversidad (Andalusian strategy for the integrated management of biodiversity). According to data from the second plan for the recovery of the Spanish fir, there are a total of 8,146 ha where *A. pinsapo* is present in varying degrees (about 1,250 ha can be considered as relatively mature, well-conserved woodland, about 3,000 are woods of *Quercus ilex* (holm oak) or *Pinus* (pine) or scrub with scattered patches of *A. pinsapo* and about 4,000 ha are woods with isolated firs. In addition, there are a further 709 ha from which *A. pinsapo* had disappeared and are currently being restored by replanting, or will be in the future. These projects date from several periods from as far back as 1957 (1959–67, 1968–1972, 1973–1983, 1986, 1988, 2001, 2004, 2005). These efforts to restore and regenerate the *A. pinsapo* woods have been based on historic sources, studies of current habitats and species distribution models (SDMs), many of which have contained inaccuracies and uncertainties.

In order to remedy this lack of accurate information, in this paper we propose that past fires, the main reason for the disappearance of *A. pinsapo*, also offer a great opportunity to carry out a precise palaeobiogeographical reconstruction of its former natural habitat, which could be a key asset for its future recovery. With this in mind, the methodological basis of the research is the analysis of the past extent of *A. pinsapo* in the Serranía de Ronda using pedoanthracology. This technique involves the search, identification and dating of the charcoal found in natural soils (not in archaeological sites), the data from which are then subjected to statistical, palaeoecological and cartographic analyses.

The initial hypothesis is that the distribution area of *A. pinsapo* was much larger in the past than it is today and the results obtained in this study have confirmed this. The palaeobiogeographical information obtained will enable new measures to be introduced to further the conservation and management of this species.

Methods

Study area

The investigation was carried out in the Serranía de Ronda, a mountainous natural area located at the southwest end of the Cordilleras Béticas, southern Spain (Fig. 1). The Serranía is bordered by the depressions of the Guadalquivir and Antequera rivers to the north, the valle de Guadalhorce to the east, the Mediterranean coast and the Strait of Gibraltar to the south and the much flatter countryside of the Campiña de Cádiz to the west. It extends over parts of the provinces of Málaga, Cádiz and Sevilla (36.5°–36.8°N; 5.5°–5°W).

The Serranía de Ronda is made up of large mountain spurs with a complex geology which converge in a high central plateau composed of dedritic materials (small fragments of sedimentary rocks) with a basin, the Depresión de Ronda, which acts as the main axis linking the different parts of the Serranía (Mauthe 1971). The plateau is surrounded by a succession of calcareous mountain ranges of which the highest peak is Torrecilla (1,919 m a.s.l.) in the Sierra de Tolox (part of the larger range, the Sierra de las Nieves). From west to east this dolomitic limestone basin is encircled by the following mountains: Sierra de Grazalema (peak, Pinar, 1,648 m), Endrinal (Reloj, 1,535 m), Líbar (Palo, 1,400 m), Jarastepar (1,427 m), Prieta (1,518 m) and Alcaparaín (Valdivia, 1,292 m). Parallel to the coast are the southernmost, mountains, the peridotite Sierra Bermeja (Abanto, 1,512 m) and Sierra Alpujata (Castillejos, 1,073 m), and the marble Sierra Blanca (Lastonar, 1,275 m) and Sierra de Mijas (1,150 m). Other mountains worthy of note on the perimeter of the Serranía de Ronda include Sierra del Aljibe (1,091 m), a sandstone massif at the southwestern end of the Serranía, and the limestone Sierras de Algodonales (Líjar, 1,051 m) and Sierra de Tablón (Terril, 1,128 m) at the northern end.

This region has a temperate, moist, mid-mountain Mediterranean climate (Gómez-Zotano et al. 2016) which is closely linked to its geographical situation near the Strait of Gibraltar and its abrupt quite distinct topography, with its main valleys and mountains running diagonally northeast to southwest. The result is that the Serranía has both oceanic and continental features of its climate, which leads, among other things, to high levels of rainfall, with over 2,000 mm of precipitation a year in the case of the Sierra del Pinar (Olmedo-Cobo and Gómez-Zotano 2017).

The area is well wooded, with the conifers *Abies* and *Pinus* and broadleaved trees such as *Quercus suber* (cork oak), *Q. faginea* (Portuguese oak), *Q. ilex* (holm oak), *Castanea sativa* (chestnut) and riverbank woods composed mainly of *Populus*, *Fraxinus*, *Ulmus* and *Salix*. The highly varied and extensive area survives as a mosaic of woodland types resulting from its situation on a biogeographical crossroads between two continents, Africa and Europe. Serranía de Ronda falls within the Baetic and Tingitano-Onubo-Algarviense biogeographical provinces which are subdivided into sectors. It covers all or part of the Rondeño, Bermejense, Antequerano and Malacitano-Axarquiense sectors of the Baetic province and the Aljíbico sector of the

