Environmental Earth Sciences (2023) 82:220
https://doi.org/10.1007/s12665-023-10912-4

ORIGINAL ARTICLE

Paleopopulations and ecological connectivity in the Natura 2000 Network: proposal for the serpentine-soil Spanish firs of Sierra Bermeja (Serranía de Ronda)

José Gómez-Zotano[1] · Rubén Pardo-Martínez[1] · José Antonio Olmedo-Cobo[1]

Received: 23 January 2023 / Accepted: 8 April 2023 / Published online: 25 April 2023

Abstract
One of the conservation priorities of the Natura 2000 Network is the ecological connectivity of forests and species of community interest to facilitate compliance with the obligations of the EU Habitats Directive. The location of paleo-populations and past distribution areas is a first step towards creating an ecological corridor which, with the protection enjoyed by Special Areas of Conservation, could positively impact the resilience of forest species in the face of Climate Change. The endangered relict forests of Spanish fir (*Abies pinsapo*) are endemic in the Serranía de Ronda (Baetic Cordillera, Southern Spain) and form a highly fragmented habitat of community interest. Amongst these forests, the Spanish fir forests that grow on serpentine soils are particularly interesting. This ultramafic mountain range has suffered the highest recurrence of forest fires in all the Serranía de Ronda, and as a result, the Spanish fir forests have been subject to processes of local extinction throughout history. In this research, we used pedoanthracology to uncover ancient locations of *Abies pinsapo*; in this way, forest fires are the main cause of the disappearance of this emblematic species in Sierra Bermeja, and their charcoal remains allowed us to make a precise reconstruction of its past distribution area. On the basis of the data obtained, an ecological corridor linking these relict forests was proposed. This corridor has now begun to be implemented with the participation of public and private social agents.

Keywords *Abies pinsapo* · Ecological corridor · Local extinctions · Pedoanthracology · Special areas of conservation

Introduction

The temperate Mediterranean Mountains of Europe host critical natural forest systems which make up habitats of interest and are a refuge for relict and/or endangered emblematic tree species located at the southern and altitudinal extremes of their geographical distribution areas (López-Albarrado and Farris 2022; Médail and Diadema 2009; Médail et al. 2019). The preservation of these orophile forests has been and continues to be an essential objective in government policies to ensure nature conservation and sustainable development in countries, such as Spain, France, Italy, Greece, or Portugal. In these countries, mountains and forests were among the first places to arouse public interest in nature protection, and their eco-cultural values were recognized in the declarations of the first National Parks. They have also been the subject of the most recent protection actions at the European level in that the EU's Natura 2000 Network is primarily made up of forests (Brambilla et al. 2015; Catalan et al. 2017; Kulakowski et al. 2017).

In this sense, and within the framework of the conservation priorities established in the management plans of the Special Areas of Conservation (SAC) of the Natura 2000 Network, declared as such because of the importance of their natural forest systems, particular emphasis is being placed on the ecological connectivity of both forest formations and species of community interest (Jongman 1995; Pino and Marull 2012; Van der Windt and Swart 2007). The preservation of montane conifer forests made up of paleo-endemic, endangered species is of particular interest, especially in the case of Mediterranean forests situated at the southern and altitudinal extremes of their geographic distribution area and included in the Natura 2000 Network (Becker et al. 2007; Holtmeier and Broll 2007; Ruíz-Labourdette et al. 2013).

✉ José Gómez-Zotano
jgzotano@ugr.es

[1] Department of Regional Geographic Analysis and Physical Geography, University of Granada, Granada, Spain

However, the degree to which the management plans set out in this European framework have been implemented varies significantly from country to country. In Spain, for example, the limited implementation of these plans has resulted in numerous Habitats of Community Interest (HCI) containing montane conifer forests suffering excessive fragmentation due to deforestation, grazing, and forest fires over the centuries. This highly fragmented forest pattern is associated with a qualitative reduction in connectivity, which harms the resilience of many organisms in the face of Climate Change (Krosby et al. 2010).

One clear example is the Spanish fir or *Abies pinsapo* Boiss. (HIC 9250), relict tree formations descended from ancient tertiary forests, which find biogeographical refuge in relatively inaccessible mountain enclaves in the Serranía de Ronda (Andalusia, Spain). These include SAC Sierra Bermeja y Real; SAC Los Reales de Sierra Bermeja; SAC Sierra de las Nieves; SAC Sierra de Grazalema; SAC Sierra Blanca. A survivor of the postglacial retreat of the southernmost Mediterranean fir forests, this species is classified as endangered under Andalusian Law (Law 8/2003, of 28th October, on Wild Flora and Fauna).

Within its small distribution area, the Spanish fir is especially endangered in the ultramafic massif of Sierra Bermeja, where a centuries-long process of local extinctions has combined with a current alarming situation of isolation of its populations due to the fragmentation of its habitat. This jeopardizes the viability and gene exchange of this circum-Mediterranean fir species on serpentine soils (Arista 1995; Gómez-Zotano and Olmedo-Cobo 2021; Guzmán et al. 2012; Linares 2011; Linares et al. 2009; Olmedo-Cobo et al. 2017; Pérez-Latorre et al. 2001). The main risk factors threatening *A. pinsapo* today are forest fires, the isolation of the populations and their monostructural characteristics, the alteration of their habitats, diseases associated with fungi and insects, and to a lesser extent, hybridization and atmospheric pollution (López-Quintanilla 2013). These factors have partially halted the recovery that the species had been showing since the mid-twentieth century once the anthropic pressure (in the form of tree felling, charcoal making and overgrazing) on its ecological niches had subsided.

Although there have been significant advances in the paleo-biogeographical knowledge of this species in recent years, there is a lack of paleo-ecological analyses that complement the small number of palynological and pedoanthracological studies so far conducted in Spanish fir refuge areas (Alba-Sánchez and López-Sáez 2013; Gómez-Zotano and Olmedo-Cobo 2021; Gómez-Zotano et al. 2017; Olmedo-Cobo et al. 2017, 2021; Pardo-Martínez 2020; Pardo-Martínez et al. 2021).

These forests are essential for the ecological continuity of this species and remain exposed to real threats which have devastated these forests in the last centuries. With this premise, a series of hypotheses were established for this research:

(a) The existence in the past of more extensive, more continuous distribution areas of *A. pinsapo* in Sierra Bermeja based on evidence from historical sources, studies of its present-day habitats, and species distribution models (SDMs).

(b) The deteriorated state of conservation of *A. pinsapo* in Sierra Bermeja is a sign that this species is on the point of local extinction and, consequently, must be treated as an endangered, highly unusual relict species.

(c) The ecological conditions of the micro-habitats where these conifers take refuge and the demographic characteristics of their populations make natural regeneration and expansion very difficult.

(d) The recovery of these conifers seems possible through the establishment of a suitable strategy for their conservation based on the protection of their ecological niches, particularly reforestation.

Bearing in mind these initial hypotheses and the conservation priorities of the SAC of forestry interest. This research aims to develop a proposal to improve the ecological and landscape quality and connectivity of the serpentine-soil Spanish fir forests of Sierra Bermeja based on past locations of *Abies* sp. discovered through pedoanthracological analysis (populations that have disappeared after being subject to recurrent fires throughout the Holocene). The data obtained enabled us to propose a solid model for an ecological corridor linking the Spanish fir forests. We also aim to transfer the results of this research to the relevant public administrations with powers to manage this emblematic forest resource to improve the ecological connectivity of the serpentine-soil Spanish fir forests of Sierra Bermeja.

Methodology

Study area

Sierra Bermeja is a mountainous area of the Serranía de Ronda, which acts as a hinterland of the Western Costa del Sol (province of Malaga). It is a medium-altitude coastal mountain range that reaches 1508 m a.s.l. (Cerro Abanto). Moreover, it is one of the most extensive ultramafic outcrops on the planet. The area is part of the Natura 2000 Network as SAC "Los Reales de Sierra Bermeja" and SAC "Sierras Bermeja y Real". They have an area of 1236 ha and 30,824 ha, respectively (Fig. 1). The natural forest systems associated with peridotites are of particular importance, creating plant associations that form HCI 9520 (*Abies* pinsapo Spanish fir forests) and HCI 9540 (Mediterranean pine forests with endemic Mesogean pines). Protecting these habitats and ecological connectivity

