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## Europe's southernmost interglacial refugia as sentinels for the local extinction of mountain conifers

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## ABSTRACT

The Serranía de Ronda is an exceptional palaeoecological laboratory for studying the dynamics of vegetation over time, due to its strategic geographical location at a biogeographical crossroads and its proven historical legacy. Many of the mountains that form part of this territory are today practically deforested, such as Sierra Blanca, whose geographic location at the heart of the Serranía de Ronda means that it has enormous potential as a biogeographical crossroads: the occasional presence of *Abies pinsapo*, *Pinus pinaster* and *Quercus rotundifolia* suggests that it was once covered by a mixed forest of conifers and broad-leaved trees. The lack of environmental research in Sierra Blanca has facilitated the installation of large quarries, which have led to its exclusion from the Sierra de las Nieves National Park, which was created in 2021. We applied the pedoanthracological methodology, which has enabled us to discover paleo-populations of *A. pinsapo* and *Pinus sylvestris*-type. The results confirm that coniferous forests previously covered a much wider area during the Holocene. These findings reinforce the role of Sierra Blanca as a high-altitude refuge for conifers during the warm stages of the Holocene and as a sentinel for the local extinction of mountain conifers. This information could help improve its management and conservation. © 2023 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

## 1. Introduction

Throughout the Holocene, landscapes have undergone important transformations in a context of Global Change, where climatic variability, paleo-ecological processes and increasing human activity have played a defining role in the last 15,000 years (Carcaillet and Thion, 1996; Cunill, 2010). In this scenario, in which mountain conifer forests have undergone quite dramatic processes of change, such as altitudinal fluctuations and extinction of populations, the cold-adapted species managed to survive in mountain refugia during the interglacial periods. This means that the comparative study of the tree line (the highest altitude that sustains trees) – a hitherto unexplored environmental frontier in the Mediterranean ranges – could offer valuable paleoenvironmental information for the bodies responsible for managing forests and the environment in general (Alba-Sánchez et al., 2021a).

One example of these taxa is the Spanish fir (*Abies pinsapo* Clemente ex Boiss.), a tree species of great ecological and landscape value, being the only fir tree that grows naturally in the South of Spain (Linares et al., 2010; López-Quintanilla, 2013). At present the only survivor species of fir in Southern Spain (*A. pinsapo*) is only found in the Western Baetic

System, and is endemic to the Rondeño and Bermejense biogeographic sectors in the Serranía de Ronda. Within this vast mountainous territory, it can be found specifically in the Sierra de las Nieves National Park and Sierra Bermeja Natural Site (province of Malaga), and in the Sierra del Pinar and the Sierra del Endrinal (province of Cádiz), within the Sierra de Grazalema Natural Park (Gutiérrez-Hernández et al., 2017; Gómez-Zotano and Olmedo-Cobo, 2021).

These mountain areas –especially those above 1000 m a.s.l.– still have similar ecological characteristics to those existing in the southernmost part of the Iberian Peninsula during the Last Glacial Maximum (Carrion et al., 2012, 2015); the altitudinal gradient of these mountains has enabled this species to migrate in altitude in search of the ideal ecological conditions for its survival (both during the Last Glacial Maximum when it moved towards the coast, and in the Holocene when it moved to higher altitudes). The migration of the Spanish fir during periods of warm conditions in the present interglacial period has been demonstrated by González-Hernández et al. (2021). These biogeographical refuges have made it possible for the Spanish fir to survive until the present day (Linares, 2011). As a consequence of its geographical isolation, the species would evolve independently from other fir trees of the Mediterranean Basin (Jaramillo et al., 2010; Cobo-Simón et al., 2020).

The reduced, fragmented distribution of *A. pinsapo* today and its much wider geographic distribution area in the past raises the following questions: Where was it found in the past? and what caused its local

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extinction in much of the Western Baetic System? It is difficult to answer these questions with any degree of certainty because our knowledge of the paleobiogeography of the species is specific to each sector and quite deficient despite the uniqueness and biogeographic originality of this species, as well as the development in recent years of new methodologies and techniques for reconstructing the past landscape. In order to answer these questions, we need to carry out a paleo-ecological study of the species in the entire Western Baetic System (Serranía de Ronda).

Several pediaanthracological studies have been carried out in this area to improve the knowledge about the past distribution area of Spanish fir and to propose a model of ecological connectivity for its relict cores (i.e; Olmedo-Cobo et al., 2019a, 2019b, 2021; Gómez-Zotano et al., 2021; Gómez-Zotano and Olmedo-Cobo, 2021; Pardo-Martínez et al., 2021). The results of the pediaanthracological analyses confirm our starting hypothesis, that the area of distribution of the Spanish fir was larger in the past, as also confirmed by the other sources of information consulted: historical sources, studies of present-day habitats, pollen and Species Distribution Models (SDMs). The palaeoecological data obtained have not only helped to improve the palaeobiogeography of *A. pinsapo* in the Serranía de Ronda, but have also confirmed the native character of *Pinus pinaster* on ultramafic soils (Gómez-Zotano et al., 2017, 2021; Olmedo-Cobo et al., 2019a, 2019b; Gómez-Zotano and Olmedo-Cobo, 2021). These findings confirm that conifers, including *A. pinsapo* and *P. pinaster*, would be the climax community in the Serranía de Ronda during the Holocene. To date, there is no pediaanthracological evidence of other potential high-elevation conifers (*P. sylvestris*-type), currently absent in the Western Baetic System.

To this end, a complete paleo-environmental reconstruction of the forests in the Serranía de Ronda is required, for which many of its mountain areas have yet to be analysed. One of these is the Sierra Blanca de Igualeja. Due to its geographical situation and its physical and environmental conditions, this mountain could be an important biogeographical hub within the heart of the Serranía de Ronda. It is particularly interesting as a potential link between two highly forested Sierras, the peridotite Sierra Bermeja and the limestone Sierra de las Nieves –recently declared a National Park–, where unconnected populations of *A. pinsapo*, continue to survive among many other species of conifers and broad-leaved trees.

Unlike the aforementioned sierras, Sierra Blanca is today practically deforested; the lack of forests makes it difficult to find out more about the climax vegetation in this area, beyond that revealed by phytosociological studies and Species Distribution Models (SDMs). The occasional presence of individual *Quercus rotundifolia*, *A. pinsapo* and *P. pinaster* trees suggests that it was once covered by a mixed forest of conifers and broad-leaved trees. However, there are no paleobiogeographic studies to determine: i) whether these species migrated to different altitudes during interglacial periods, ii) whether they are autochthonous to this area or iii) the role they may have played in connecting different species.

In order to fill this knowledge gap, pediaanthracological analysis is applied for the first time in Sierra Blanca. The results corroborate our initial hypothesis that coniferous forests previously covered a much wider area during the Holocene. Paleo-populations of *A. pinsapo* have been found, as well as a taxonomic group of *Pinus* that is now extinct throughout the Serranía de Ronda (*P. sylvestris*-type). These findings reinforce the role played by high-elevation conifers during the Holocene.