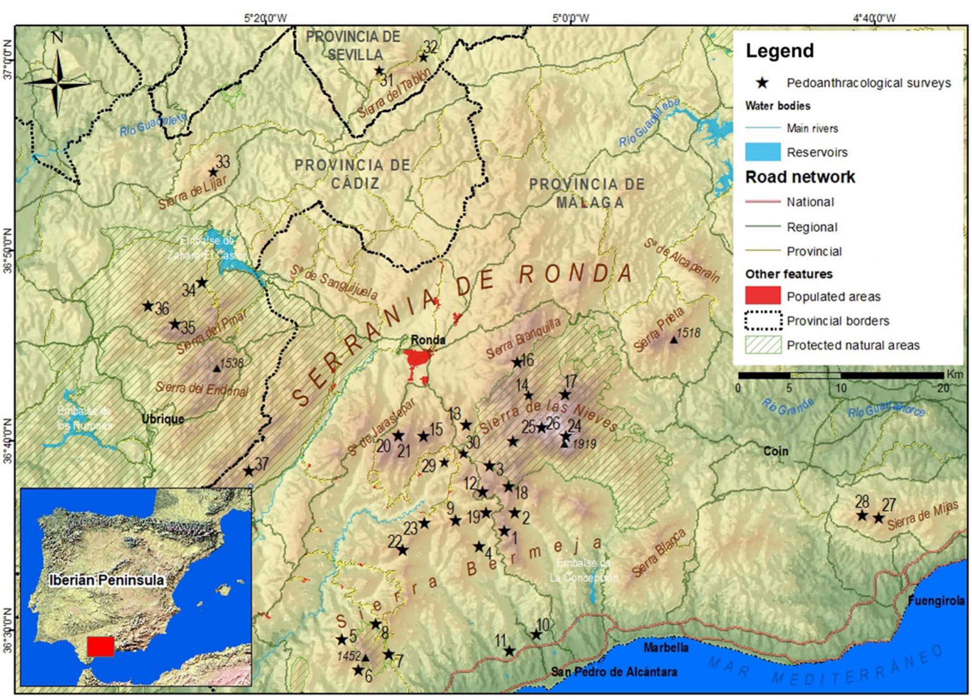


Fig. 1 Topographic map of the study area showing the sampled sites (numbers and sites in Table 1)

Tingitano-Onubo-Algarviense province (Pérez Latorre et al. 2019).

There are up to four altitudinal zones (bioclimatic levels) in the Serranía because of its height and extent, thermo-, meso-, supra- and oromediterranean. The *A. pinsapo* woodland corresponds with the Paeonio broteroi-Abieteto pinsapi series phytosociological plant community (serie supra-mesomediterránea rondeña calcícola de *A. pinsapo*), and Burio Macucae-Abieteto pinsapi series (serie meso-supramediterránea bermejense serpentinícola de *A. pinsapo*) (Pérez Latorre et al. 1998).

According to research by Gómez-Zotano and Olmedo-Cobo (2020), this area has been subjected to a long process of human activity with many good and bad decisions affecting the woodland management, and it has suffered not only from traditional human activities in mountain areas, such as tree felling, burning and charcoal making, subsistence agriculture, conversion to grazing land, livestock farming or the selection of dominant trees, but also from the exceptional demand for timber by the Spanish navy, and from the early attempts at industrialisation in Júzcar and Marbella. Wood was also required for building the Ronda to Algeciras railway, and large swathes of woodland were lost in a proliferation of large forest fires from the second half of the 20th century onwards. These numerous negative effects have been countered in recent years by an increasing level of protection and more effective management and organization of this valuable shared woodland heritage.

Human beings have therefore played a fundamental role in the past and present distribution of wooded, cleared and re-wooded areas in the Serranía, in this way giving rise to the large areas of woodland that currently enrich the extensive ecological and cultural heritage of this area.

For all these reasons, the unusual geographical and historical framework of the Serranía de Ronda makes it an interesting experimental area for the identification of changes to the woodland in space and through time, and for exploring the problems arising from conservation and management policies.

Methodology

The main research method used in our study of *A. pinsapo* was pedoanthracological (soil charcoal) analysis, and in particular the method proposed by Carcaillet and Thinon (1996) and Talon et al. (1998), and later adapted by Cunill (2010) and Cunill et al. (2013). This consists of the following stages:

Fieldwork. A total of 37 soil pits were dug at the 25 sampling sites (Fig. 1, ESM), which enabled us to cover a large part of the mountainous area in the study area. The sites were strategically distributed across the whole of the Serranía de Ronda, in places chosen because they may have acted as ecological niches for *A. pinsapo* during the Holocene according to the various sources of information available, species distribution models (SDMs), pollen studies and historical accounts. A sampling pit was dug at each site down to bedrock level, from which soil samples of between 3 kg and 15 kg per sampling level were taken. Phytosociological surveys of the local flora and plant communities were made for each of the sites.

Anthracological (charcoal) analysis. The second stage of our work took place in the laboratory and involved the following phases:

- The samples were wet sieved with mesh sizes of 0.8 mm, 2 mm and 5 mm. The soil fraction of the samples was gradually broken down, using water and a paintbrush, and poured through the sieve, leaving behind stones and possible charcoal fragments. The material collected by each of the three sieve sizes was left to dry in a space prepared for this purpose in the laboratory.
- The charcoal fragments were sorted from the sieved material and identified using a stereo microscope and the residual mineral fraction was then discarded. Before being discarded, all stone fragments of >5 mm were weighed for subsequent inclusion in the calculation of the amount of charcoal (anthracomass).
- Anthracomass analysis. This analysis compares the weight of the charcoal found in the soil (in mg) with the weight of the whole soil sample (in kg), as the absolute anthracomass (in mg/kg), having also calculated the specific anthracomass of *Abies* sp. for the samples in which it was found. For this calculation, the weight of the stony material trapped in the 5 mm mesh was subtracted from the initial weight of the soil sample.
- Taxonomic identification of the selected charcoals was done using a Nikon SMZ445 stereo zoom microscope and reflected light optical microscopy using an Olympus BX51 at 10–200×. The taxa represented by the charcoal fragments were identified by consulting various atlases of comparative anatomy of wood (Jacquiot et al. 1973; Schweingruber 1990; Vernet et al. 2001), and also by comparing them with the collection of carbonized wood fragments stored in the anthracotheque at the laboratory of Physical Geography Department of Granada University. The maximum number of pieces of charcoal in each sample varied between 50 and 100 fragments and a total of 5,649 pieces of charcoal were identified.
- Radiocarbon dating of 47 charcoal fragments of *Abies* sp. was done by the Poznań radiocarbon laboratory (Poznań, Poland) and Alfred-Wegener-Institut (Bremerhaven, Germany) and calibrated with Oxcal v. 4.4 (Oxcal 2021) using the IntCal20 database (Reimer et al. 2020), to 2 sigma (95% probability).