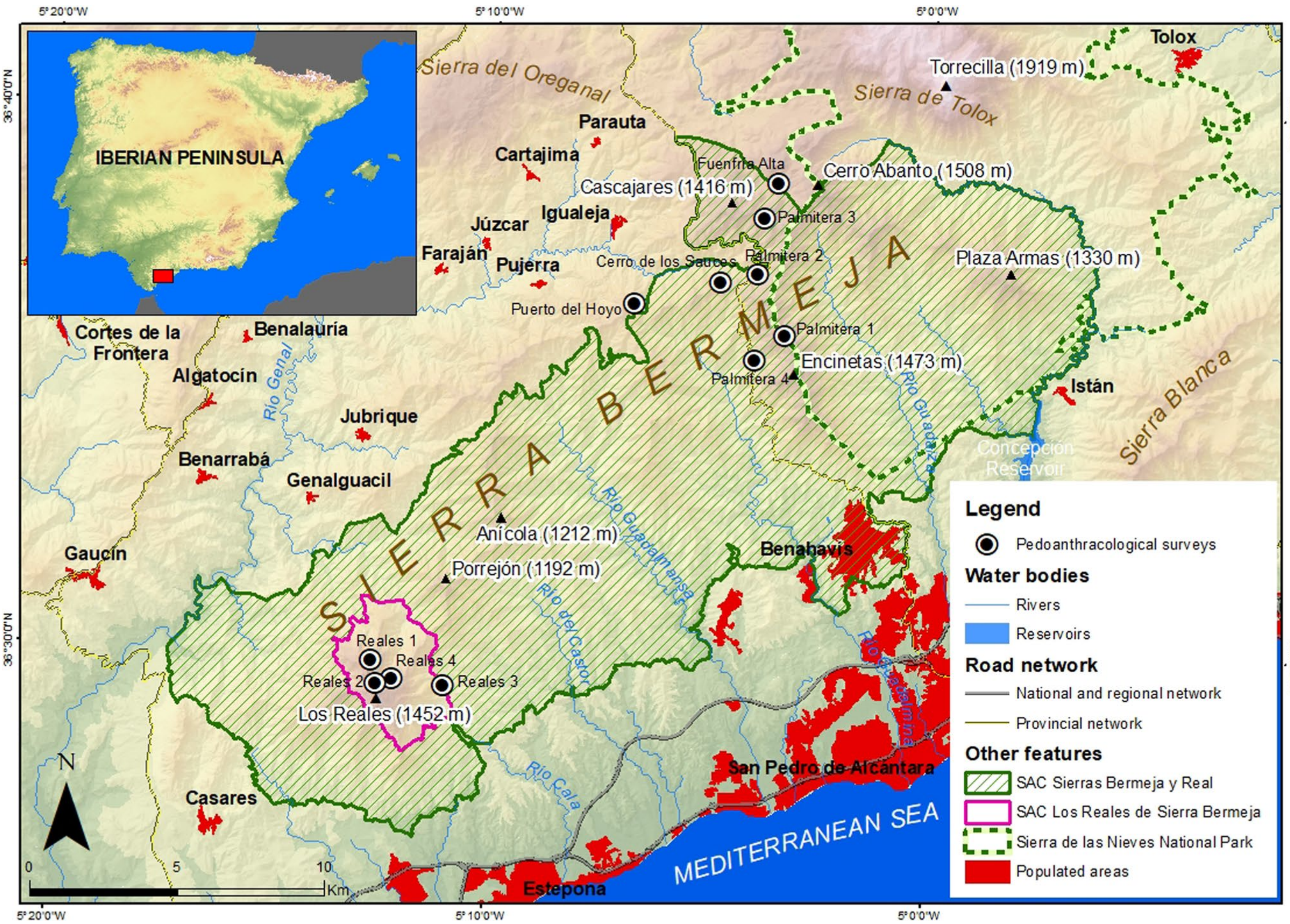

Fig. 1 Study area and location of the pedoanthracological surveys conducted during this research. Source: Andalusia Spatial Data Network

are the two main Conservation Priorities identified in the SACs' management plan and the reason for the declaration of Los Reales de Sierra Bermeja as a protected Natural Space in 1989. Of all these forest habitats, the HCI 9520 stands out in that it is classified in the Plan as very rare; the Spanish fir forests that grow on serpentine soils are a relict plant community that is unique in the world (Cabezudo et al. 1989; Gómez-Zotano et al. 2014; Pérez-Latorre and Hidalgo-Triana 2017; Pérez-Latorre et al. 2020). Due to its high natural and cultural values, this area is part of the Andalusia (Spain)—Morocco Intercontinental Biosphere Reserve of the Mediterranean. Recently, the eastern half of Sierra Bermeja was included in the Sierra de las Nieves National Park.

Method

The first phase of the method involves the analysis of all those earlier sources of information that enable us to estimate the past, present, and potential future distribution area of *A. pinsapo*, as represented above all in the studies by Becerra (2006), Gil (2002), Gómez-Zotano (2004), Gómez-Zotano and Olmedo-Cobo (2021), Guzmán et al. (2012) and López-Quintanilla (2013), and to characterize its habitat in geographical and phytogeographical terms.

The second phase of the method is based on pedoanthracological analysis. In this research, we followed the pedoanthracological protocols established by Talon et al. (1998) and adapted by Cunill et al. (2012). According to the basic information, 11 pedological surveys were conducted in areas considered potential hosts of serpentine-soil Spanish fir forests in Sierra Bermeja (Fig. 1). Between one and eight sampling levels were identified in each site. These were partly delimited using soil horizons, and between 3 and 15 kg of soil were collected for each level. The samples were then processed in the laboratory using the water-sieving technique (mesh sizes of 5, 2, and 0.8 mm) (Fig. 2). Later, once the mineral fraction collected in the meshes during the sieving process had dried, we conducted manual triage of the charcoal it contained with the help of a binocular magnifying glass. After calculating the absolute anthracomass (mg of charcoal/kg of mineral residue) for each sampling level, we then conducted a detailed study of the three anatomical sections of the wood (transversal, longitudinal radial, and longitudinal tangential) using an incident light episcopic microscope (differential interference contrast of 50×, 100×, 200×, and 500×). The next stage was to try to identify the taxa of the charcoal samples we had collected using the wood anatomy identification keys provided by Schweingruber (1990) and Vernet et al. (2001), and by comparing them with the charcoal samples from the reference collection at the anthracotheque at the Terra Laboratory at the University of Granada. A total of 3565 fragments were analyzed, of which 28 were sent for C^{14} AMS radiometric dating at two specialized laboratories: Poznań Radiocarbon Laboratory (Poznań, Poland) and Alfred-Wegener-Institut (Bremerhaven, Germany). They were then calibrated with Oxcal v. 4.4 using the IntCal20 database (Reimer et al. 2020), to 2 sigma (95% probability). Figure 2 shows some of the tasks conducted during this second phase of the pedoanthracological method.

This method's third and final phase involved designing and mapping a proposal for the ecological connectivity of *A. pinsapo* based on the results of the previous two phases.

Results

Analysis of the information sources

A few diachronic studies have been conducted to reconstruct the evolution of the Spanish fir forest in Sierra Bermeja over time. The most interesting for these purposes is the historical data set out in Gómez-Zotano (2004), Gómez-Zotano and Olmedo-Cobo (2021), Guzmán et al. (2012), and Junta de Andalucía (2012). These studies highlighted increased fragmentation of Spanish fir habitats and a decline in its surface area since the eighteenth century, most specifically in the Spanish fir forests in Los Reales, Abanto, Armas, and Corona. They also confirmed the extinction of other smaller forest formations in Trincheruelas, Duque, and Cerro del Pollo. The main risk factors that have endangered populations of *A. pinsapo* in the recent past are forest fires (especially the ones in 1991 and 2021), the isolation of the populations and their monostructural characteristics, the modification of their habitats, the diseases associated with fungi and insects, and, to a lesser extent, hybridization and atmospheric pollution (López-Quintanilla 2013). These factors have helped halt, at least in part, the expected recovery since the mid-twentieth century, once the anthropic pressure on its ecological niches (tree felling, traditional charcoal production, and overgrazing) had declined.

Regarding the research into this species' habitats and ecological niches, the phytogeographic studies by Gómez-Zotano et al. (2017) and Pérez-Latorre and Hidalgo-Triana (2017) are especially interesting. These studies described the singularity of the vegetation in the bermejense sector (biogeographical territory of Sierra Bermeja). At a broader scale, Liétor et al. (2003) analyzed the causal relations established between the characterization of the edaphic medium and the availability of the macro- and micro-nutrients required for the development of *A. pinsapo*. Torres-Cabañete et al.

Fig. 2 Photographs illustrating the pedoanthracological method applied at the "Palmitera 1" site: **a** carrying out the survey; **b** preparing the edaphological profile; **c** charcoal sample; **d** sieving; **e** selected charcoal fragments

(2009) centred their research on the flows of the nutrients of the Spanish fir forest, concluding that the structural modifications of the microbial community present in the soils inhabited by *A. pinsapo* depended on the biogeochemical variability between the different types of Spanish fir forests. Other research studies, such as those carried out by Carreira de la Fuente et al. (2013) and Lázaro-Gimeno et al. (2013), respectively, analyzed the effects of atmospheric pollution and of tropospheric ozone on Spanish fir populations. The phytosanitary state of the forest masses of this species was explored by Cobos-Suárez et al. (2013), who concluded that the population density and state of conservation of the serpentine-soil Spanish fir forest varied considerably from one place to another.

For their part, the main SDMs applied to *A. pinsapo* (Alba-Sánchez and López-Sáez 2013; Alba-Sánchez et al. 2010; Gonzalo et al. 2004; Gutiérrez-Hernández 2017, 2018; López-Tirado and Hidalgo 2014; Navarro et al. 2006) have been based on suitability patterns and multivariable regressions for establishing different degrees of the potentiality of this species in the mountains in the South and Southeast of Spain. As regards Sierra Bermeja, these models indicate a high number of habitable areas for the Spanish fir in almost all its territory above 800–1000 m a.s.l., covering all the mountain ridges that link the present-day Spanish fir forests that have taken refuge in the peripheral peaks of the massif. From a prospective point of view, the models applied by the Regional Government of Andalusia are of particular interest (Junta de Andalucía 2014). These models show a significant reduction in the habitat suitability area of the Spanish fir at the end of the current century. In this way, the high levels of suitability manifested in the previous years are now giving way to medium and low values, so revealing how climate change is ushering in an uncertain future for the survival of this species (González-Hernández 2021; Lenoir and Svenning 2014).

Pedoanthracological analysis

In this study, we analyzed 3565 charcoal fragments (Fig. 3), of which 2341 (62.8%) were correctly identified. The remaining 1224 fragments (34.3%) were impossible to identify. The most frequent causes preventing us from identifying the taxa of these fragments included vitrification processes, the deformation of the anatomical structure of the wood, and/or the presence of fungi.

We identified up to 144 *Abies* fragments in 4 of the 11 sites sampled. Palmitera 1 and Fuenfría Alta were considered to be *Abies* paleo-populations (Fig. 4), as, in both sites, this genus is not present today. The specific anthracomasses were relatively small, with values varying between 233.6 mg/kg in Palmitera 1, 37.5 mg/kg in Reales 2, 9.8 mg/kg in Fuenfría Alta, and 8.4 mg/kg in Reales 1.