Studies of this kind are important for four main reasons: i) to reconstruct past forest ecosystems; ii) to study the dynamics of these ecosystems during different paleohistoric phases, identifying the main disturbances (climatic and/or anthropic); iii) to discover local extinctions due to anthropic or climatic action; iv) for their potential application in present-day forest management.

## 2. Methods

### 2.1. Study area

The research has been conducted in Sierra Blanca, a limestone massif in the Western Baetic System (Serranía de Ronda). It is bordered to the south/southeast by the Sierra Bermeja, by the Genal Valley to the south and west, and by the Sierra de las Nieves to the north/northwest (36°37' 55"N, 5°05'04"W). Its highest point is in Cerro Cascajares (1416 m.a.s.l.) and it is the source of important rivers in this area such as the Genal (río Seco and Nacimiento de Igualeja) and the Guadiaro (Arroyo de la Fuenfría-Guadalevín) (Fig. 1).

Sierra Blanca belongs to the Frontier Units of the Inner Zone of the Baetic System. It is part of the unit of Las Nieves (previously known as the Rondaide domain), essentially carbonated and partially affected by contact metamorphism in the area near the intrusion of peridotites in Sierra Bermeja. The contact halo is composed from south to north by massive white saccharoid marbles (after which the Sierra is named), massive, white-blue crystalline limestones and black layered limestone with loamy levels (Serrano-Lozano and Guerra-Merchán, 2004; Instituto Geológico y Minero de España, 2007).

According to Gómez-Zotano et al. (2019), the relief of Sierra Blanca is strongly associated with the tectonic and structural elements. A typical karst formation can be observed on its steep slopes, which is dominated by bare limestone pavements with sinkholes, drains, caves, upwellings, travertines and scree (active and cemented).

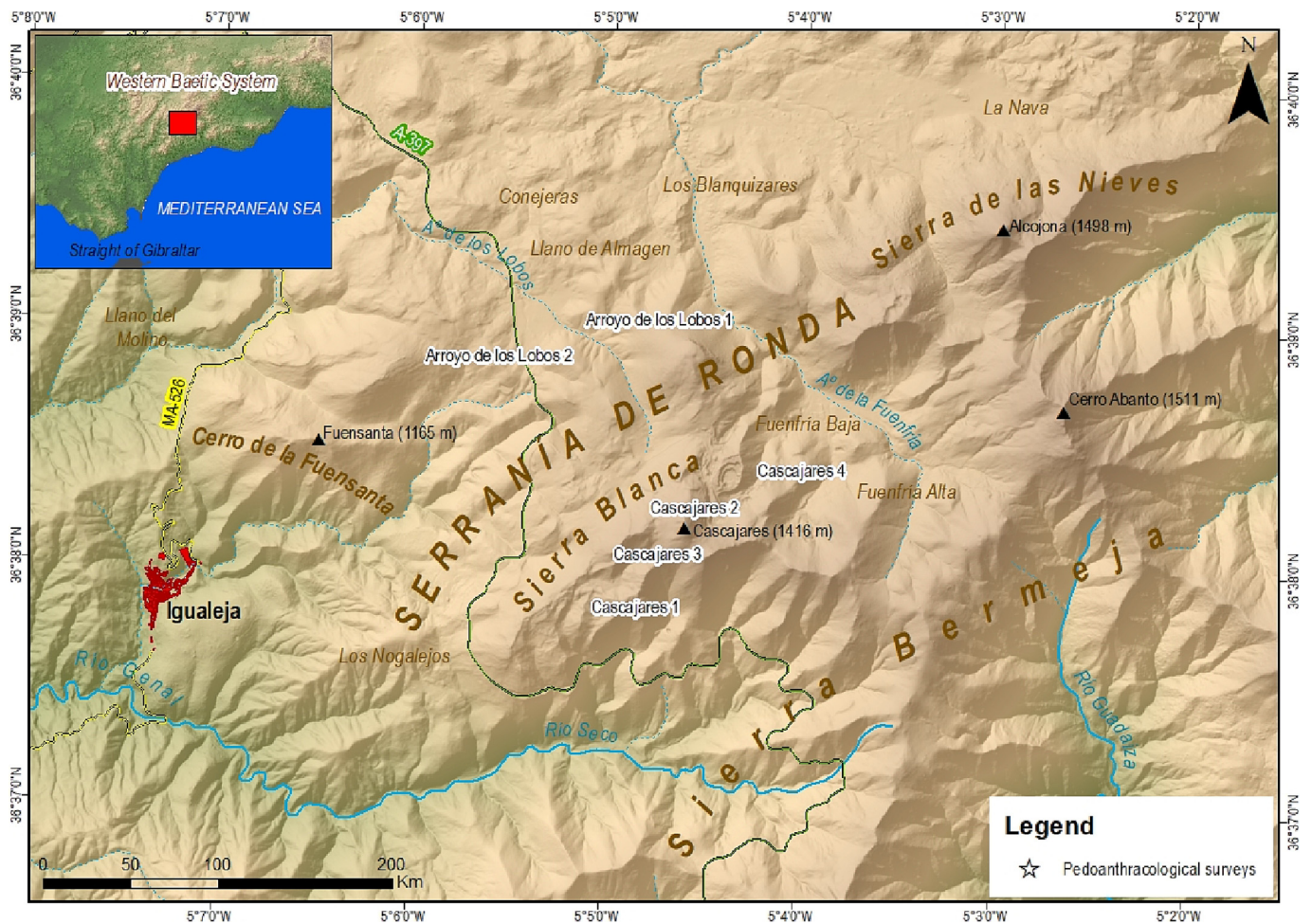
This mountain has a humid semi-continental Mediterranean climate (Gómez-Zotano et al., 2016). It is a temperate-cool, mid-mountain climate that is noticeably humid thanks to the strong Atlantic influence, and also to the easterly, rain-bearing winds that create crypto-precipitation due to the low, lingering clouds in the Strait of Gibraltar. In any case, rainfall and temperature are locally affected by differences in altitude and by varying exposure to the sun/shade, which determines its classification as a semi-continental climate within the context of Serranía de Ronda (index levels 15 to 16; Olmedo-Cobo and Gómez-Zotano, 2017).

The soils vary considerably and the most common association is lithosolic Leptosol-Regosol. These display generally and exclusively an ochric epipedon, with brown to red colours, which very occasionally could be classified as mollic. The larger cracks and gaps are filled with a fine matrix, where discontinuous illuvation cutans with uneven development can be observed. This soil type is defined as lepti-chromic luvisols (pink earth) (Guerra-Merchán, 1998).