- Interpretation of the anthracological data.

Results

Taxon identification and anthracomass values

5,649 charcoal fragments were analysed during the course of this research. However, in a large number of these we were only able to distinguish between angiosperms and gymnosperms, 12.1% and 5% of the total, respectively. In a further 24.2% of the samples it was impossible to make an identification of any kind, due to either the deformation of the charcoal fragments, or the fact that the anatomical characteristics of the wood were practically invisible as a result of the carbonisation process, the actions of fungi and/or vitrification processes (glassy appearance of some charcoals). It is important to note that large amounts of vitrified charcoal were discovered in some of the samples studied. It has should clarified that charcoal vitrification is a process that has yet to be fully explained by the scientific community (Vaschalde et al. 2011), makes it impossible to carry out any kind of taxonomic identification. This means that certain taxa may be over- or underestimated, which would result in incomplete palaeoecological interpretations.

From a general perspective, the taxa most frequently found from the Serranía de Ronda sites as a whole are *Quercus* sp. (23.2%) and *Pinus pinaster* (14.2%). We also identified, albeit in much smaller percentages, genera such as *Pinus* (2.5%) or families such as Lamiaceae (2.5%), Fabaceae (2.3%) and Rosaceae (1.3%). Other categories were also detected, and between families, genera and species a total of 28 taxa were identified. The percentages of each of the remaining categories were practically negligible, ranging from between 1% and 0.04%. In most cases these identifications coincide with taxa currently present at the sampling sites. However, our analysis of the charcoal fragments also revealed various taxa that are not present today at some of the sampling sites. These new taxa include *Fraxinus* and *Salix* at Cañada de Enmedio, *Pinus* in the Sierra del Pinar in an area currently dominated by *A. pinsapo* and *Pinus* and *Abies* at Jarastepar 2.

Using the pedoanthracological analysis procedure described above, we managed to identify 194 charcoal fragments belonging to *Abies* sp., 3.4% of the total, from nine of the 25 sites: Los Reales 1 and 2, Puerto de los Valientes, Cañada de Enmedio, Sierra del Pinar 1 and 2, Palmitera 1, Jarastepar 2 and Fuenfría Alta (Fig. 2). The last three were considered to represent past populations of *A. pinsapo* as it is no longer present in these areas.

The charcoal concentration has been analysed in 37 soil samples collected since 2014 from a total of 25 pedoanthracological sites. Within this extensive sampling network, the charcoal values vary enormously from one site to the next (Table 1).

The specific anthracomass values for *Abies* sp., from sites where it occurred, range from 441.9 mg/kg in Sierra del Pinar 1 mg/kg to 0.8 mg/kg in Jarastepar 2.

Charcoal dates

Table 2 shows the various radiocarbon ages obtained for the 47 fragments of *Abies* sp. dated in this research, ranging from 9,931 cal BP to 9,616 cal BP up to sub-recent dates <500 years old of as little as 276–78 cal BP.

The oldest dates are from Palmitera 1, Jarastepar 2, Los Reales 1 and Fuenfría Alta, with ages very close to 10,000 cal BP (ranging between 9,931–9,616 cal BP and 9,619 cal BP), while the most recent sub-recent dates are from Los Reales 1 (326–208 cal BP and 294–102 cal BP), Los Reales 2 (295–103 cal and 282–82 cal BP) and Puerto de los Valientes (383 cal BP and 380 cal BP).

The site with the most complete chronological range is Palmitera 1, with 15 dates ranging from 9,931–9,916 cal BP to 5,441–5,145 cal BP, thus covering a substantial part of the early and middle Holocene. By contrast, Cañada de Enmedio has a limited chronological range with exclusively sub-recent dates, ranging from 326–208 cal BP to 276–78 cal BP. Other sites with sub-recent dates are Los Reales 1 (three dates between 326–208 cal BP and 294–102 cal BP), Los Reales 2 (three dates between 295–103 cal BP and 282–82 cal BP) and Puerto de los Valientes (two dates between 383 cal BP and 380 cal BP).

Discussion

New data on the past distribution of *Abies* in southern Spain

The results obtained in this research make a valuable contribution to palaeobiogeographic knowledge of this taxon in southern Spain by offering a more accurate and detailed picture of its former distribution there. In particular, the discovery of charcoal of *Abies* sp. from three sites in the Serranía de Ronda where it is not currently present enables us to corroborate our initial hypothesis, that *A. pinsapo* once had a wider distribution than it has today. This confirms the assertions of Linares (2011) who, on the basis of fossil records of *Abies* spp. from around the Mediterranean, suggested the existence of a common ancestor which was widely distributed across the western Mediterranean during the Cenozoic. The fragmentation of this original population probably took place in the Oligocene about 30–25 Ma, as a result of the tectonic processes that produced the break-up of the ancient Hercynian Belt of mountains in Spain (Magri et al. 2017),

