

# Past and present potential distribution of the Iberian *Abies* species: a phytogeographic approach using fossil pollen data and species distribution models

Francisca Alba-Sánchez<sup>1,\*</sup>, José A. López-Sáez<sup>2</sup>, Blas Benito-de Pando<sup>1</sup>, Juan C. Linares<sup>3</sup>, Diego Nieto-Lugilde<sup>1</sup> and Lourdes López-Merino<sup>2</sup>

<sup>1</sup>Dpto. de Botánica, Facultad de Ciencias, Campus Universitario de Fuente Nueva, Universidad de Granada, 18071 Granada, Spain, <sup>2</sup>GI Arqueobiología, Instituto de Historia, CCHS, CSIC, Albasanz 26-28, 28037 Madrid, Spain, <sup>3</sup>Dpto. Sistemas Físicos, Químicos y Naturales, Universidad Pablo de Olavide, Ctra. Utrera Km 1, 41013 Sevilla, Spain

## ABSTRACT

**Aim** Quaternary palaeopollenological records collected throughout the Iberian Peninsula and species distribution models (SDMs) were integrated to gain a better understanding of the historical biogeography of the Iberian *Abies* species (i.e. *Abies pinsapo* and *Abies alba*). We hypothesize that SDMs and *Abies* palaeorecords are closely correlated, assuming a certain stasis in climatic and topographic ecological niche dimensions. In addition, the modelling results were used to assign the fossil records to *A. alba* or *A. pinsapo*, to identify environmental variables affecting their distribution, and to evaluate the ecological segregation between the two taxa.

**Location** The Iberian Peninsula.

**Methods** For the estimation of past *Abies* distributions, a hindcasting process was used. *Abies pinsapo* and *A. alba* were modelled individually, first calibrating the model for their current distributions in relation to the present climate, and then projecting it into the past—the last glacial maximum (LGM) and the Middle Holocene periods—in relation to palaeoclimate simulations. The resulting models were compared with Iberian-wide fossil pollen records to detect areas of overlap.

**Results** The overlap observed between past *Abies* refugia—inferred from fossil pollen records—and the SDMs helped to construct the Quaternary distribution of the Iberian *Abies* species. SDMs yielded two well-differentiated potential distributions: *A. pinsapo* throughout the Baetic mountain Range and *A. alba* along the Pyrenees and Cantabrian Range. These results propose that the two taxa remained isolated throughout the Quaternary, indicating a significant geographical and ecological segregation. In addition, no significant differences were detected comparing the three projections (present-day, Mid-Holocene and LGM), suggesting a relative climate stasis in the refuge areas during the Quaternary.

**Main conclusions** Our results confirm that SDM projections can provide a useful complement to palaeoecological studies, offering a less subjective and spatially explicit hypothesis concerning past geographic patterns of Iberian *Abies* species. The integration of ecological-niche characteristics from known occurrences of *Abies* species in conjunction with palaeoecological studies could constitute a suitable tool to define appropriate areas in which to focus proactive conservation strategies.

## Keywords

*Abies alba*, *Abies pinsapo*, Iberian Peninsula, PMIP, Quaternary refugia, SDMs.

\*Correspondence: Francisca Alba-Sánchez, Dpto. de Botánica, Facultad de Ciencias, Campus Universitario de Fuente Nueva, Universidad de Granada, 18071 Granada, Spain.  
E-mail: falba@ugr.es