The vegetation of Sierra Blanca has been characterised by Gómez-Zotano et al. (2019). According to other studies of this area (Pérez-Latorre et al., 1998, 2021), the potential formations must have belonged to the Baetic series of meso-Mediterranean holm oak forest with the typical particularities, of the Rondense biogeographical subsector. This series is characterised by the presence of holm oak forest as the most evolved community, typical of soils with basic pH (such as the leptosols and regosols which have formed on top of marbles), whose degradation in increasingly xeric environments and increasingly poor soils has led to the progressive appearance of kermes oak, retama, esparto, rosemary and thyme fields (Consejería de Medio Ambiente, 2004).

Gómez-Zotano et al. (2019) identified different variants of this holm oak forest at the altitudinal gradient between Río Seco (740 m) and Cascajares (1416 m), and a marked sun/shade orientation. These form an altitude-based series of present-day vegetation made up of the following formations (Fig. 2): in thermophile and edapho-xerophile environments in the base area and the most exposed hillsides, with strong sunlight, the wild olive (*Olea europea* subsp. *sylvestris*) is often present with *Chamaerops humilis*. Scattered remains can be found of basophile holm oak forest, of which robust examples can be found near Los Nogalejos. In the coolest environments, together with the holm oaks, thorn bushes typical of the pre-forest border of humid forests appear. These are mainly formations of *Berberis vulgaris* subsp. *australis*,

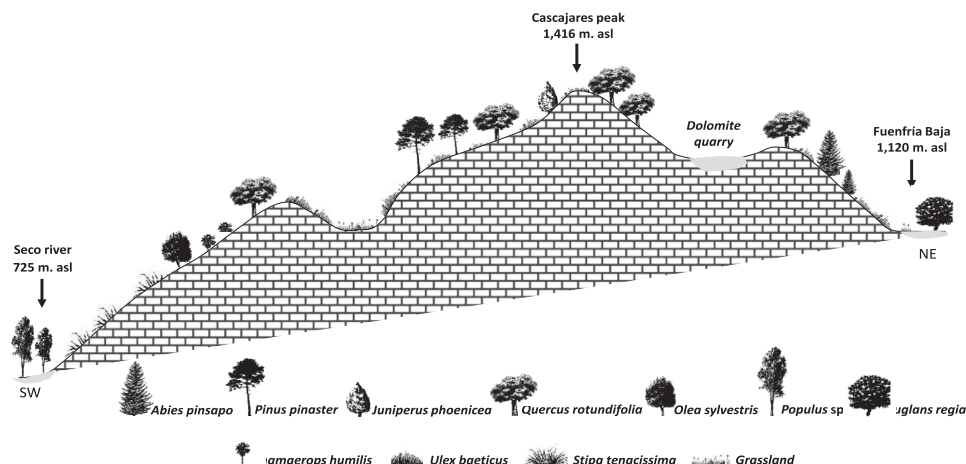




**Fig. 1.** Sites sampled during this research (numbers and sites in Table 1). Source: drawn up by the authors using information from the Andalusian Institute of Statistics and Cartography (Instituto de Estadística y Cartografía de Andalucía).

*Crataegus monogyna* and *Rosa canina*, which specifically indicate the potentiality of the *A. pinsapo* Spanish fir forest of which a few examples still remain on a shady hillside situated to the south-east of Fuenfría Baja and others near the Llano de Almagen. Given the scarcity of trees, these areas are dominated by some of the substitution stages referred to above, essentially gorse (*Ulex baeticus* subsp. *Baeticus*) and juniper

bushes (*Juniperus communis*) accompanied by *Cistus albidus*, *Rosmarinus officinalis*, *Lavandula lanata* or *Phillyrea latifolia*. *Arenaria erinacea* appears in meadows, crests and windy hillsides. Finally, the most xeric hillsides are colonised by espartos, where *Stipa tenacissima* dominates together with other perennial tillered gramineae such as *Helictotrichon filifolium* subsp. *arundanum*.



**Fig. 2.** Altitudinal zonation of the current vegetation in Sierra Blanca de Igualaja.

In hillsides exposed to sunlight, with steep slopes and poor soils that lead to low availability of soil moisture, isolated tesserae of *Pinus halepensis* and *P. pinaster* appear, which take the place of the mature stage of the holm oak in these conditions of low humidity and precipitation. The relict presence of Phoenician juniper (*Juniperus phoenicea*), of great biogeographical interest in this area, reinforces the role of the conifers as permanent communities on crests and steep hillsides on soils that have evolved little, where they probably took the place of the holm oak forest. In the case of the Phoenician juniper, the presence of abundant remains of wood from this Cupressaceae in a nearby old marble quarry, shows that it had a more significant role in quite recent times, which indicates that the edapho-xerophile formations have also suffered massive deforestation. It is also important to point out that *P. pinaster*, unlike the green pine forests which grow on the peridotites, display a more yellowish colour which may be symptomatic of iron chlorosis, although they reach much greater ages and sizes than the pine forests in Sierra Bermeja.

Sierra Blanca is a publicly-owned mountain range belonging to the Town Council of Igualaja (province of Malaga), which has been subject to very intense anthropic use over the course of history. According to Gómez-Zotano (2004, 2006a, 2006b) and Gómez-Zotano et al. (2019) there has been severe deforestation over the centuries with several episodes of particular note: a) the installation and start-up in 1730 of the Royal Tinplate Factory in San Miguel de Júzar, which led to the felling of a large part of the forests in the Genal Valley to supply wood; b) the exploitation of marble quarries and magnetite mines in contact with the peridotites during the 18th and 19th centuries; c) the process of expropriation carried out during the 19th century, which led to the ploughing of areas of wild vegetation around the new farmhouses established on publicly owned land in the mountains; d) continuous livestock grazing, charcoal production, lime extraction or the collection of esparto among other traditional mountain activities. The simultaneous pressure from all these different activities meant that by the mid-20th century, the Sierra was completely bare and had largely been abandoned due to the incipient rural exodus. The rare efforts to repopulate the forests in subsequent decades fell victim to the forest fire of 31 July 2004, which affected an area of 94 ha.

Nowadays, the Sierra is used for extensive farming of sheep and goats, sufficient to prevent the spontaneous regeneration of the vegetation. In addition, there has been a resurgence in quarrying activity in response to the demand from the booming construction industry on the Costa del Sol. The quarrying of marble and aggregates has had a strong impact on the environment and landscape of Sierra Blanca, without this being tackled in any way by environmental or landscape restoration measures.

As a result, Sierra Blanca was not included in the recently declared Sierra de las Nieves National Park, so failing to achieve the only protection status that could have halted the environmental deterioration of the Sierra. Other attempts to protect it have proved ineffective, in that for example Sierra Blanca is fully integrated into the Intercontinental Biosphere Reserve of the Mediterranean: Andalusia (Spain) – Morocco, and also belongs to the Natura 2000 network with three Special Areas of Conservation (ES6170010 Sierras Bermeja y Real, ES6170006 Sierra de Las Nieves and ES6170016 Valle del Río del Genal), without this having resulted in any effective form of protection.