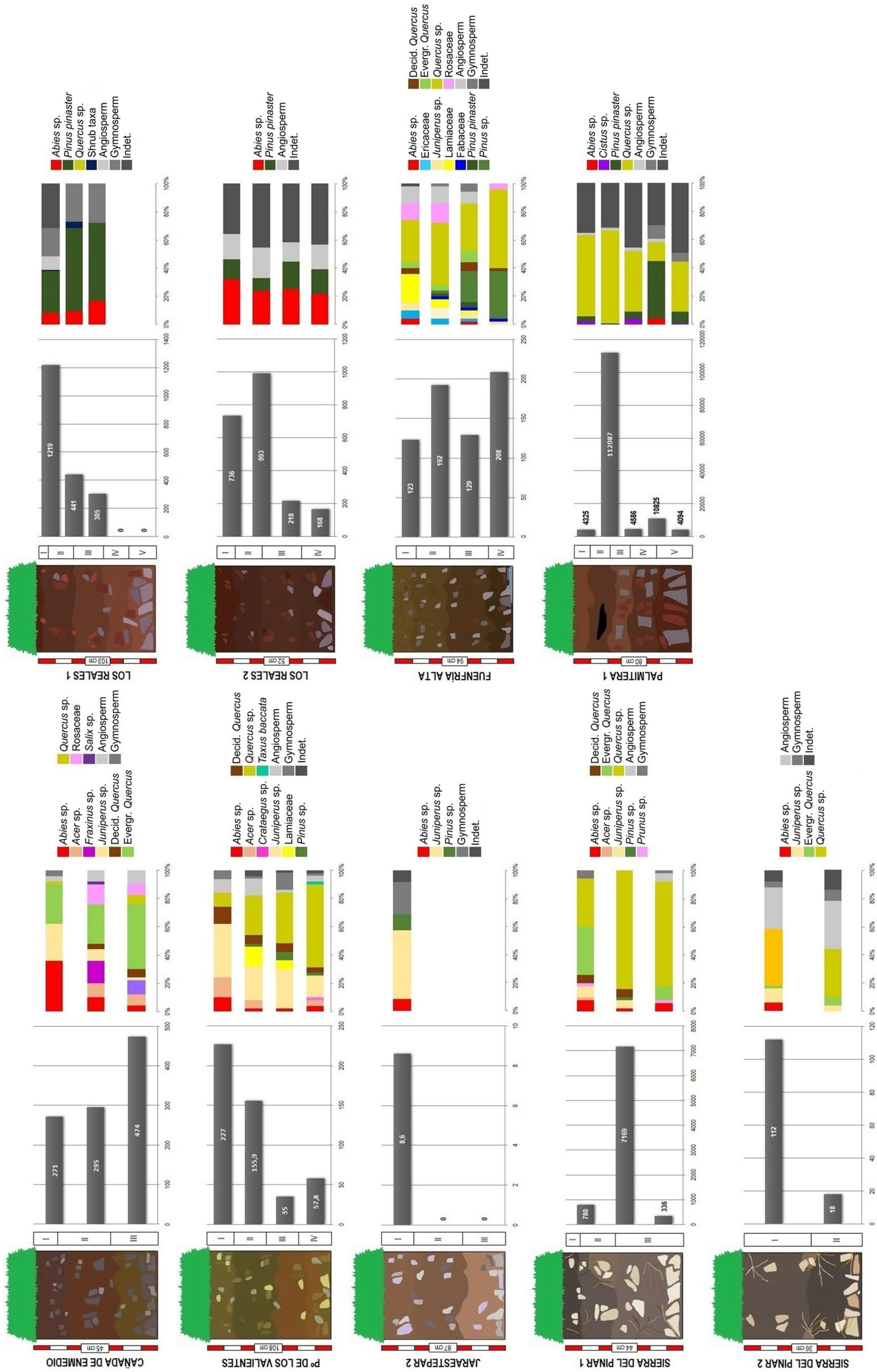


Fig. 2 Percentages of charcoal taxa identified, by sampling levels, from each of the sites where *Abies* sp was identified

Table 1 Charcoal values in mg/kg soil sample, number of samples and specific anthracomass of *Abies* sp

No	Sites	Total anthracomass (mg/kg)	*Abies* sp. (no. of fragments	Specific anthracomass of *Abies* sp. (mg/kg)
1	Palmitera 1	137,379.3	23	233.6
2	Palmitera 2	7066.3	–	–
3	Palmitera 3	7831.6	–	–
4	Palmitera 4	99.6	–	–
5	Los Reales 1	1965	20	8.4
6	Los Reales 2	2115.2	98	37.5
7	Los Reales 3	197.1	–	–
8	Los Reales 4	98.4	–	–
9	Puerto del Hoyo	413.7	–	–
10	Majada del Toro	1.4	–	–
11	Arroyo del Toro	15.3	–	–
12	Cascajares	17.6	–	–
13	Navacillo	39.7	–	–
14	Cañada de Enmedio	1039.4	23	159.3
15	Cancha de Almola	25.7	–	–
16	Puerto de Lifa	9,6	–	–
17	Cañada del Cuerno	27.5	–	–
18	Fuenfria Alta	651.7	3	9.8
19	Cerro de los Sauces	287.5	–	–
20	Jarastepar 1	25	–	–
21	Jarastepar 2	9.3	3	0.8
22	Jardón 1	289.5	–	–
23	Jardón 2	185.2	–	–
24	Puerto de los Valientes	475.7	9	21.4
25	Pilones 1	118.4	–	–
26	Pilones 2	143	–	–
27	Puerto de la Encina	234.3	–	–
28	Cerro Barretos	1461.1	–	–
29	Navacillo 1 (base)	22	–	–
30	Navacillo 2 (base)	136.5	–	–
31	Terril (summit)	49.7	–	–
32	Tablón (base)	186.4	–	–
33	Líjar	5.2	–	–
34	Llanos de Rabel	80.3	–	–
35	Sierra del Pinar 1	8285	8	441.9
36	Sierra del Pinar 2	129.8	3	10.2
37	Sierra de los Pinos	30.8	–	–
	TOTAL		190	470.8

so causing the division of this ancestral *Abies* into separate species in geographically and genetically isolated populations (Rosenbaum and Lister 2004).