The most frequently identified taxon in the pedoanthracological record was *P. pinaster* with 765 charcoal fragments (21.5% of the total). Its specific anthracomass values ranged between 14,295.2 mg/kg for Palmitera 1 and 7.3 mg/kg for Palmitera 4.

The second most common genus was *Quercus* with 679 fragments identified (19% of the total). This genus was found in seven out of the 11 surveys conducted. The anthracomass values varied between 63,601.5 mg/kg in Palmitera 1 and 8.4 mg/kg in Reales 4.

The pedoanthracological record was completed by families and genera such as *Pinus* (1.3%), Lamiaceae (0.7%), *Juniperus* (0.5%), Leguminosae (0.5%), Rosaceae (0.4%),

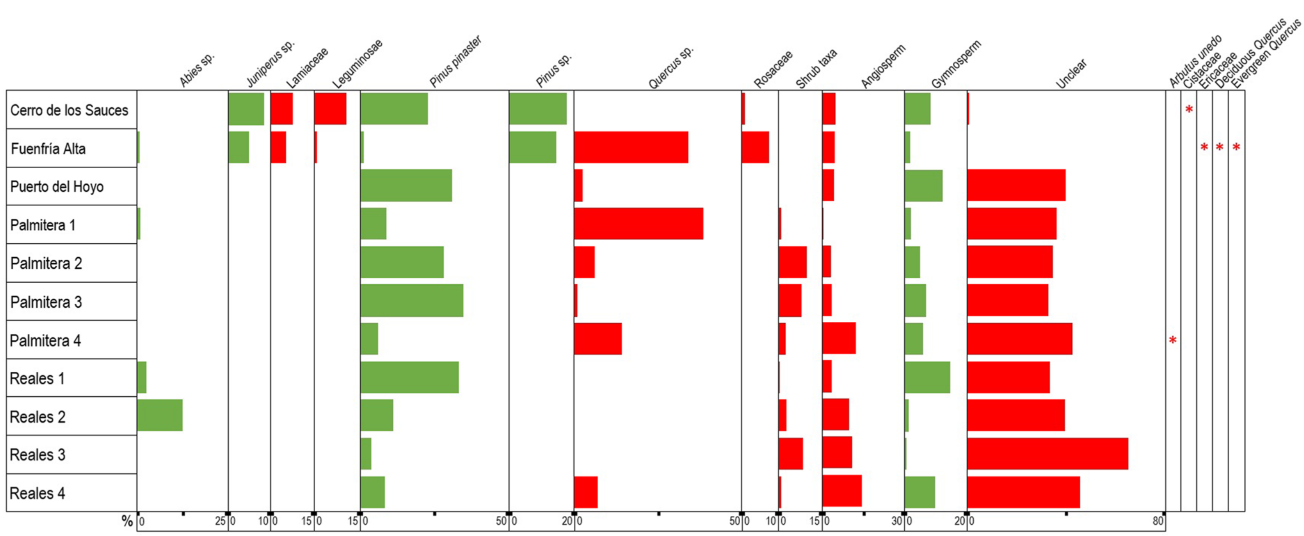

Fig. 3 Taxonomic identifications in each of the sampling sites in Sierra Bermeja

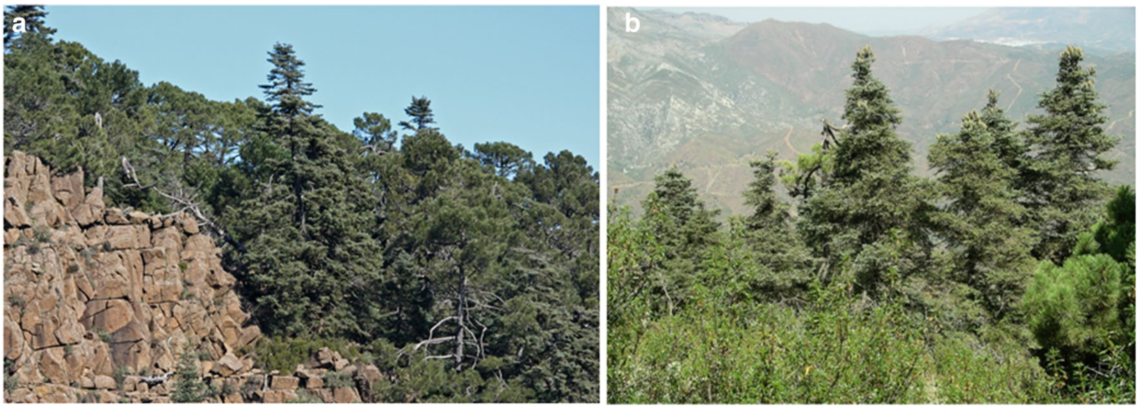

Fig. 4 Core areas for the serpentine-soil Spanish fir corridor (**a** Los Reales; **b** Plaza de Armas)

evergreen *Quercus* (0.3%), deciduous *Quercus* (0.2%), Ericaceae (0.2%), and Cistaceae (0.1%).

Regarding radiocarbon dating, 28 fragments of *Abies* were dated, obtaining chronologies ranging between 9931 and 9616 years cal BP and 282–82 years cal BP (Table 1).

Table 1 Chronologies obtained by radiocarbon dating for samples of *Abies* sp

Survey	Laboratory code	Conventional age (C14 years BP)	Calibrated age (years cal BP) (95%)
Palmitera 1	5173.1.1	8707 ± 37	9931–9616
	5174.1.1	8573 ± 35	9719–9551
	5176.1.1	8549 ± 36	9552
	5175.1.1	8300 ± 40	9266–9206
	5177.1.1	8155 ± 39	9245–9076
	5170.1.1	8003 ± 128	9236–8615
	5171.1.1	8057 ± 111	8672
	Poz-83921	7300 ± 50	8342–8053
	5169.1.1	7142 ± 34	8001–7944
	Poz-78851	6480 ± 40	7516–7356
	5172.1.1	6239 ± 35	7224–7085
	Poz-78852	5710 ± 40	6651–6473
	Poz-83920	5840 ± 40	6607–6573
	Poz-83922	5770 ± 40	6553–6523
	Poz-83924	4605 ± 35	5441–5145
Reales 1	Poz-83919	8860 ± 50	9810
	Poz-83918	6160 ± 40	7014
	Poz-78858	200 ± 30	326–208
	Poz-78859	195 ± 30	325–143
	Poz-78885	60 ± 30	294–102
Reales 2	Poz-82525	3270 ± 30	3516–3476
	Poz-82527	1800 ± 30	1832–1674
	Poz-83914	45 ± 30	295–103
	Poz-83913	40 ± 30	295–103
	Poz-83912	110 ± 30	282–82
Fuenfría Alta	Poz-113780	8740 ± 50	9619
	Poz-113779	4970 ± 35	5897–5668
	Poz-113778	5015 ± 35	5726–5679

Proposal for the connectivity

Following the results of the pedoanthracological analysis and the previous information analyzed, we propose setting up an ecological corridor for the Spanish fir forests that grow on serpentine soils to create a continuous habitat connecting its two core areas (Figs. 4, 5 and 6). Core Area A is at the western end and hosts the largest Spanish fir forest, located on the peak known as Los Reales (1452 m a.s.l.). For its part, Core Area B, at the Eastern end, is made up of the little Spanish fir forest in the Plaza de Armas (1330 m a.s.l.). Between the two, an isoaltitudinal ridge runs parallel to the coast from which various peaks of over 1000 m a.s.l. jut out (these include, from southwest to northeast, Porrejón 1192 m a.s.l., Anícola 1212 m a.s.l., Canalizo 1166 m a.s.l., Caballo 1092 m a.s.l., and Sauces 1157 m a.s.l.). This ridge occupies the western half of the massif. In its eastern half, various peaks reach higher altitudes than Sierra Bermeja, namely Sierra Palmitera (Encinetas 1473 m a.s.l.), Cerro del Duque (1342 m a.s.l.), Cerro Abanto (1508 m a.s.l.), and Cerro Corona (1299 m a.s.l.). In the first of these enclaves, charcoal fragments from paleo-populations of Spanish fir were found, while in the others, there are a few surviving remains of Spanish fir forests (individual trees and small copses), most of which were seriously damaged by the big fire of 1991.