## 2.2. Methodology

In this research we followed the protocols for the pedoanthracological method established by Thion (1978) and adapted by Talon et al. (1998) and Cunill (2010). To this end we carried out six pedological sampling, which covered almost the entire study area (Fig. 1, Table 1). In each sampling, we identified between one and four sampling levels, coinciding with the different soil horizons. We then collected between 3 and 15 kg of soil for each level. The soil was processed in the laboratory using the sieving-with-water technique (mesh

sizes of 5, 2 and 0.8 mm). Later, once the mineral fraction collected in the mesh after the sieving process had dried, the charcoal contained in the mineral fraction was selected manually by using a binocular magnifying glass. The absolute anthracomass (mg of charcoal/kg of mineral residue) was then calculated for each sampling level.

After a detailed study of the three wood faces (transverse, longitudinal radial and longitudinal tangential) using an incident light episcopic microscope (differential interference contrast, 50×, 100×, 200× and 500×), we tried to identify the taxa corresponding to the charcoal samples using the wood anatomy guides provided by Schweingruber (1990) and Vernet (2001), and with the help of the reference collection of charcoals at the Laboratorio Terra of Granada University. A total of 940 fragments were analysed, 15 of which (1 *Abies* fragment, 5 *Pinus* and 9 *P. sylvestris*-type) were subjected to radiometric C14 AMS dating in specialised laboratories at the Poznań Radiocarbon Laboratory (Poznań, Poland) and the Alfred-Wegener-Institut (Bremerhaven, Germany). Calibration of the dated samples was carried out with Oxcal v.4.4. In particular, the IntCal20 database – 2 sigma, 95% probability – was used (Reimer et al., 2020).

## 3. Results

### 3.1. Taxa identification and anthracomass values

Fig. 3 offers a summary of the pedoanthracological results obtained in this research.

### 3.2. Charcoal dating results

Table 2 shows the results for the 15 samples dated in this research (1 fragment of *Abies* sp., 5 of *Pinus* sp. and 9 of *P. sylvestris*-type).

## 4. Discussion

The results of this research have enabled us to discover previously unknown ancient populations of *P. sylvestris*-type and *A. pinsapo* in enclaves considered as interglacial refugia, something that had previously been identified in palynological studies in mountain ranges in south-eastern Iberia such as the Sierra de Baza (Carrion et al., 2007), Sierra de María (González-Ramón et al., 2012), Sierra de Segura (Carrion, 2002), Sierra Nevada (Alba-Sánchez et al., 2021a; Jiménez-Moreno et al., 2022) and Sierra de las Nieves (Alba-Sánchez et al., 2019, 2021b).

These findings provide new data on the past distribution area of coniferous forests in the Western Baetic System. According to various different wood anatomy atlases (Schweingruber, 1990; Vernet, 2001), *P. sylvestris* and *Pinus nigra* have very similar anatomical characteristics, which makes it impossible to distinguish them (Fig. 4). This methodological difficulty can also be extended to other disciplines of a paleo-ecological nature such as palynology (Mander and Punyasena, 2014). However, other authors suggest the possibility of discriminating at a species level when there is a large volume of macro-remains of adult trees in a good state of preservation (Jaquiot, 1955; García-Esteban and Guindeo, 1989).

Most of the charcoal fragments collected in this study are smaller than 2 mm in size, a fact which in many cases has made it impossible to identify the species. In spite of this limitation, the results confirm the role of Sierra Blanca as a refuge for high mountain pine forests during the early stages of the Holocene, with various fragments of *P. sylvestris*-type dated between 11,210–10,565 and 8340–7940 years cal BP in north-facing locations (Table 2). This hypothesis confirms the conclusions obtained by Alba-Sánchez et al. (2021b) in the nearby Sierra de las Nieves, where pollen analysis detected the presence of *P. sylvestris*-type in the late Holocene. At a regional level, various different studies have confirmed the presence of high-elevation pine forests in basal areas of the extreme south-west of the Baetic System during the last millennia. In particular, the remains of pollen attributed to



**Table 1**  
Geographic characteristics of the sampling sites.

Name	Coordinates	Altitude (m a.s.l.), thermotype and ombrotype	Geo-ecological environment	Substrata and soil type	Depth of the survey (cm) / sampling levels	Flora and vegetation
Cascajares 1	36°37'55"N; 05°05'04"W (X = 313,640; Y = 4,056,081)	1236 Mesomediterranean subhumid	Bottom of sinkhole S (gradient of 0%) - Basophilic grassland	Clays and massive white marbles; hemic Histosol type soil	112 / 3	<i>Poo bulbosae-Astragalium sesamei</i> : Grassland (4), <i>Phlomis crinita</i> (+), <i>Phlomis lychnitis</i> (+), <i>Ulex parviflorus</i> (+).
Cascajares 2	36°38'11"N; 05°04'45"W (X = 314,115; Y = 4,056,550)	1319 Mesomediterranean humid	NE mountainside (gradient less than 5%) - Basophilic grassland	Massive white marbles; leptosol type soil	23 / 3	<i>Paeonio coriaceae-Quercetum rotundifoliae</i> : Grassland (3), <i>Phlomis crinita</i> (2), <i>Bupleurum spinosum</i> (1), <i>Ulex baeticus</i> (1), <i>Arenaria erinacea</i> (+).
Cascajares 3	36°38'08"N; 05°04'40"W (X = 314,218; Y = 4,056,458)	1351 Mesomediterranean subhumid	W mountainside (gradient of 5%) - Basophilic grassland	Massive white marbles; leptosol type soil	42 / 2	<i>Paeonio coriaceae-Quercetum rotundifoliae</i> : Grassland (3), <i>Ulex baeticus</i> (2), <i>Bupleurum spinosum</i> (1), <i>Thymus mastichina</i> (1), <i>Carduncellus</i> sp. (1), <i>Phlomis crinita</i> (1), <i>Rhamnus pumila</i> (1).
Cascajares 4	36°38'19"N; 05°04'09"W (X = 314,999; Y = 4,056,795)	1260 Mesomediterranean humid	NW mountainside (gradient of 10%) - Scrub with pines on slope	Massive white marbles; regosol type soil	97 / 3	<i>Paeonio coriaceae-Quercetum rotundifoliae</i> : <i>Ulex baeticus</i> (3), <i>Cistus albidus</i> (2), <i>Phlomis crinita</i> (1), <i>Pinus pinaster</i> (1), <i>Pteridium aquilinum</i> (1), <i>Thymus mastichina</i> (1), <i>Bupleurum spinosum</i> (+), <i>Crataegus</i> sp. (+), <i>Daphne gnidium</i> (+), <i>Ptilostemum hispanicum</i> (+), <i>Quercus rotundifolia</i> (sapling) (+), <i>Rhamnus pumila</i> (+), <i>Rubia peregrina</i> (+).
Arroyo de los Lobos I	36°38'56"N; 05°05'06"W (X = 313,607; Y = 4,057,953)	1122 Mesomediterranean humid	N mountainside (gradient of 2%) - Basophilic grassland	Black layered limestone with loamy levels; Luvisol type soil	82 / 4	<i>Paeonio coriaceae-Quercetum rotundifoliae</i> : Grassland (4), <i>Phlomis purpurea</i> (3), <i>Cistus albidus</i> (1), <i>Daphne gnidium</i> (1), <i>Helichrysum stoechas</i> (1), <i>Pinus pinaster</i> (1), <i>Quercus rotundifolia</i> (+), <i>Thymus mastichina</i> (1), <i>Crataegus monogyna</i> (+), <i>Lavandula lanata</i> (+), <i>Ulex parviflorus</i> (+).
Arroyo de los Lobos II	36°38'57"N; 05°05'12"W (X = 313,497; Y = 4,057,929)	1142 Mesomediterranean humid	N mountainside (gradient of 7%) - Scrub	Black layered limestone with loamy levels; Luvisol type soil	40 / 4	<i>Paeonio coriaceae-Quercetum rotundifoliae</i> : <i>Cistus albidus</i> (3), <i>Pinus pinaster</i> (2), <i>Daphne gnidium</i> (1).