Alba-Sánchez and López-Sáez (2013) noted that pollen from *Abies* has been found in different parts of the Cordillera Bética from ponds, peat bogs or caves in Málaga, Granada, Almería, Jaén, Alicante, Valencia, Castellón and Gibraltar, and that this almost certainly belonged to *A. pinsapo*, the only fir that grows naturally in southern Spain, so raising the possibility that it was much more widely distributed in the past (Alba-Sánchez et al. 2018). In the south of the Iberian Peninsula, there is a great deal of pollen-based evidence of *Abies* sp. during the Holocene, from a range of sites across Andalucía, including Antas (Almería), Cueva del Cucú (Almería), Roquetas de Mar (Almería), Cueva del Boquete de Zafarraya (Granada), Cueva de las Ventanas (Granada), Laguna del Padul (Granada), Laguna de Río Seco (Granada), Cueva del Bajondillo (Málaga) and Gorham's Cave (Gibraltar). The last two sites are the closest to the present day distribution area of *A. pinsapo*. In many cases, the pollen

Table 2 ^{14}C dates of *Abies* sp. by sites. Dates by Poznań radiocarbon laboratory (Poznań, Poland) and Alfred-Wegener-Institut (Bremerhaven, Germany)

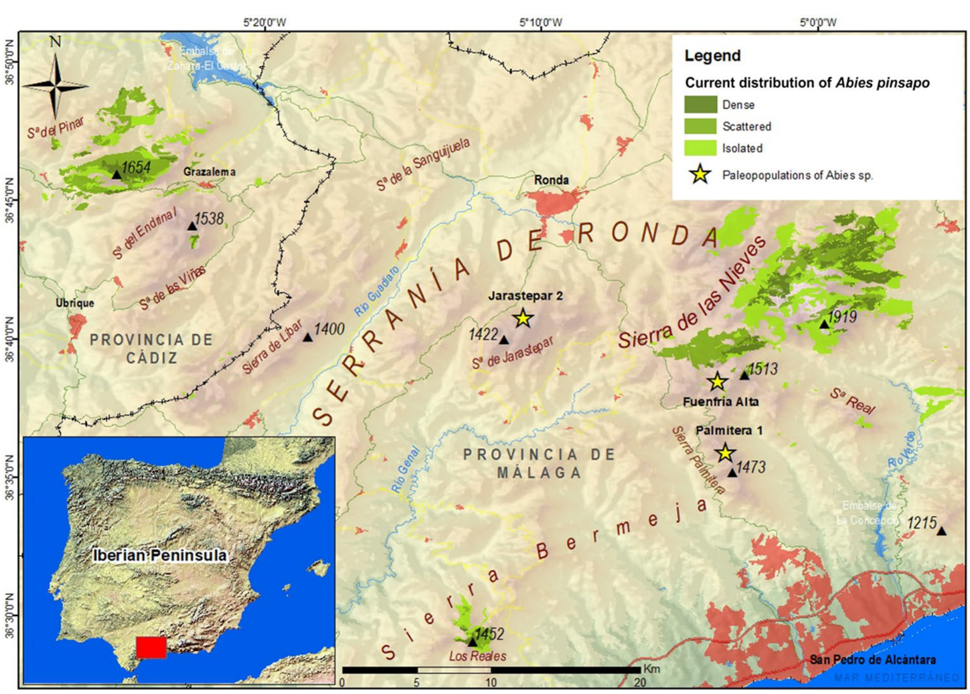
Site	Level	^{14}C age (BP)	Cal. age, 2σ (cal BP)	Lab. Code
Palmitera 1	V	8,707 ± 37	9,931–9,616	5173.1.1
	V	8,573 ± 35	9,719–9,551	5174.1.1
	V	8,549 ± 36	9,552	5176.1.1
	V	8,300 ± 40	9,266–9,206	5175.1.1
	V	8,155 ± 39	9,245–9,076	5177.1.1
	V	8,003 ± 128	9,236–8,615	5170.1.1
	V	8,057 ± 111	8,672	5171.1.1
	V	7,300 ± 50	8,342–8,053	Poz-83921
	IV	7,142 ± 34	8,001–7,944	5169.1.1
	IV	6,480 ± 40	7,516–7,356	Poz-78851
	V	6,239 ± 35	7,224–7,085	5172.1.1
	IV	5,710 ± 40	6,651–6,473	Poz-78852
	V	5,840 ± 40	6,607–6,573	Poz-83920
	IV	5,770 ± 40	6,553–6,523	Poz-83922
	IV	4,605 ± 35	5,441–5,145	Poz-83924
Los Reales 1	III	8,860 ± 50	9,810	Poz-83919
	II	6,160 ± 40	7,014	Poz-83918
	I	200 ± 30	326–208	Poz-78858
	I	195 ± 30	325–143	Poz-78859
	I	60 ± 30	294–102	Poz-78885
Los Reales 2	IV	3,270 ± 30	3,516–3,476	Poz-82525
	III	1,800 ± 30	1,832–1,674	Poz-82527
	I	45 ± 30	295–103	Poz-83914
	II	40 ± 30	295–103	Poz-83913
	II	110 ± 30	282–82	Poz-83912
Cañada de En medio	III	200 ± 30	326–208	Poz-113828
	I	180 ± 30	322–137	Poz-113846
	II	180 ± 30	322–137	Poz-113848
	II	170 ± 30	320–131	Poz-113827
	I	50 ± 30	295–103	Poz-113270
	II	15 ± 30	295–103	Poz-113784
	II	80 ± 30	291–79	Poz-113847
	II	115 ± 30	280–80	Poz-113829
	II	125 ± 30	276–78	Poz-113826
Puerto de los Valientes	IV	1,197 ± 73	1,030	5160.1.1
	IV	360 ± 30	491–385	Poz-113772
	I	345 ± 30	383	Poz-113771
	I	335 ± 30	380	Poz-113773
Fuenfría Alta	III	8,740 ± 50	9,619	Poz-113780
	I	4,970 ± 35	5,897–5,668	Poz-113779
	I	5,015 ± 35	5,726–5,679	Poz-113778
Jarastepar 2	I	9,038 ± 121	9,830	5162.1.1
	I	8,861 ± 122	9,669–9,629	5163.1.1
	I	8,637 ± 40	9,606	5161.1.1