Overall, the ridge forming the backbone of Sierra Bermeja shows a high level of ecological homogeneity:

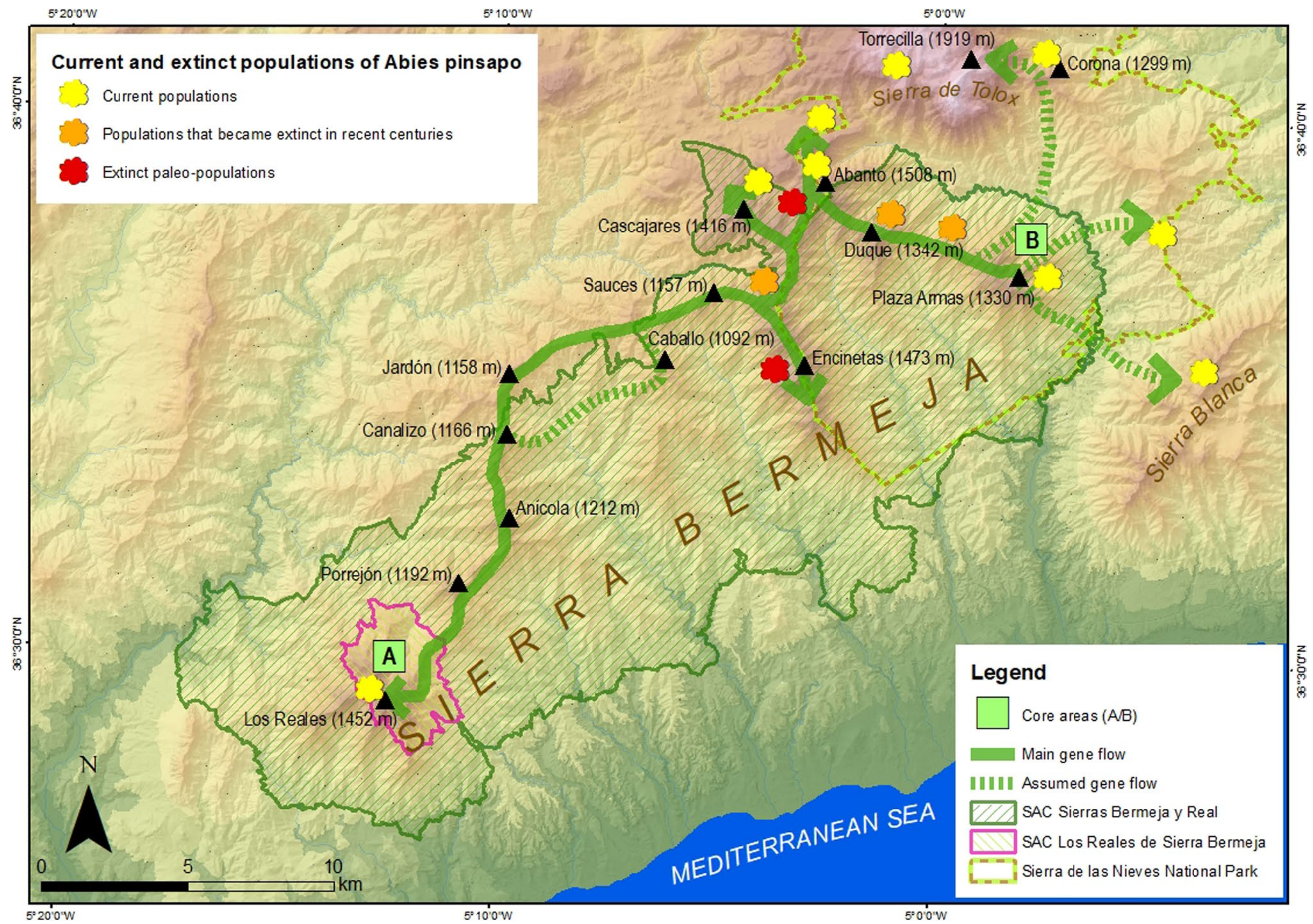

Fig. 5 Map of the corridor for the serpentine-soil Spanish fir and its main gene flow. Source: drawn up by the authors using layers of geographic information from the Andalusia Spatial Data Network as the cartographic base

Fig. 6 Ridge of Sierra Bermeja which would form part of the ecological corridor of the serpentine-soil Spanish fir forest

serpentine soils, humid–hyperhumid ambrotype, non-rainfall water inputs, and a meso-supramediterranean bioclimatic stage (the latter at altitudes of over 1200–1400 m a.s.l.). This mesological continuity is only interrupted at the headwaters of the River Guadalmansa, where metamorphic materials (gneisses and schists) appear along about 6 km of the drainage divide. Aside from the lithological differences, the cold temperatures and humidity are also important factors as the ridge continues at altitudes of over 1000 m a.s.l. (Cerro Jardón, 1158 m a.s.l.). This sector, which belongs to the SAC Valle del Genal, was excluded from the SAC Sierra Bermeja y Real, because it hosts plantations of sweet chestnut (*Castanea sativa*) and Monterey pine (*Pinus radiata*).

The ridge forming the ecological corridor has a minimum length of 36 km, interrupted only by narrow mountain passes, such as Peñas Blancas (972 m a.s.l.), Chaparral (932 m a.s.l.), Hoyo (963 m a.s.l.), Allanadillas

(1065 m a.s.l.), and Refriega (916 m a.s.l.), which act as minor natural barriers to gene exchange (passage of individuals, seeds, pollen, spores, etc.), without this creating an obstacle for the future viability of the naturally disjointed populations. No remains of *Abies sp.* were identified in the pedoanthracological survey conducted in Puerto del Hoyo.

The ecological corridor has clear, well-defined boundaries to the northwest (Genal Valley) and south (Mediterranean coast). In the East and Northeast, there might be exchanges with Spanish fir populations that grow on carbonated and schistose soils in Sierra Blanca de Marbella, Bornoque, and Sierra de las Nieves, included in the SAC. In addition, the extension of the corridor towards Sierra Blanca de Igualeja (Cascajares, 1416 m a.s.l.) in the north is necessary to connect the isolated Spanish fir forests in this marble-stone mountain, which also belongs to the SAC Sierra Bermeja y Real.

Reforestation activities

The transfer of the results of this research to the Public Administrations and to private actors with competencies in this field has enabled us to implement the proposal for a network of ecological corridors of *A. pinsapo*, which connect their fragmented populations in Sierra Bermeja. Using the pedoanthracological data, in combination with SDMs (Navarro et al. 2006), the species has been reintroduced in 15 localities where it no longer grew, through the Plan for the Recovery of the Spanish Fir being implemented by the Department of Agriculture, Livestock-Farming, Fishing and Sustainable Development of the Regional Government of Andalusia (Fig. 7).

The reforestation activities involved a combination of seeding (7200 seeds planted in the shaded areas of Jubrique, Pujerra and Igualeja from the end of 2020 to January 2021) and direct plantation from 2019 of 1094 plants with 3–7

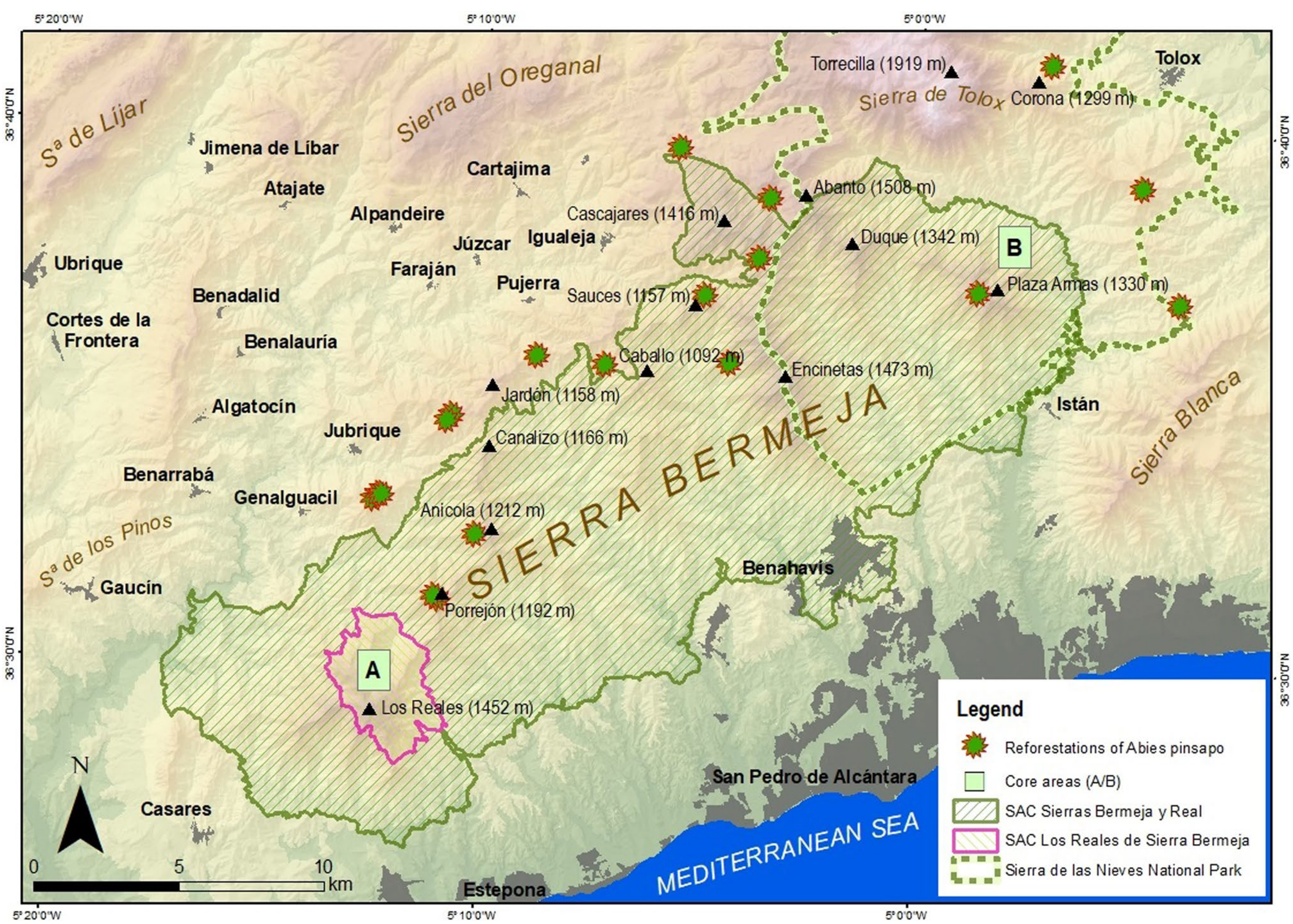

Fig. 7 Localities in which *A. pinsapo* has been reintroduced. Source: Andalusia Spatial Data Network

internodes in publicly owned mountainsides (880 plants from Core Area A between Jubrique and Igualeja and 214 from Core Area B in the Sierra Real de Istán), and 13–15 internodes in private estates. In the latter, which made up 2 of the 15 localities, the work was carried out with the active collaboration of the Asociación El Glaucal de La Nava and an extensive volunteer network. Projects of particular interest include planting Spanish firs in the Venta del Madroño and the project known as "Bosque Eterno" or Eternal Forest involving sponsoring Spanish firs (Fig. 8). All these actions have brought about a significant improvement in the local environment, given the minimal territorial representation of *A. pinsapo*, the threats to which it is exposed and the ecological requirements which have led to it being classified as an endemic species with a very closely confined distribution area.