*P. sylvestris*-type found in the archaeological site of Pirulejo (Cordoba), with different nonsequential chronologies which range from the Older Dryas to the Holocene (López-Sáez et al., 2008). In Gorham Cave (Gibraltar), the anthracological record has also revealed the existence of cryophilic pine forests during the Last Glacial Maximum (Carrión et al., 2008; Finlayson et al., 2008). In the Cave of Nerja (Malaga), various fragments of charcoal attributed to Black Pines (*P. nigra*), were found with dates from the Gravettian until 11,930 years cal BP, coinciding with the Pleistocene–Holocene transition (Badal, 1991; Aura et al., 2002). From that point on a progressive reduction in Black Pine can be

noted, which might indicate its movement towards higher altitudes. Likewise, the fact that the latter site is relatively near the study area, together with the greater proximity of certain relict masses of *P. nigra* compared to *P. sylvestris* (Euforgen, 2022), could help attribute the charcoal fragments identified as *P. sylvestris*-type to *P. nigra* (Fig. 5).

In addition, the identification of charcoal from *Abies* in Arroyo de los Lobos 2 —a locality in which this genus is currently absent— would confirm the presence of the Spanish fir in Sierra Blanca as recently as 143–25 years cal BP. Fig. 6 contrasts the data obtained with other available geo-reference sources such as pedoanthracological

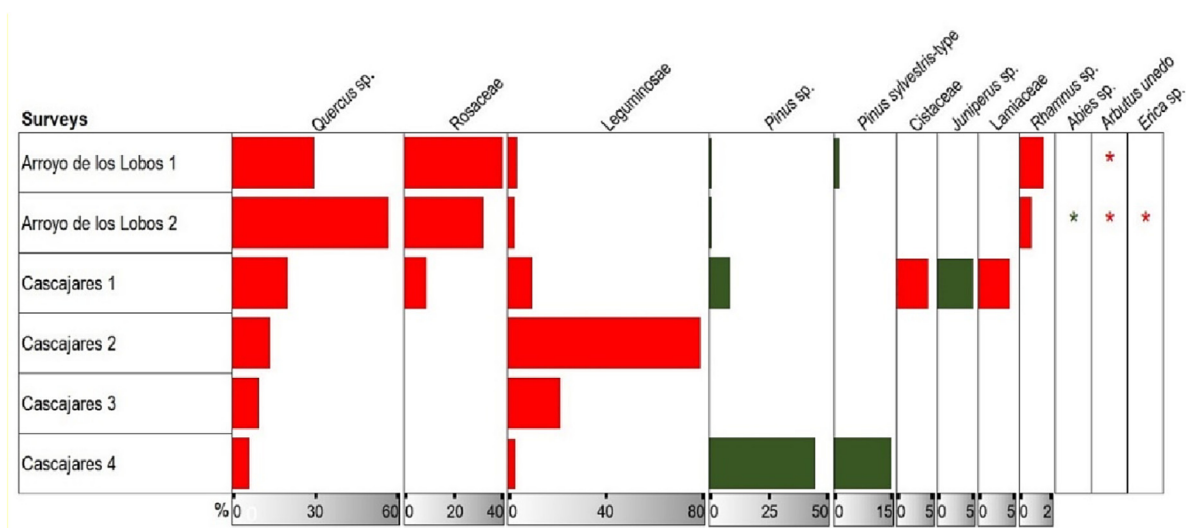


Fig. 3. Taxa identified in each one of the six pedoanthracological surveys conducted (expressed in %).

**Table 2**  
Charcoal dating.

Taxa	Lab. Code	Level	MS <sup>14</sup> C age (years BP)	Cal. age BP
Arroyo de los Lobos 1				
<i>Pinus sylvestris</i> -type	7990.1.1	III	9560 ± 124	11,210–10,565
Arroyo de los Lobos 2				
<i>Abies</i> sp.	6792.1.1	III	108 ± 23	143–25
Cascajares 1				
<i>Pinus</i> sp.	6253.1.1	III	9261 ± 88	10,605–10,240
<i>Pinus</i> sp.	6251.1.1	III	9153 ± 97	10,581–10,158
<i>Pinus</i> sp.	6252.1.1	III	8583 ± 94	9825–9421
<i>Pinus</i> sp.	6250.1.1	II	7473 ± 84	8416–8162
<i>Pinus</i> sp.	6249.1.1	I	139 ± 56	154–0
Cascajares 4				
<i>Pinus sylvestris</i> -type	7992.1.1	II	7472 ± 26	8365–8279
<i>Pinus sylvestris</i> -type	7997.1.1	III	7473 ± 25	8366–8280
<i>Pinus sylvestris</i> -type	7993.1.1	II	7352 ± 25	8198–8032
<i>Pinus sylvestris</i> -type	6793.1.1	III	7361 ± 23	8153–8033
<i>Pinus sylvestris</i> -type	7996.1.1	II	7405 ± 28	8333–8172
<i>Pinus sylvestris</i> -type	7995.1.1	II	7386 ± 25	8324–8166
<i>Pinus sylvestris</i> -type	7998.1.1	III	7335 ± 25	8184–8034
<i>Pinus sylvestris</i> -type	7994.1.1	II	7300 ± 104	8340–7940