count for *Abies* sp. accounted for over 3–5% of the total pollen from a particular period at a site, which together with the very low dispersion capacity of *A. pinsapo* pollen, just a few dozen kilometres, suggests its past presence near these sites (Alba-Sánchez and López-Sáez 2013). The pollen analysis from Gorham's Cave revealed the presence of *Abies* during the Upper Palaeolithic, around 16,000–19,000 cal BP, so demonstrating that this area in the south of the Iberian Peninsula acted as a refuge for *A. pinsapo* and for a large number of mesophilous and thermophilous taxa (Alba-Sánchez and López-Sáez 2013). The dates obtained from the Cueva del Bajondillo show that *Abies* sp. was present there around 7,400 cal BP, during one of the coldest and wettest phases of the early Holocene (Reed et al. 2001; Alba-Sánchez and López-Sáez 2013). This probably confirms the presence of *A. pinsapo* in some areas of the Cordillera Bética during the early and middle stages of the Holocene, as also demonstrated by pedoanthracological analysis, before later receding to its current relict distribution area (Linares 2011). *A. pinsapo* was present in the cirque of Río Seco in the Sierra Nevada (about 3,000 m) at 1,200–1,100 cal BP, which suggests that it moved to higher altitudes in the southernmost Cordillera Bética mountains during recent millennia (Alba-Sánchez and López-Sáez 2013; Alba-Sánchez et al. 2018). Other species of conifers have shown similar dynamics and are also considered as Holarctic relicts in the Cordillera Bética, including *Taxus baccata* (yew) and *Pinus sylvestris* (Scots pine), whose populations have been declining over the last few millennia as a result of habitat loss (Olmedo-Cobo 2012; Olmedo-Cobo and Gómez-Zotano 2014). Intense human pressure together with a warmer climate are the main reasons for the progressive confinement of these taxa to their current relict distribution areas, whose natural southern boundary is in the westernmost physiographic areas of the Cordillera Bética in Spain and Rif mountains in Morocco (Ruiz de la Torre 2006).

Together with the evidence from pollen records, the pioneering development of studies of soil charcoal in Serranía de Ronda, focusing on the peridotite (ultramafic igneous rock) area of Sierra Bermeja, developed by Gómez-Zotano et al. (2017, 2018 and Olmedo-Cobo et al. (2016, 2017, 2019a, b) has resulted in the discovery for the first time of charcoal fragments of *Abies* in an area where *A. pinsapo* is not found today. This site, Palmitera 1, provided the first palaeoecological evidence probably of *A. pinsapo* from pedoanthracological analysis on Sierra Bermeja. Further charcoal remains of *Abies* sp. were also discovered in Fuenfría Alta and Jarastepar 2 (Fig. 3). These finds together with dating of the charcoal fragments enabled us to obtain a more accurate picture of its distribution at various sites in the south of the Iberian Peninsula at various times in the Holocene. Of the 194 fragments of *Abies* charcoal from these three sites, 47 were dated to over 1,000 cal BP and many were much older, spanning practically all the Holocene. This confirms the role of certain mountain refuges for *Abies* during the constant climatic changes which caused advances and retreats of glaciers, and also the reduction and fragmentation of the distribution areas of the taxa best adapted to temperate climates (van der Veken et al. 2007; Alba-Sánchez and López-Sáez 2013). One of these refuges was the site referred to here as Jarastepar 2, in the centre of the Serranía de Ronda, which acted as an important link in the chain during the westward migration of *A. pinsapo*, connecting the populations in the Sierra de Grazalema (Cádiz) with the Sierra de las Nieves (Málaga). The fir populations indicated by the sites Palmitera 1 and Fuenfría Alta then connected this population at Sierra de las Nieves to the southernmost place with of *A. pinsapo* on the Iberian Peninsula, on the serpentine rock area of Sierra Bermeja.

The dates of the charcoal fragments confirm the absence of stratification in the mountain soils of the Cordillera Bética, as with their Alpine and sub-Alpine counterparts

Fig. 3 Current distribution of *Abies pinsapo* and ancient populations of *Abies* sp. discovered in this research



(Carcaillet 2001). The result is that charcoal fragments that date from rather recent times were found at relatively deep levels at some sites, such as for example Level III of Cañada de Enmedio (326–208 cal BP) or Level IV of Puerto de los Valientes (491–385 cal BP). At other sites quite the opposite occurred, with charcoal fragments aged several thousand years old being found near the surface, such as in Level I of Fuenfría Alta (5,897–5,668 cal BP). Differently aged fragments can also be found within the same level as a result of plant growth and bioturbation (Carcaillet and Thinon 1996).