Discussion

Paleo-ecological bases

The application of the pedoanthracological method in different locations of Sierra Bermeja has enabled us to propose a model of ecological connectivity based on the following paleo-ecological aspects: (1) enhanced knowledge of the present and potential future distribution of *A. pinsapo* in Sierra Bermeja; (2) the confirmation through the analysis of the soil charcoal uncovered in the surveys that *A. pinsapo* once had a larger distribution area in Sierra Bermeja; (3) a more precise knowledge of the dynamics of the Spanish fir forests after the Last Glacial Maximum, the causes that led to its local extinction, and the consequent shrinking of its past distribution area to its current one; (4) the assessment of the role played by climate and of the autochthonous nature of the conifer forest during the Holocene in Sierra Bermeja; (5) the verification of the critical role played by fire in the configuration of the plant landscape during the last millennia in this area; (6) the confirmation using charcoal fossil records of the veracity of the historic sources and of the SDMs.

The identification of various fragments belonging to the *Abies* genus (presumably *A. Pinsapo*) in Palmitera 1 and Fuenfría Alta, localities where this genus is no longer present today, enabled us to confirm that the Spanish fir once covered a much larger area. This idea, first raised by Linares (2011), was later reinforced by the findings of different paleo-pollen records from the Holocene in various different locations of the South and East of the Iberian Peninsula (see Alba-Sánchez and López-Sáez 2013; Alba-Sánchez et al. 2018), although the very limited representation of this taxon in the pollen diagrams did not enable this claim to be verified with a sufficient degree of certainty (see Carrión 2013). This hypothesis was later ratified by the discovery of up to four extinct populations of *Abies* in the Serranía de Ronda as a whole (Palmitera 1, Fuenfría Alta, Jaraestepar 2,

Fig. 8 **a** Seeding work in the publicly owned mountainside of Sierra Bermeja de Igualeja; **b** seeds classified according to the Spanish fir forest of origin; **c** and **d** private Spanish fir plantation project in the Venta del Madroño; **e** and **f** reforestation activities for the creation of the Bosque Eterno (Eternal Forest)

and Arroyo de los Lobos 2), after the application of pedoanthracological analysis (Olmedo-Cobo et al. 2021; Pardo-Martínez et al. 2021), a paleo-ecological discipline with a high spatial resolution which verifies the local presence of the identified taxa (Cunill et al. 2012; Talon et al. 1998).

In general, our findings reveal the important role played by Sierra Bermeja as a postglacial refuge for different species of conifers (such as *A. pinsapo* and *P. pinaster*) after the Last Glacial Maximum. This discovery enabled us to fill an important gap in our knowledge of the southern part of the Iberian Peninsula. This is because, until relatively recently, a large percentage of the paleo-ecological studies carried out in this region focused on the Southeast (see Anderson et al. 2011; Carrión et al. 2007; Gil-Romera et al. 2010), or coastal areas and/or areas at relatively low altitude in the Southwest of the Iberian Peninsula (see Carrión, 2013). Besides, the bermejense sector and the Serranía de Ronda as a whole form an interesting biogeographical crossroads (Gómez-Zotano and Olmedo-Cobo 2021), which gives it a great variety of climatic and historic singularities—within its regional context—all of which make it a unique space from a paleo-biogeographical point of view (Gómez-Zotano 2004). The data obtained have also confirmed that both species make up the climax vegetation in Sierra Bermeja, so revealing that *P. pinaster* is an autochthonous species on ultramafic soils, thus bringing to an end a debate that had long divided the scientific community (Olmedo-Cobo et al. 2019).

On the one hand, the radiocarbon dating of 28 charcoal fragments belonging to the *Abies* genus has made it possible to theorize about the dynamics of the Spanish fir in the bermejense sector after the Last Glacial Maximum; and on the other hand, these data confirm the critical role played by fire in the configuration of the plant landscape of Sierra Bermeja, and how for thousands of years fire has been one of the leading causes of local extinction of *A. pinsapo* in areas where this fir no longer grows. The Spanish fir forest in Sierra Bermeja was affected by up to five episodes of fire in the first stages of the Holocene, with chronologies dating from 9931–9616 to 9552 years cal BP. This time interval coincided with a period of maximum heat and dryness around the Alboran Sea approximately 9500 years ago (Cacho et al. 2001; Jalut et al. 2000), which, together with the still limited representation in the paleo-pollen diagrams of agricultural practices in locations near the study area (Aura et al. 2002; Cortés-Sánchez et al. 2008; Jordá and Aura 2008; López-Sáez et al. 2007), suggests that natural factors caused these perturbations. It seems likely that these episodes of fire became more intense during the mid-Holocene, coinciding with a period in which there is evidence of an increase in the prehistoric population—and of associated agricultural and livestock farming activity—in areas near the coast of Andalusia and the Ronda Depression (Castaño-Aguilar 2021; Fernández et al. 2007; Ramos-Muñoz et al. 2017). The aridity of the Mediterranean climate was also increasing at that time (Jalut et al. 2000). This dynamic, which can be viewed within the context of the progressive aridification of the environment, may have favoured the conifers that best adapted to xeric conditions such as *P. pinaster*. The decline of *A. pinsapo* continued until about 5500 years ago when it disappeared from the pedoanthracological record in Palmitera 1 and Fuenfría Alta. This finding, together with the progressive decline in *Abies* pollen in most of the fossil records from the south of the Iberian Peninsula over the last few thousand years (Carrión 2013), could help explain the extinction of the Spanish fir in these two localities in Sierra Bermeja.

At a nearer timescale, the statistics on forest fires show that they have affected a larger area and have been especially devastating in recent decades (Stephen et al. 2013). In Spain, the risk factors that give rise to forest fires have increased in recent years, although the number of fires, many of which are started deliberately, has fallen in most Spanish provinces (Urbieta et al. 2019). Unfortunately, Sierra Bermeja is not following this positive trend and is currently one of the areas of the Iberian Peninsula most affected by fire (MITECO, 2022), with 46,227 ha burnt since 1950 (Martos-Martín and Gómez-Zotano 2021). Five major forest fires have affected the serpentine-soil Spanish firs since the 1950s (1956, 1966, 1969, 1991, and 2021), causing the loss of ± 4494 trees. The last of these fire episodes was the most devastating, affecting almost 10,000 ha and destroying ± 3000 *A. pinsapo* trees. Forest fires cause severe damage in terms of the direct disappearance of thousands of individual trees and the destruction of potential habitat areas for the natural dispersion of this species, with the resulting negative effects on connectivity (Martín-Martín et al. 2013).

Connectivity

The results of the historical and pedoanthracological analyses verified the existence of historic and paleo-populations of *A. pinsapo* in four enclaves in S. Bermeja. The secondary-succession scrub typical of the serpentine-soil forests of *A. pinsapo* can also be found in these ecological niches (Gómez-Zotano et al. 2014). These findings show that these areas have the right ecological conditions to establish an ecological corridor that would facilitate the regeneration of existing Spanish fir forests and the links between them. To this end, within the framework of the Natura 2000 Network, it is necessary to implement both a more ambitious strategy for the protection/regeneration of the ecological conditions of these habitats—including those where the species currently finds refuge—and a plan for the reforestation of the species given the demographic characteristics of its populations, which typically have a limited capacity for natural regeneration and expansion. To date, the various actions taken to restore and recover the Spanish fir forest have been based on historical sources, studies of the present-day habitats and SDMs, which are not free of uncertainties and inaccuracies. The pedoanthracological approach provides much more accurate answers to the unknowns that inevitably arise in theoretical modelling.

In this sense, the restoration of ecosystems of this kind, understood as a set of activities aimed at re-establishing the functionality and the capacity of ecosystems to develop towards a mature state (Law 42/2007—State Agency, Official State Gazette, 2007), must guarantee the maintenance and improvement of connectivity so as to ensure the conservation of these ecosystems in a profoundly disturbed territory (basically by forest fires) faced with the threat of Climate Change, which will bring about an increase in temperatures and a decline in rainfall.

This connectivity would bring about the recovery of forests that have been affected by fire for millennia and would improve the habitats that sustain the Spanish fir as an endangered emblematic species. The ecological corridor for the Spanish fir in Sierra Bermeja would reduce the isolation of the different local populations and promote gene exchange, enhancing genetic variability. At the same time, it would prevent phenomena, such as endogamy and genetic drift. It would also help the small populations in decline, halting trends towards local extinction. In addition, it would enable the recolonization of habitats, the re-establishment of populations after episodes of local extinction, and the maintenance of greater richness and diversity of native species. Finally, it would provide a habitat, a refuge and other necessary resources for numerous forest species.

With these results, it will also be possible to complement and expand the "Green Corridor for the Spanish Fir" proposed by Gavira (2006), which was designed to connect the calcicole Spanish Fir forests in the Sierra de las Nieves National Park with those in the Sierra de Grazalema Natural Park. In addition, Sierra Bermeja could also become a wider ecological corridor for other plant and animal species. The connectivity study for the development of flora, some of which is endemic and exclusive to Sierra Bermeja, is also of great interest (Gómez-Zotano et al. 2014). For example, according to Pérez-Latorre and Hidalgo-Triana (2017), three species of endemic serpentinophyte flora are present exclusively in Core Area A of Los Reales (*Peucedanum officinale* subsp. *brachyradium*, *Centaurea lainzii* and *Euphorbia flavicoma* subsp. *bermejense*), which could benefit from the ecological corridor. In general, Sierra Bermeja, as an essential refuge area for flora and one of the most important speciation areas for Mediterranean vegetation in typological, landscape, and physiographical terms (Cabezudo et al. 1989; Gómez-Zotano 2004), could therefore be considered an ecological corridor of utmost importance.