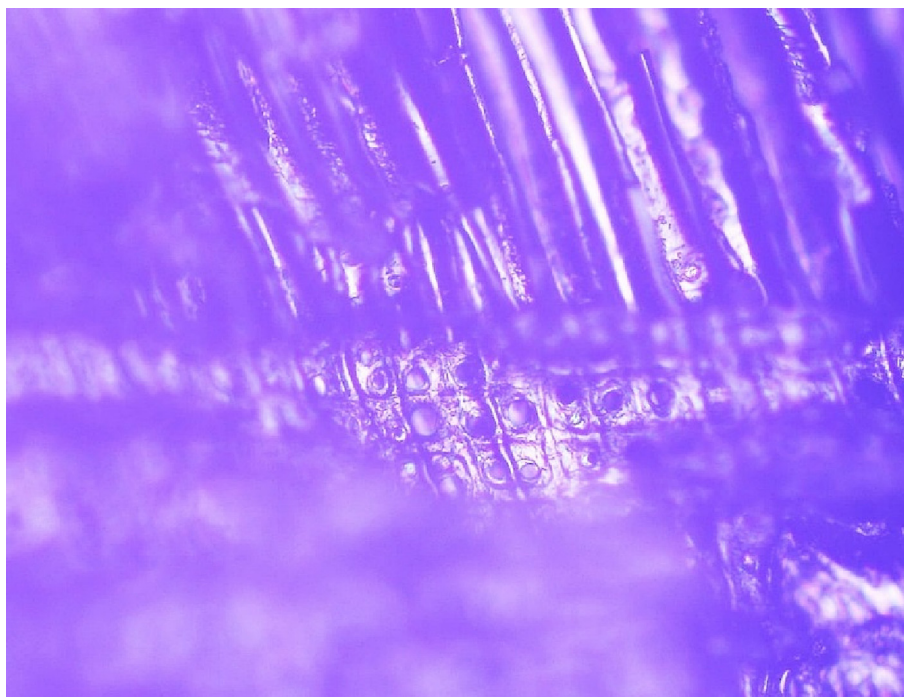
and palynological records and Species Distribution Models (SDM) (Navarro-Cerrillo et al., 2006; Sánchez-Salguero, 2007; Alba-Sánchez and López-Sáez, 2013; Gutiérrez-Hernández, 2018; Pardo-Martínez et al., 2021). The paleo-locality identified complements the paleo-biogeographical reconstruction of *Abies* conducted for the Serranía de Ronda as a whole by Pardo-Martínez et al. (2021), who found three paleo-populations with chronologies included within the Holocene. The location of these extinct populations offers us an insight as to the role that certain mountain ranges, such as Sierra del Oreganal or Sierra Palmitera, may have played as a refuge during the migration of this fir over the course of the last millennia. Both these ranges could have acted as links between the three separate disconnected Spanish fir forests existing today (Gómez-Zotano et al., 2019, 2021).

The different paleo-populations of Spanish fir discovered so far fall within the potential domain established by the models together with the other larger mountain ranges (Fig. 6).

In the same way, the palynological studies indicate a wider distribution of Spanish fir in the past in certain areas of the Serranía de Ronda, as confirmed by the results obtained by Alba-Sánchez et al. (2021b) in the nearby Sierra de las Nieves National Park. At a wider scale, there is also evidence of a broader extension of Spanish fir in the Baetic System, with records from the late Pleistocene and Holocene in locations such as the Bajondillo Cave (province of Málaga), the Gorham Cave (Gibraltar) or the Boquete de Zafarraya Cave (province of Granada) (Carrión et al., 2012, 2015; Alba-Sánchez et al., 2010; Alba-Sánchez and López-Sáez, 2013; Alba-Sánchez et al., 2018), as well as Vanguard Cave in Gibraltar (Carrión et al., 2018), Abrigo 3 del Complejo del Humo (Ochando et al., 2020), Padul (Camuera et al., 2019) and El Asperillo (Fernández et al., 2021).

The dating records for *Abies* sp. obtained by Pardo-Martínez et al. (2021), once they had been contextualised with information from other available sources, enable us to theorise about the dynamic of the Spanish firs since the Last Glacial Maximum. The migration to higher altitudes verified for *A. pinsapo* (Alba-Sánchez et al., 2018), together with a favourable scenario for fire as a consequence of the progressive aridification of the climate once the Holocene began (Jalut et al., 2000; Combourieu et al., 2009), may have ended up triggering the gradual regression of the Spanish fir forests. In fact, there is evidence of a total of 14 episodes of fire between 9931 and 9616 and 8001–7944 years cal BP in medium-altitude mountain ranges (Sierra del Oreganal, Sierra de las Nieves and Sierra Palmitera), so reinforcing the hypothesis regarding the role played by disturbances of natural origin in the distribution of *A. pinsapo* during the Early Holocene.

This dynamic may have accentuated during the mid-Holocene, as a result of the aridification of the Mediterranean climate about 6000 years ago (Mauri et al., 2015), and due to increasing anthropization at the beginning of the Neolithic, which from then on would be particularly important in areas near the Mediterranean coast and in the Ronda depression (Ramos-Muñoz et al., 2017; Castaño-Aguilar, 2021).



**Fig. 4.** Radial section of a charcoal fragment of *P. sylvestris*-type. One of its main anatomical characteristics is the existence of rays with large fenestriform pits.