Another source of information on *A. pinsapo* comes from historical sources, including various references to Spanish fir since the 16th century, recording a wider distribution area than we know today (Guzmán et al. 2013). These sources include historical data collected by Gil (2002), Gómez-Zotano (2004, 2006) and Becerra (2006) in documents such as the municipal ordinances of the city of Ronda and its jurisdictional area in 1508; the ordinances of the town of Zahara de la Sierra in 1575; inventories of timber to supply the navy or for building houses in Villaluenga in 1754 and 1766; news about the "Pino del Oso" used to mark the border between Ronda and Tolox in 1635, 1809 and 1870; general and specific questions from the *Catastro del Marqués de la Ensenada* (land survey of the marquis of Ensenada) for the different villages in the area in the middle of the 18th century; geographical and general maps of the villages and their main wooded areas in the provinces of the navy in the mid 18th century, considered as the first quantitative attempt to measure the area of *A. pinsapo* woods, the *Diccionario de Andalucía* by Tomás López published in 1780; the *Diccionario Enciclopédico* by Pascual Madoz of 1845–1850 and finally the written accounts of travellers, hunters, engineers and naturalists such as William Bowles in 1752, Simón de Rojas Clemente in 1809, Charles Edmond Boissier in 1837, Samuel Edward Cook Widdrington in 1829 and 1839, Moritz Willkomm in 1844, Antonio Laýnez in 1858, Mariano Laguna in 1868, Abel Chapman and Walter J. Buck in 1907, Luís Ceballos and Manuel Martín Bolaños in 1928 and 1930, A. Barbey in 1930 and Luís Ceballos and Carlos Vicioso in 1933 (Guzmán et al. 2013). Both general and specific references increased greatly from the end of the 19th century and in the first half of the 20th.

Various studies have been made of the habitats and ecological niches of *A. pinsapo*. These include the phytogeographic studies by Rivas-Martínez (1973) and Asensi and Rivas-Martínez (1976) on the woods of Paeonio broteroi-Abietetum pinsaponis in the Rondeño part of the Sierra de las Nieves; a reference study on the Bermeja part of Sierra Bermeja of the community Bunio macucae-Abietetum pinsaponis was made by Pérez Latorre et al. (1998); Ceballos and de Cordoba (1966) were pioneers in the study of *A. pinsapo* in the Sierra del Pinar in Grazalema, also considered part of the Rondeño. Subsequent studies (Ruiz de la Torre 1990; Ruiz de la Torre et al.1994; Oria de Rueda et al. 1991; Pérez Latorre et al. 1998; Navarro et al. 2006a; Valladares 2009; López-Quintanilla 2015) have revealed that, scattered around these main areas with *A. pinsapo*, there are also small populations and isolated individual trees within other types of woodland, together with other smaller woods in Ojen, Monda, Istán, etc.

The main species distribution models (SDMs) applied to *A. pinsapo* (Navarro-Cerrillo et al. 2006a; Alba-Sánchez et al. 2010; Alba-Sánchez and López-Sáez 2013; Gutiérrez-Hernández 2018) were based on suitability patterns and multivariable regressions to establish different degrees of potential for this species to grow in particular mountain areas in the south and southeast of Spain, covering an area that was much larger than the Serranía de Ronda (in that it also included the Sierras de Almijara-Tejeda, Sierra Nevada, Sierras de Cazorla-Segura and Sierra de Aitana). In this study area, these models showed a high level of suitability for *A. pinsapo* almost everywhere above 800–1,000 m. This means that it could potentially thrive in a large part of the vast limestone and peridotite area that surrounds the current *A. pinsapo* woods sheltered among some of the peaks of the Serranía de Ronda. The areas of high potential described by these models include the three ancient populations of *Abies* sp. discovered in our pedoanthracological survey. However, the current global climate change suggests that in the future there could be a progressive loss of suitable ecological niches for *A. pinsapo*, above all due to rising temperatures, a change that would cause it to migrate to higher altitudes, so resulting in increasing fragmentation of habitat and vulnerability to forest fires (Gutierréz Hernández 2018). This information from SDMs which was later mapped is an ideal framework for our research, as a starting point for the selection of possible sites for future soil charcoal excavations. In turn, the results of our research have offered accurate answers to some of the unknowns that form an inevitable part of theoretical modelling procedures.

The role of fire in forming the plant landscape of the Serranía de Ronda

Fire has been one of the most important agents of change in the plant landscape over the course of history and is a key factor in the great diversity of vegetation associated with the Mediterranean climate (Bond and Keeley 2005). The high charcoal values (137.379 mg/kg) from the Palmitera 1 site situated in the peridotite area of Sierra Bermeja reveal the significance of past fires for the vegetation of this mountainous area throughout the Holocene. In fact, fires continue to be a regular feature of the Sierra Bermeja, where Vega-Hidalgo (1999) found a recurrence period of 14.5 years. This frequent burning, together with the unusual topography of Palmitera 1 in the form of an enclosed basin helps explain the vast concentration of charcoal found there. By contrast, sites on calcareous soils such as Jarastepar 1 and 2, among others, have shown very low levels of charcoal, and low charcoal has also been noted in studies of dolomitic limestone soils in the north of the Iberian Peninsula, such as those in the Sierra del Aramo, Cantabria (Beato-Bergua et al. 2019). This could be because limestone does not readily form soils and these do not retain much charcoal, above all in areas with a moderate to steep slopes which have an effective soil formation during the Holocene of less than 1 cm (Farrús et al. 2002). However, larger quantities of materials may accumulate in low lying areas, so encouraging soil formation (Daniels and Hammer 1992). Although this correlation could be used to reject certain locations for future soil charcoal analysis, the relatively small number of sites studied so far on sedimentary materials in Spain obliges us to be cautious about rejecting sites.