This proposal for ecological connectivity would enable compliance with one of the legal requirements established by the Habitats Directive, i.e., the preservation of the ecological connectivity and integrity of the natural areas included in the Natura 2000 Network (García-Quiroga and Abad-Soria 2014). It would also allow certain endangered species of flora, such as the Spanish Fir, to consolidate and expand their distribution areas. This is an essential prerequisite for complying with one of the fundamental principles of the biogeographic conservation theory, namely that protected areas must have the greatest possible surface area to improve their interconnection (Worboys et al. 2010). All this is within a context in which habitat fragmentation is one of the main causes of worldwide biodiversity loss (Farjalla et al. 2018). This explains why guaranteeing gene exchange between the different populations of the species concerned has been a common task in the defence of biodiversity conservation for decades. Within this context, implementing ecological corridors has proved the most effective option for restoration work and improving the connections between vegetal organisms (Bennet 2004; Morera et al. 2021).

The lack of validation procedures with accessible data can inhibit the evaluation of the effectiveness of ecological corridors (Lalechère and Bergès 2021). However, a wide array of experiences in different parts of the world, with representation of all kinds of ecosystems (see Hilty et al. 2020), endorse the positive effects of these mechanisms in the management of biodiversity, especially when compared to other methods, such as assisted migration (Gurrutxaga and Lozano-Valencia 2008; Krosby et al. 2010; Morera et al. 2021). Most of the species involved respond positively to initiatives of this kind (Gilbert-Norton et al. 2010), which have proved especially effective in the case of vulnerable species such as *A. pinsapo*, with a low dispersal capacity (Merenlender et al. 2022), something that should be monitored periodically (Rudnick et al. 2012). It is also important to incorporate human activities when planning corridors of this kind, especially in a context in which the study of ecological processes must necessarily go beyond the traditional ecosystem level and be addressed from a holistic approach to landscape (Martín-Martín et al. 2013).

To guarantee the successful fulfilment of these objectives, authors, such as Hodgson et al. (2009) and Krosby et al. (2010), argue that it is essential to increase the number of protected areas in both quantitative and qualitative terms. In this sense, the inclusion of Sierra Bermeja as a whole within the recently declared Sierra de las Nieves National Park should be viewed as a priority, especially if we take into account that National Parks are generally equipped with greater public resources to prevent and fight forest fires, the main threat to which the Spanish fir is exposed (Rodríguez-Rodríguez and Martínez-Vega 2017). This would bestow a higher degree of protection on the only Spanish fir Forest on peridotites in the world, which, combined with reinforcing environmental education and awareness in a heavily populated area, would guarantee real progress in safeguarding ecological and landscape values that are unique in the world.

Conclusions

The location of paleo-populations and past distribution areas provides a significant advance on the current state of scientific knowledge for the conservation and sustainability of *Abies pinsapo,* as a basis for the ecological and socio-cultural coherence of its populations in the south of the Iberian Peninsula and as a model for sustainable human development. By transferring this knowledge to the relevant authorities and the wider general public, this project aspires to contribute to the safeguarding of the Spanish fir, a symbolic tree that provides valuable ecosystem services and enhances the well-being of the societies that live in its vicinity.

The results of this research could be of interest to environmental volunteer networks and local companies working in the forestry sector, who could apply the pedoantracological methodology in their research. It could also help solve various technical problems arising in forest restoration and treatment (reconversion of reforestations to native masses of Spanish fir, broadleaved, pine forest, mixed masses, etc.). The results obtained could also help resolve other issues related to the processes that take place within the biota, the ecological function of biodiversity (co-evolutionary mechanisms, connectivity, or isolation of species) or the identification of new present or past populations.

In this sense, it is worth highlighting the possibilities offered by this project for the application of the principle of ecological connectivity contained in Law 42/2007 of 13th December on Natural Heritage and Biodiversity: Article 20 of Title I "Ecological corridors and mountain areas" states that "Public Administrations shall provide, in their environmental planning or in the natural resource management plans, mechanisms to achieve the ecological connectivity of the territory, establishing or re-establishing corridors, in particular within the protected areas of the Natura 2000 Network and the natural areas of special importance for biodiversity". This objective is also included in the Management Plans of the Special Areas of Conservation (SAC) declared due to the importance of the Natural Habitats of Community Interest Type 9520 "Abies pinsapo forests" (a habitat listed as very rare in the case of serpentine fir forests); these plans emphasize the ecological connectivity of both the species and its forests.

Author contributions JG-Z conceived, designed and led the research. JG-Z, RP-M and JAO-C carried out the fieldwork and collected field data.JG-Z, RP-M and JAO-C analysed the data.JG-Z and RP-M writted the manuscript principal body.JAO-C assisted with analyses and writing the paper.JG-Z, RP-M and JAO-C produced the figures.JG-Z, RP-M and JAO-C reviewed the manuscript and contributed to the final draft.JG-Z and RP-M reviewed the first version of manuscript submitted to journal.

Funding Funding for open access publishing: Universidad de Granada/CBUA. This research has been supported by a contract for University Teacher Training (Formación de Profesorado Universitario) (Ref. 18/03023) from the Spanish Ministry of Education, Culture and Sports (Ministerio de Educación, Cultura y Deportes del Gobierno de España), and research projects financed by the State Research Agency (SRA) and European Regional Development Fund (ERDF): PALEOPINSAPO (CSO2017-83576-P), MED-REFUGIA (RTI2018-101714-B-I00) and TED2021-132631B-I00; Andalusian Plan for Research, Development and Innovation: Oromed-Refugia (P18-RT- 4963); and ERDF Operational Programme in Andalusia (EU regional programme): ForestMed (A-RNM-688-UGR20).

Data availability The authors declare that all data supporting the findings of this study are available within the article (and its supplementary information files).

Declarations

Conflict of interest The authors declare no competing interests.

References

Alba-Sánchez F, López-Sáez, JA (2013) Paleobiogeografía del pinsapo en la Península Ibérica durante el Cuaternario. In: López-Quintanilla J (ed) Los Pinsapares en Andalucía: Conservación y sostenibilidad en el siglo XXI. Consejería de Agricultura, Pesca y Medio Ambiente de la Junta de Andalucía, Sevilla, pp 33–52

Alba-Sánchez F, López-Sáez JA, Benito B, Linares JC, Nieto-Lugilde D, López-Merino L (2010) Past and present potential distribution of the Iberian *Abies* species: a phytogeographic approach using fossil pollen data and species distribution models. Divers Distrib 16(2):214–228. https://doi.org/10.1111/j.1472-4642.2010.00636.x

Alba-Sánchez F, Abel-Schaad D, López-Sáez JA (2018) Paleobiogeografía de *Abies* spp. y *Cedrus atlantica* en el Mediterráneo occidental (península Ibérica y Marruecos). Revista Ecosistemas 27:26–37. https://doi.org/10.7818/ECOS.1441

Anderson RS, Jiménez-Moreno G, Carrión JS, Pérez-Martínez C (2011) Postglacial history of alpine vegetation, fire, and climate from Laguna de Río Seco, Sierra Nevada, southern Spain. Quatern Sci Rev 30:1615–1629. https://doi.org/10.1016/j.quascirev.2011.03.005

Arista M (1995) The structure and dynamics of an *Abies pinsapo* forest in southern Spain. For Ecol Manage 74:81–89

Aura JE, Jordá JF, Pérez M, Rodrigo MJ, Badal E, Guillem P (2002) The far south: The Pleistocene-Holocene transition in Nerja Cave (Andalucía, Spain). Quatern Int 93:19–30. https://doi.org/10.1016/S1040-6182(02)00004-6

Becerra M (2006*)* Ordenación y aprovechamiento de los pinsapares rondeños durante el siglo XIX. La memoria de Antonio Laýnez. Editorial La Serranía, Alcalá del Valle.

Becker A, Körner C, Brun JJ, Guisan A, Tappeiner U (2007) Ecological and land use studies along elevational gradients. Mt Res Dev 27:58–65. https://doi.org/10.1659/0276-4741(2007)27[58:EALUSA]2.0.CO;2

Bennett G (2004) Linkages in practice: a review of their conservation practice. IUCN, Gland and Cambridge

Brambilla M, Bergero V, Bassi E, Falco R (2015) Current and future effectiveness of Natura 2000 network in the central Alps for the conservation of mountain forest owl species in a warming climate. Eur J Wildl Res 61:35–44. https://doi.org/10.1007/s10344-014-0864-6

Cabezudo B, Nieto JM, Pérez-Latorre A (1989) Contribución al conocimiento de la vegetación edafófilo-serpentinícola del sector Rondeño (Málaga, España). Acta Botánica Malacitana 14:291–294

Cacho I, Grimalt J, Canals M, Sbaffi L, Shackleton NJ, Schönfeld J, Zahn R (2001) Variability of the western Mediterranean Sea surface temperature during the last 25,000 years and its connection with the Northern Hemisphere climatic changes. Paleoceanography 16:40–52. https://doi.org/10.1029/2000PA000502

Carreira de la Fuente JA, Salido MT, Torres-Cabañete P, Blanes-Campos C, Viñegla B, García-Ruíz, R (2013) Efectos de la contaminación atmosférica en los Pinsapares de Andalucía. In: López-Quintanilla J (ed) Los Pinsapares en Andalucía: Conservación y sostenibilidad en el siglo XXI. Consejería de Agricultura, Pesca y Medio Ambiente de la Junta de Andalucía, Sevilla, pp 375–387

Carrión JS (2013) Paleoflora y paleovegetación de la península Ibérica e islas Baleares: Plioceno-Cuaternario. Ministerio de Economía y Competitividad, Madrid

Carrión JS, Fuentes N, González-Sampériz P, Sánchez-Quirante L, Finlayson C, Fernández S, Andrade A (2007) Holocene environmental change in a montane region of southern Europe with a long history of human settlement. Quatern Sci Rev 26:1455–1475. https://doi.org/10.1016/j.quascirev.2007.03.013

Castaño-Aguilar JM (2021) Poblamiento antiguo en los bosques de la Serranía de Ronda. In: Gómez-Zotano J, Olmedo-Cobo JA (eds) Los bosques de la Serranía de Ronda. Una perspectiva espacio-temporal. Editorial La Serranía, Alcalá del Valle, pp 59–75

Catalan J, Ninot JM, Aniz MM (2017) High Mountain Conservation in a Changing World. Springer Nature, Cham.