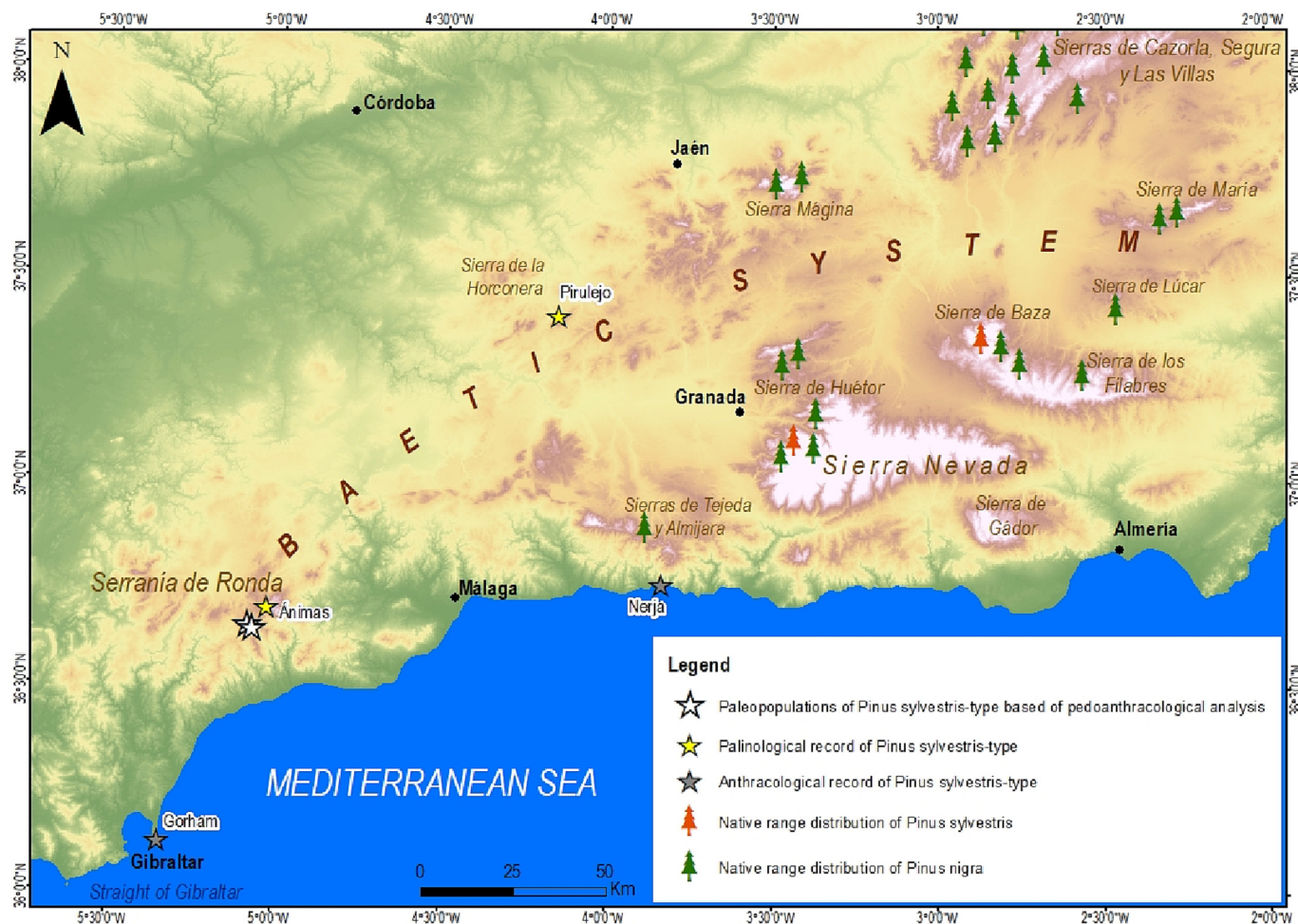


Fig. 5. Paleo-populations of *P. sylvestris*-type found during the research, other evidence of its past presence and current distribution range of *P. nigra* and *P. sylvestris* in the south of the Iberian Peninsula. Source: drawn up by the authors using information from the Andalusian Institute of Statistics and Cartography (Instituto de Estadística y Cartografía de Andalucía).

*A. pinsapo* seems to have declined much more sharply in recent times. Disturbances of anthropic origin would seem to be one of the main factors that help to explain the reduction of the distribution of Spanish fir to its current range (Guzmán et al., 2013; Alba-Sánchez et al., 2019). One of the main threats to the Spanish fir forests is fire (Blanca et al., 2001). The results have enabled us to identify up to 23 episodes of fire affecting *A. pinsapo* over the last 1000 years in the Serranía de Ronda (Pardo-Martínez et al., 2021).

Taken together, the pedoanthracological data indicate that the intense fragmentation and degradation of the habitat as a result of both anthropogenic activities and climate events have reduced the population of conifers (*A. pinsapo* and *P. sylvestris*-type) in Europe's Southernmost mountain refuges, and increased the risk of extinction of these taxa, so endorsing the conclusions reached for other Iberian conifers (Linares and Carreira, 2009; Sánchez-Salguero et al., 2017). They also enable us to confirm the hypothesis regarding the migration of certain conifers, such as *A. pinsapo* and *P. sylvestris*-type, to higher altitudes in Sierra Blanca (in shady areas) and by extension, in the Western Baetic System during the Pleistocene–Holocene transition. The Serranía de Ronda may have formed the southwestern boundary of certain high-elevation pine forests during the Holocene, before the continuous climatic oscillations of the last millennia and anthropic-related disturbances caused its definitive decline at the southwestern end of the Baetic System, where it was reduced to its current distribution range (Catalan-Bachiller, 1991; Castro et al., 2005).

In this way, the regressive dynamics experienced by the high-elevation pine forests in the Serranía de Ronda, which may possibly have resulted in their local extinction would be an excellent indicator of the vulnerability of other relict species such as *A. pinsapo* (Camarero et al., 2015; Talluto et al., 2017), a species which has already moved to higher altitudes due to climate change, leading to the contraction of its already reduced natural distribution area (González-Hernández et al., 2021).

At the same time, the pedoanthracological evidence confirms the native character of *P. pinaster* on the ultramafic soils of Sierra Bermeja (bordering on Sierra Blanca), considered a refuge area for this taxa during the Last Glacial Maximum (Olmedo-Cobo et al., 2019a, 2019b), formations of which may have occupied the sunny hillsides of Sierra Blanca together with other edapho-xerophile communities of *P. halepensis* and *J. phoenicea*.

In addition, the dates obtained from the radiocarbon dating of 15 fragments of charcoal from Sierra Blanca offer an exceptional framework of reference to enhance our knowledge of the geohistory of forest fires in the south-western end of the Baetic System, with high spatial and temporal resolution (Carracedo-Martín et al., 2017). All of this in an area for which there is a marked lack of information on this question, as can be deduced from Harrison et al. (2021), Global Paleofire Database (2022) and Sweeney et al. (2022), unlike other mountain systems in the North and centre of the Iberian Peninsula (Pérez-Obiol et al., 2016; López-Sáez et al., 2018).

The dissemination of the data obtained would reinforce the proposals made by Gómez-Zotano et al. (2017), Olmedo-Cobo et al.