The dates of charcoal fragments from Jarastepar 2, Los Reales 1, Fuenfría Alta and Palmitera 1 revealed that some were almost 10,000 years old, coinciding with the beginning of the climatic recovery which took place after the Late Glacial period (López and López 1999). Various taxa began to spread at this time including *A. pinsapo*, which found a habitat in some of these places in the south of the Iberian Peninsula (Carrión et al. 2003). During this period before the Neolithic, the lack of palaeoenvironmental evidence indicates that the hunter-gatherers had virtually no influence on the natural vegetation (Fernández Rodriguez et al. 2007). It is therefore very likely that at the start of the Holocene the fires in these ancient habitats of *A. pinsapo* could have been due to natural causes, resulting from increasingly warm and arid conditions in this area (Jalut et al. 2000; Cacho et al. 2001). In the following period, during the Neolithic, a total of nine signs of fire were detected in three of the four sites mentioned above (Los Reales 1, Fuenfría Alta and Palmitera 1), but none in Jarastepar 2. These nine episodes of fire were concentrated in the part of the study area on ultramafic rock and are dated to between 7,014 cal BP in Reales 1 cal BP and 5,441–5,145 cal BP in Palmitera 1. These fires may have been the result of human activity, from the progressive increase in the population in coastal areas very near Sierra Bermeja (Navarro et al. 1993; Fernández Rodriguez et al. 2007). The existence of a particularly intense Neolithic settlement process (8,000–6,000 cal BP) associated with caves in karst landscapes would help support this theory (Romo et al. 2008).

There is very little evidence of fire in the study area from the end of the Neolithic about 5,000 years ago up to just a couple of centuries ago. Just two episodes were detected in Los Reales 2, from 3,516–3,476 cal BP to 1,832–1,674 cal BP, as well as evidence of one last ancient fire in Puerto de los Valientes (Sierra de las Nieves), which was dated to 1,345–1,040 cal BP. However, over the last few centuries, as shown by various different documentary sources (Vega-Hidalgo 1999; Gómez-Zotano 2004, 2006), the signs of fire intensified again, especially from the eighteenth century onwards and 18 charcoal samples were dated between 491–385 cal BP and 276–78 cal BP.

The role of soil charcoal in palaeoecological studies

The application of pedoanthracological analysis in various Spanish mountain ranges has enabled us to make significant progress in the reconstruction of their past environments. This was first applied in the Pyrenees of Catalonia by Cunill (2010) and since then has been extended to the Cordillera Bética, the Sistema Central and the Cordillera Cantábrica. In the Pyrenees mountains, Cunill et al. (2012, 2013) analysed the changes in the landscape above 2,000 m, paying particular attention to changes in the tree line, while in the Sierra de Gredos (Sistema Central), García Álvarez et al. (2017) concentrated on changes in the tree canopy during the Holocene, and especially to the role played by forest fires in the formation of the current plant landscape. Research by Beato-Bergua et al. (2019) in the Cordillera Cantábrica increased biogeographical knowledge of both the present and past situation of *Taxus baccata* (yew) trees in the central mountains of Asturias, so making a decisive contribution to the conservation of a relict species in danger of extinction.

The present research helps to consolidate the efforts made so far in the application of soil charcoal in palaeoecological studies in different parts of the Cordillera Bética. This technique has not only enabled us to find out more about the past of *A. pinsapo*, in both biological and geographical terms, but has also helped resolve some of the long-standing phytosociological questions about the plant community. In this way the pedoanthracological analysis carried out at various sites in Sierra Bermeja together with evidence from pollen, phytogeographical studies and species distribution models (SDMs) have enabled researchers to confirm the native character of *Pinus pinaster* on ultramafic soils (Olmedo-Cobo et al. 2019a, b), so confirming the role of the conifers *A. pinsapo* and *P. pinaster* in climax woodland in the Serranía de Ronda during the Holocene.

The discovery of ancient populations of *A. pinsapo* in mountainous areas where it is currently absent, and outside protected natural areas or those covered by the plan for the recovery of *A. pinsapo*, makes an excellent contribution to identifying the complex past distribution of this species with a view to its effective future management. However, our knowledge of the palaeo-biogeography of *A. pinsapo* is far from complete in spite of the widespread development of methodologies and techniques for the restoration of the landscape in recent years.

The results of this research also make an important contribution to the Programa de Actuación del Plan de Recuperación del Pinsapo (Programme of action for the recovery of the Spanish fir) (2015–2019) (Junta de Andalucía 2011). In particular they have been integrated into the Líneas Estratégicas del Programa Sectorial del Plan Andaluz de Investigación, Desarrollo e Innovación (Strategic Lines of Action for the Sectorial Programme of the Andalusian Plan for Research, Development and Innovation) for carrying out research projects which can help enhance the management of Spanish fir and associated species: (a) archaeobotanical studies which help us to understand the dynamics of *A. pinsapo* associated with changes in the climate during the Quaternary; (b) historical records of distribution of *A. pinsapo*.

Conclusions

The results of this research have enabled us to 1, discover the present and potential area and distribution of *A. pinsapo* by using available sources of information and by characterising the study area in both geographical and phytogeographical terms; 2, determine the past area of *A. pinsapo* by analysing soil charcoal fragments, providing new data about its ancient distribution area; 3, discover more about the dynamics of *A. pinsapo* during the Holocene, the factors affecting it (climatic or human) and the successive stages through which the fir woods must have passed before being confined to their current restricted habitats; 4, compare the soil charcoal records with historical data and the species distribution models, and above all the characteristics of the natural habitats and ecological niches currently occupied by this species as a basis for its conservation and management.

The results obtained in this research, once they have been compared with those obtained from geohistorical, botanical and palaeoenvironmental (above all palaeoclimatic) studies could be of great importance as a basis for developing a strategy for the preservation and regeneration of *A. pinsapo*. These new possibilities for conservation and management could be applied in both the places where *A. pinsapo* is found today, and in others that have high potential as a future habitat for it, as established using suitability models and multivariate regressions.

For all these reasons, future efforts must focus on transferring the results of research to public administrations and private companies with responsibilities in the management of this emblematic woodland resource. Palaeobiogeographical reconstruction of the past distribution of *A. pinsapo* could also be used to develop a model for the ecological connectivity of existing *A. pinsapo* areas, an effective tool for the future preservation of this fir and its woods.

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