Cobos-Suárez P, Martínez-Saavedra G, Gutiérrez-Tejada GA, Miguel-Martínez FJ, Cobos-Suárez JA (2013) Estado fitosanitario de las masas de *Abies pinsapo* Boiss. In: López-Quintanilla J (ed) Los Pinsapares en Andalucía: Conservación y sostenibilidad en el siglo XXI. Consejería de Agricultura, Pesca y Medio Ambiente de la Junta de Andalucía, Sevilla, pp 415–441

Cortés-Sánchez M, Morales-Muñiz A, Simón-Vallejo MD, Bergadà-Zapata MM, Delgado-Huertas A et al (2008) Palaeoenvironmental and cultural dynamics of the coast of Málaga (Andalusia, Spain) during the Upper Pleistocene and early Holocene. Quatern Sci Rev 27:2176–2193. https://doi.org/10.1016/j.quascirev.2008.03.010

Cunill R, Soriano JM, Bal MC, Pèlachs A, Pérez-Obiol R (2012) Holocene treeline changes on the south slope of the Pyrenees: a pedoanthracological analysis. Veg Hist Archaeobotany 21(4–5):373–384. https://doi.org/10.1007/s00334-011-0342-y

Farjalla V, Coutinho R, Gómez-Aparicio L, Navarrete S, Aliny PF, Pires M, Soares AT, Mariana V (2018) Pérdida de biodiversidad: causas y consecuencias para la humanidad. In: Marquet P, Valladares F, Magro S, Gaxiola A, Enrich-Prast A (eds) Cambio Global. Una Mirada desde Iberoamérica. ACCI Ediciones, Madrid, pp 89–110

Fernández LE, Suárez J, Tomassetti JM, Navarro I (2007) Corominas, una necrópolis megalítica en el ámbito litoral malagueño. Mainake 29:513–540

García-Quiroga F, Abad-Soria J (2014) Los corredores ecológicos y su importancia ambiental. Observatorio Medioambiental 17:253–298. https://doi.org/10.5209/rev_OBMD.2014.v17.47194

Gavira ON (2006) Análisis de un corredor florístico entre los Parques Naturales Sierra de Grazalema y Sierra de las Nieves (Cádiz y Málaga, España). Anales De Biología 28:45–72

Gil A (2002) Simón de Rojas Clemente. Viaje a Andalucía. Historia Natural del Reino de Granada. GBG Editora, Almería-Barcelona

Gilbert-Norton L, Wilson R, Stevens JR, Beard KH (2010) A meta-analytic review of corridor effectiveness. Conserv Biol 24:660–668. https://doi.org/10.1111/j.1523-1739.2010.01450.x

Gil-Romera G, Carrión JS, Pausas JG, Sevilla-Vallejo M, Lamb HF, Fernández S, Burjachs F (2010) Holocene fire activity and vegetation response in South-Eastern Iberia. Quatern Sci Rev 29:1082–1092. https://doi.org/10.1016/j.quascirev.2010.01.006

Gómez-Zotano J (2004) El papel de los espacios montañosos como traspaís del litoral mediterráneo andaluz: el caso de Sierra Bermeja (provincia de Málaga). Dissertation, University of Granada

Gómez-Zotano J, Olmedo-Cobo JA (2021) Los bosques de la Serranía de Ronda: una perspectiva espacio-temporal. Editorial La Serranía, Alcalá del Valle

Gómez-Zotano J, Róman F, Hidalgo N, Pérez-Latorre A (2014) Biodiversidad y valores de conservación de los ecosistemas serpentínicos en España: Sierra Bermeja (provincia de Málaga). Boletín de la Asociación de Geógrafos Españoles 65:187–206. https://doi.org/10.21138/bage.1749

Gómez-Zotano J, Olmedo-Cobo JA, Cunill-Artigas R, Martínez-Ibarra E (2017) Descubrimiento y caracterización geográfica de una depresión ultramáfica en Sierra Bermeja: nuevos datos geomorfoedáficos, fitogeográficos y paleoecológicos. Pirineos 172. https://doi.org/10.3989/Pirineos.2017.172001

González-Hernández A (2021) Biogeografía y conservación de dos especies de la flora relicta del Mediterráneo Occidental: *Abies pinsapo* Boiss. y *Cedrus atlantica* (Endl.) Carrière. Dissertation, University of Granada

Gonzalo J, García JM, Allué C (2004) Potencialidades y adecuaciones fitoclimáticas de *Abies pinsapo* Boiss. en España. Montes 77:24–32

Gurrutxaga M, Lozano-Valencia PJ (2008) Evidencias sobre la eficacia de los corredores ecológicos: ¿Solucionan la problemática de fragmentación de hábitats? Observatorio Medioambiental 11:171–183

Gutiérrez-Hernández O (2017) El nicho ecológico fundamental de *Abies pinsapo* en la Serranía de Ronda. Takurunna 6–7

Gutiérrez-Hernández O (2018) Impacto del calentamiento global en la distribución y supervivencia del pinsapo (Serranía de Ronda).

Boletín de la Asociación de Geógrafos Españoles 76:504–549. https://doi.org/10.21138/bage.2532

Guzmán JR, Catalina MA, Navarro RF, López J, Sánchez R (2012) Los paisajes del pinsapo a través del tiempo. In: López-Quintanilla J (ed) Los Pinsapares en Andalucía: Conservación y sostenibilidad en el siglo XXI. Consejería de Agricultura, Pesca y Medio Ambiente de la Junta de Andalucía, Sevilla, pp 111–158

Hilty J, Worboys GL, Keeley A, Woodley S, Lausche B et al (2020) Guidelines for conserving connectivity through ecological networks and corridors. IUCN, Gland

Hodgson JA, Thomas CD, Wintle BA, Moilanen A (2009) Climate change, connectivity and conservation decision making: back to basics. J Appl Ecol 46:964–996. https://doi.org/10.1111/j.1365-2664.2009.01695.x

Holtmeier FK, Broll G (2007) Treeline advance – driving processes and adverse factors. Landscape Online 1:1–33. https://doi.org/10.3097/LO.200701

Jalut G, Amat AE, Bonnet L, Gauquelin T, Fontugne M (2000) Holocene climatic changes in the Western Mediterranean, from southeast France to southeast Spain. Palaeogeogr Palaeoclimatol Palaeoecol 160:255–290. https://doi.org/10.1016/S0031-0182(00)00075-4

Jongman R (1995) Nature conservation planning in Europe: developing ecological networks. Landsc Urban Plan 32:169–183. https://doi.org/10.1016/0169-2046(95)00197-O

Jordá JF, Aura JE (2008) 70 fechas para una cueva. Revisión crítica de 70 dataciones C14 del Pleistoceno Superior y Holoceno de la Cueva de Nerja (Málaga, Andalucía, España). Espacio, Tiempo y Forma. Serie I. Nueva Época Prehistoria y Arqueología 1:239–256. https://doi.org/10.5944/etfi.1.2008.1922

Junta de Andalucía (2012) Guía de los paisajes del pinsapar. Un recorrido histórico a partir de las referencias históricas previas al siglo XXI. Consejería de Agricultura, Pesca y Medio Ambiente, Sevilla

Junta de Andalucía (2014) Escenarios locales de cambio climático. Clasificación del Índice de distribución potencial del Pinsapo (*Abies pinsapo*). http://www.juntadeandalucia.es/medioambiente/rediam. Accessed 13 Jan 2023

Krosby M, Tewksbury J, Haddad N, Hoekstra J (2010) Ecological connectivity for a changing climate. Conserv Biol 24:1686–1689. https://doi.org/10.1111/j.1523-1739.2010.01585.x

Kulakowski D, Seidl R, Holeska J, Kuuluvainen T, Nagel TA et al (2017) A walk on the wild side: disturbance dynamics and the conservation and management of European mountain forest ecosystems. For Ecol Manage 388:120–131. https://doi.org/10.1016/j.foreco.2016.07.037

Lalechère E, Bergès L (2021) A validation procedure for ecological corridor locations. Land 10:1320. https://doi.org/10.3390/land10121320

Lázaro-Gimeno D, Luque JA, Ibars AM, García-Nogales A, Rodríguez JPG, Fernández-Golfín JI, Merino-Ortega JA (2013) Impacto del ozono troposférico en *Abies pinsapo* Boiss. In: López-Quintanilla J (ed) Los Pinsapares en Andalucía: Conservación y sostenibilidad en el siglo XXI. Consejería de Agricultura, Pesca y Medio Ambiente de la Junta de Andalucía, Sevilla, pp 389–399

Lenoir J, Svenning JC (2014) Climate-related range shifts—a global multidimensional synthesis and new research directions. Rev Palaeobot Palynol 62:403–415. https://doi.org/10.1111/ecog.00967

Liétor J, Linares JC, Martín-García JM, García-Ruíz R, Carreira JA (2003) Relaciones suelo-planta en bosques de *Abies pinsapo* Boiss. Disponibilidad de nutrientes y estatus nutricional. Acta Botánica Malacitana 28:89–104. https://doi.org/10.2431/abm.v28i0.7269

Linares JC (2011) Biogeography and evolution of *Abies* (Pinaceae) in the Mediterranean Basin: the roles of long-term climatic change and glacial refugia. J Biogeogr 38:619–630. https://doi.org/10.1111/j.1365-2699.2010.02458.x

Linares JC, Camarero JJ, Carreira JA (2009) Interacting effects of changes in climate and forest cover on mortality and growth of the southernmost European fir forests. Glob Ecol Biogeogr 18:485–497. https://doi.org/10.1111/j.1466-8238.2009.00465.x

Lopez-Albarado J, Farris E (2022) Ecology and evolution of plants in the Mediterranean basin: perspectives and challenges. Plants 11:1584. https://doi.org/10.3390/plants11121584

López-Quintanilla J (2013) Los pinsapares en Andalucía (*Abies pinsapo* Boiss.): conservación y sostenibilidad en el siglo XXI. Consejería de Agricultura, Pesca y Medio Ambiente de la Junta de Andalucía, Sevilla.