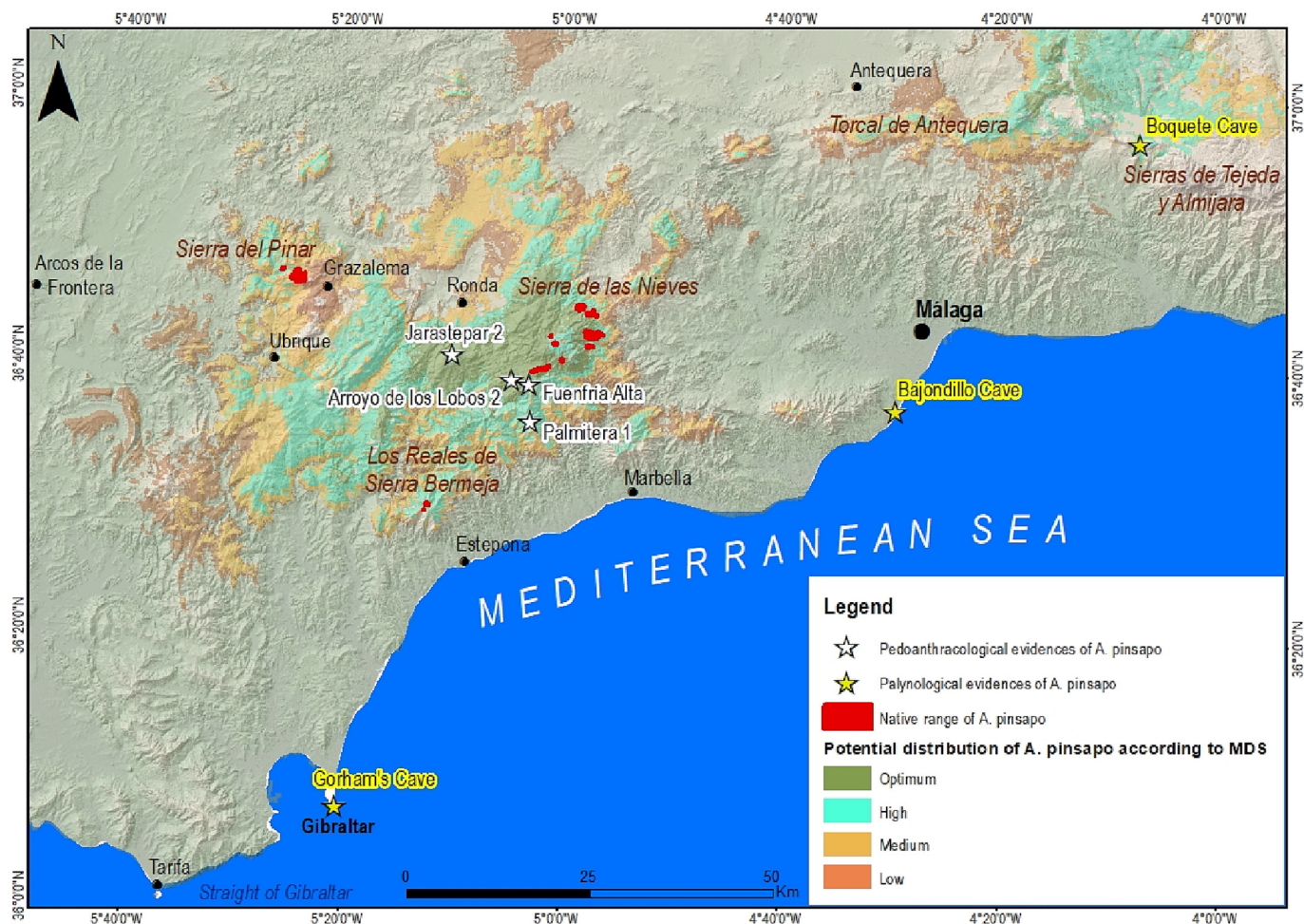


Fig. 6. Pedoanthracological and palynological evidence of *A. pinsapo* and native range and potential distribution of *A. pinsapo*. Source: drawn up by the authors using information from the Andalusian Institute of Statistics and Cartography (Instituto de Estadística y Cartografía de Andalucía).

(2019a, 2019b) and Pardo-Martínez et al. (2021) for the creation of an ecological corridor for *A. pinsapo*, complementing and broadening the Green Corridor for the Spanish Fir proposed by Gavira (2006), designed to connect the calcicolous Spanish firs in the Sierra de las Nieves National Park and the Sierra de Grazalema Natural Park. Together with the discovery of very ancient charcoal fragments of *Abies* in the Sierra del Oreganal —as the principal nexus joining the two enclaves—, the existence of ancient Spanish fir populations in Sierra Blanca and Sierra Palmitera raises the possibility of extending this ecological network to include the peridotite sector of the Serranía de Ronda (Gómez-Zotano et al., 2021). In this way it would be possible to connect the three separate, disjointed forest masses of Spanish Fir, so guaranteeing greater viability of ecosystems that are very sensitive to the current process of global change (López-Quintanilla, 2013). The implementation of these proposals would help secure the recovery of forests that have been affected by fire for thousands of years, as well as enhancing the habitats that sustain species such as the fir. This ecological corridor would reduce the isolation of local populations and would enhance the genetic exchange between the populations and the genetic variability. It would enable the supplementation of small populations in decline and would allow the recolonization of habitats and the re-establishment of populations in areas that have suffered episodes of local extinction. It would also help maintain a much greater wealth and diversity of native species and would provide a habitat, refuge and other necessary resources for numerous wild species (Quiroga and Abad, 2014; UNEP, 2019; Hilty et al., 2020).

In addition, the data obtained could enable the reintroduction of extinct high mountain pine forests (*P. nigra* or *P. sylvestris*), in those places in which evidence has been found of their previous presence. All this would give Sierra Blanca an unrivalled paleo-environmental and paleo- biogeographical role in the context of the western Baetic System, which would justify the cessation of quarrying activity, the restoration of the area and its inclusion in the Spanish National Parks network.

For all these reasons, Sierra Blanca is an exceptional palaeoecological laboratory for studying the dynamics of vegetation over time, and for exploring the problems arising from environmental conservation and management policies.

### 5. Conclusions

The results of this research have enabled us to: i) determine new paleopopulations of *A. pinsapo* and *P. sylvestris*-type by analysing soil charcoal fragments, so providing new data about its ancient distribution area; ii) discover more about the Holocene dynamics of *A. pinsapo* and *P. sylvestris*-type, the factors (climatic or human) involved and the successive stages through which the high mountain coniferous forests may have passed before being confined to their current habitats; iii) compare the soil charcoal records with pollen evidences and the species distribution models, and above all the characteristics of the natural habitats and ecological niches currently occupied by these species as a basis for their conservation and adaptative management; iv) consider the extent of the interglacial refuges as sentinels for certain relict conifer species



such as *A. pinsapo* and *P. sylvestris*-type, in a context in which a combination of natural and anthropic factors is threatening their survival.

Paleoecological evidence obtained in this research, once it has been compared with that information from other sources such as geohistorical, botanical and paleoenvironmental (above all paleoclimatic) and genetic studies, could be the basis for developing of strategies for the preservation and regeneration of *A. pinsapo*, as well as for the reintroduction of certain orophile pine species such as *P. nigra* or *P. sylvestris*.

These new possibilities for conservation and management could be applied in both the places where *A. pinsapo* is found today, and in others that show high potential as a future habitat for this species, as established paleoecological sources and suitability models. This involves to disseminate the results of this research to public administrations and private companies with responsibilities in the management of these emblematic forest resource. Paleo-biogeographical 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 forests.

Likewise, the first evidence of *P. sylvestris*-type discovered in the Serranía de Ronda by using analysis of the charcoal present in the soil, constitutes an unprecedented informative resource in the context of the Western Baetic Cordillera. This finding reinforces the idea of glacial refuge played by the Serranía de Ronda during the last millennia for certain conifers forests. The palaeoecological information obtained can be used as an indicator of the dynamics that certain relict mountain pine forests may experience in a context of Global Change such as the present one, helping their adaptive management.

#### Author contributions

J.G. conceived, designed and led the research; J.G., R.P. and J.A.O. carried out the fieldwork and collected field data; R.P., J.A.O. and F.A.S. analysed the data; J.G. took the lead in writing the manuscript; R.P., J.A.O. and F.A.S. assisted with analyses and writing the paper; R.P. and J.A.O. produced the figures; F.A.S. led the funding acquisition and project administration; all authors reviewed the manuscript and contributed to the final draft.

#### Data availability

The data for this paper will be freely available from the corresponding author.

#### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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