López-Sáez JA, López-García P, Cortés-Sánchez M (2007) Paleovegetación del Cuaternario reciente: Estudio arqueopalinológico. In: Cortés-Sánchez M (ed) Cueva Bajondillo (Torremolinos). Servicio de Publicaciones de la Universidad de Málaga, Málaga, Secuencia cronocultural y paleoambiental del Cuaternario reciente en la Bahía de Málaga, pp 139–156

López-Tirado J, Hidalgo P (2014) A high resolution predictive model for relict trees in the Mediterranean-mountain forests (*Pinus sylvestris* L., *P. nigra* Arnold and *Abies pinsapo* Boiss.) from the south of Spain: A reliable management tool for reforestation. For Ecol Manage 330:105–114. https://doi.org/10.1016/j.foreco.2014.07.009

Martín-Martín C, Bunce RGH, Saura S, Elena-Roselló R (2013) Changes and interactions between forest landscape connectivity and burnt area in Spain. Ecol Ind 33:119–138. https://doi.org/10.1016/j.ecolind.2013.01.018

Martos-Martín J, Gómez-Zotano J (2021) Sierra Bermeja y los grandes incendios forestales. In: Gómez-Zotano J, Olmedo-Cobo JA (eds) Los bosques de la Serranía de Ronda. Una perspectiva espacio-temporal. Editorial La Serranía, Alcalá del Valle, pp 391–437

Médail F, Diadema K (2009) Glacial refugia influence plant diversity patterns in the Mediterranean Basin. J Biogeogr 36:1333–1345. https://doi.org/10.1111/j.1365-2699.2008.02051.x

Médail F, Monnet AC, Pavon D, Nikolic T, Dimopoulos P et al (2019) What is a tree in the Mediterranean basin hotspot? A critical analysis. Forest Ecosystems 6:17. https://doi.org/10.1186/s40663-019-0170-6

Merenlender AM, Keeley A, Hilty J (2022) Ecological corridors for which species? Therya 13(1):45–55. https://doi.org/10.12933/therya-22-1162

Morera-Beita C, Sandoval-Murillo F, Alfaro L (2021) Ecological corridors in Costa Rica: an evaluation applying landscape structure, fragmentation-connectivity process, and climate adaptation. Conserv Sci Practice 3:e475. https://doi.org/10.1111/csp2.475

Navarro RM, Lara A, Blanco P, Calzado C, López-Quintanilla J, Fernández-Cancio A, Guzmán JR, Sánchez-Salguero R (2006) Aproximación a la definición del hábitat fisiográfico del *Abies pinsapo* Boiss. Andalucía. Investigación agraria. Sistemas y recursos forestales 15(1):137–152. https://doi.org/10.5424/srf/200615S1-00988

Olmedo-Cobo JA, Cunill R, Martínez-Ibarra E, Gómez-Zotano J (2017) Paleoecología de *Abies* sp. en Sierra Bermeja (sur de la Península Ibérica) durante el Holoceno medio a partir del análisis pedoantracológico. Bosque 38(2):259–270. https://doi.org/10.4067/S0717-92002017000200004

Olmedo-Cobo JA, Cunill R, Gómez-Zotano J (2019) The native status of *Pinus pinaster* on serpentine soils: charcoal analysis and palaeoenvironmental history in Sierra Bermeja (southern Iberian Peninsula, Spain). Veg Hist Archaeobot 28:417–432. https://doi.org/10.1007/s00334-018-0701-z

Olmedo-Cobo JA, Pardo-Martínez R, Gómez-Zotano J (2021) First data about the Holocene composition of mountain forests in the

Sierra de las Nieves Natural Park (Ronda Mountains, Spain) through pedoanthracological analysis. Boletín de la Asociación de Geógrafos Españoles. https://doi.org/10.21138/bage.3099
Pardo-Martínez R (2020) La pedoantracología en España: una revisión bibliográfica. Pirineos 175:e059. https://doi.org/10.3989/pirineos.2020.175009
Pardo-Martínez R, Gómez-Zotano J, Olmedo-Cobo JA (2021) The history of *Abies pinsapo* during the Holocene in southern Spain, based on pedoanthracological analysis. Veg Hist Archaeobot 31:307–321. https://doi.org/10.1007/s00334-021-00855-w
Pérez-Latorre A, Hidalgo-Triana N (2017) Los hábitats de Sierra Bermeja: exclusividad en vegetación y ecosistemas a nivel europeo y mediterráneo. Takurunnna 6–7:89–106
Pérez-Latorre A, Cabezudo B, Gálán de Mera A, Carrión J (2001) El papel de las gimnospermas en la vegetación forestal de Andalucía. Medio Ambiente 38:30–33
Pérez-Latorre A, Hidalgo-Triana N, Cabezudo B (2020) Biogeografía y bosques de la Serranía de Ronda (Cádiz-Málaga-Sevilla). In: Gómez-Zotano J, Olmedo-Cobo JA (eds) Los bosques de la Serranía de Ronda. Una perspectiva espacio-temporal. Editorial La Serranía, Alcalá del Valle, pp 11–58
Pino J, Marull J (2012) Ecological networks: Are they enough for connectivity conservation? A case study in the Barcelona Metropolitan Region (NE Spain). Land Use Policy 29(3):684–690. https://doi.org/10.1016/j.landusepol.2011.11.004
Ramos-Muñoz J, Siles-Guerrero F, Gutiérrez-López, Martínez-Enamorado V, Martín-Ruíz JA (2017) Actas del I Congreso internacional de historia de la Serranía de Ronda: las ocupaciones por sociedades prehistóricas, protohistóricas y de la antigüedad en la Serranía de Ronda y Béticas Occidentales. Editorial La Serranía, Alcalá del Valle
Reimer PJ, Austin W, Bard E, Bayliss A, Blackwell PG et al (2020) The IntCal20 northern hemisphere radiocarbon age calibration curve (0–55 cal kBP). Radiocarbon 62(4):725–757. https://doi.org/10.1017/RDC.2020.41
Rodríguez-Rodriguez D, Martínez-Vega J (2017) Assessing recent environmental sustainability in the Spanish network of National Parks and their statutory peripheral areas. Appl Geogr 89:22–31. https://doi.org/10.1016/j.apgeog.2017.09.008
Rudnick DA, Ryan SJ, Beier P, Cushman SA, Dieffenbach F et al (2012) The role of landscape connectivity in planning and implementing conservation and restoration priorities. Issues Ecol 16:1–20
Ruiz-Labourdette D, Schmitz M, Pineda F (2013) Changes in tree species composition in Mediterranean mountains under climate change: Indicators for conservation planning. Ecol Ind 24:310–323. https://doi.org/10.1016/j.ecolind.2012.06.021
Schweingruber FH (1990) Anatomy of European woods. Kessel, Bern
Stephens SL, Agee JK, Fule PZ, North MP, Romme WH, Swetnam TW, Turner MG (2013) Managing forests and fire in changing climates. Science 342:41–42. https://doi.org/10.1126/science.124029
Talon B, Carcaillet C, Thinon M (1998) Études pédoanthracologiques des variations de la limite supérieure des arbres au cours de l´Holocene dans les Alps françaises. Géog Phys Quatern 52:195–208
Torres-Cabañete P, Hinojosa MB, García-Ruíz R, Daniell T, Carreira JA (2009) Relación entre variabilidad biogeoquímica y rasgos estructurales de la comunidad microbiana en suelos forestales: Bosques de *Abies pinsapo* como caso de estudio. Ecosistemas 18(2):91–102
Urbieta IR, Franquesa M, Viedma O, Moreno JM (2019) Fire activity and burned forest lands decreased during the last three decades in Spain. Ann for Sci 76:90. https://doi.org/10.1007/s13595-019-0874-3
Van der Windt HJ, Swart JAA (2007) Ecological corridors, connecting science and politics: the case of the Green River in the Netherlands. J Appl Ecol 45:124–132. https://doi.org/10.1111/j.1365-2664.2007.01404.x
Vernet JL, Ogereau P, Figueiral I, Machado C, Uzquiano P (2001) Guide d'identification des charbons de bois préhistoriques et récents, Sud-Ouest de l'Europe: France, Péninsule ibérique et Îles Canaries. CNRS, Paris
Worboys GL, Francis WL, Lockwood M (2010) Connectivity conservation management: a global guide. Earthscan, London