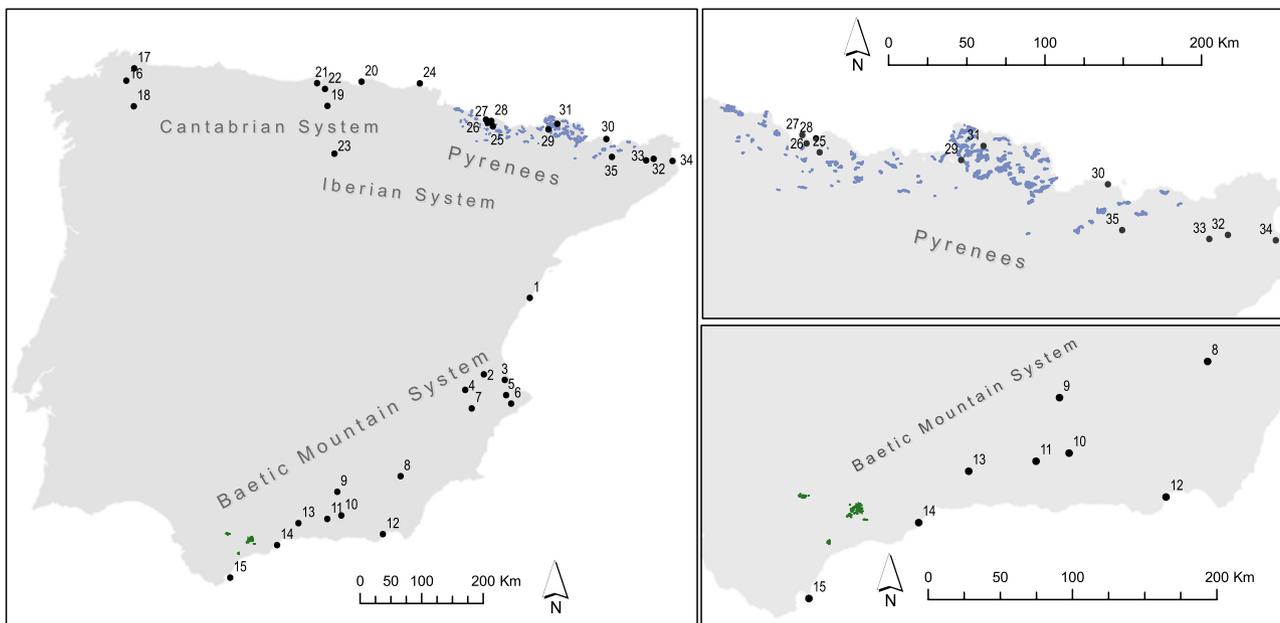
## INTRODUCTION

The geographical proximity of two *Abies* species in the Iberian Peninsula (*Abies alba* and *Abies pinsapo*), with contrasting environmental requirements as well as different morphological traits (Farjon & Rushforth, 1989), constitutes an unsolved biogeographic and palaeobotanic enigma. Currently, *A. alba* is located exclusively in the Pyrenees mountain Range in the north-eastern Iberian Peninsula (Costa Tenorio *et al.*, 1997), which has a warm temperate climate with a rainy and warm summer (Cfb Climate class: Köppen-Geiger climate classification by Kottek *et al.*, 2006). *Abies pinsapo* (Spanish populations) is found only in southern Spain, specifically in the south-western Baetic mountain Range (Fig. 1), in a wet Mediterranean climate with a hot and dry summer (see Csa climate class: Köppen-Geiger climate classification by Kottek *et al.*, 2006).

*Abies* is currently distributed around the Mediterranean basin with nine species and one natural hybrid (Vidakovic, 1991). The age and timing of circum-Mediterranean *Abies* speciation events as well as their subsequent migrations has been the subject of extensive debate and analysis in the literature, with recent opinions indicating that the most important speciation event took place during the Pliocene, when a regional drying trend led to geographic isolation of drought-sensitive taxa (Hewitt, 1996; Willis & McElwain, 2002). According to Krussmann (1972) and Farjon & Rushforth (1989), the successive migrations and fragmentations would have favoured the differentiation of two *Abies* groups: (1) archaic firs, represented by subsection *Pinsapones* Franco, with species having archaic morphological features (indicating an earlier speciation) such as *Abies pinsapo*; and (2) modern

firs, represented by subsection *Albae* (Franco) Franco, these species having modern morphological characteristics, indicating a later speciation, such as *A. alba*. These populations, restricted to moist mountainous habitats during most of the Quaternary, would diverge to the current diversity of related species (Linares, 2008).

Understanding Quaternary refuge distributions of species has been a core task in historical biogeography for several reasons. For example, refugia based on biogeographic evidence can guide palaeoenvironmental reconstructions, or accurate knowledge of distributional responses to past climate change can provide an excellent calibration for predictions of the consequences of present-day climate change (Waltari *et al.*, 2007). In the Iberian Peninsula, Quaternary refugia have been identified based on different types of historical biogeographic evidence, especially palaeoecological studies, in which glacial refugia for emblematic taxa, such as *Carpinus betulus* L., *Castanea sativa* Mill., *Fagus sylvatica* L., *Juglans regia* L. and evergreen oaks (*Quercus suber* L., *Quercus ilex* L. and *Quercus coccifera* L.), have been reported for the most critical periods of the Pleistocene (Carrión & Sánchez-Gómez, 1992; Carrión *et al.*, 2003; Krebs *et al.*, 2004; López de Heredia *et al.*, 2007; López-Merino *et al.*, 2008). Nevertheless, in the case of *Abies*, given that fir species cannot be distinguished in palynological analyses, previous studies related to their glacial refugia or past distribution usually refer to the entire genus (Terhürne-Berson *et al.*, 2004). So far, the fossil records of *Abies* have been interpreted based on the presumption that the pollen grains of the *Abies* morphotype documented in pollen sequences of south and south-eastern Spain refer to *A. pinsapo* (Carrión *et al.*, 2008; Cortés-Sánchez *et al.*, 2008), whereas the pollen grains from north and north-eastern Spain refer to *A. alba*



**Figure 1** Current *Abies* distribution in the Iberian Peninsula: *Abies pinsapo* in the Baetic Range and *Abies alba* in the Pyrenees Range. Pollen deposits with the code indication are shown (see complementary information in Table 1).

populations (Huntley & Birks, 1983). However, this geographic dichotomy lacks reliable ecological support.

The emerging field of species distribution models (SDMs) offers an independent perspective on these questions. These models can be used to predict potential distributional patterns for a given species and to assess the degree of ecological segregation among different taxa (Guisan & Thuiller, 2005). An SDM represents an approximation of a species' ecological niche in the environmental dimension being examined, translated into the geographic space. Based on the environmental conditions of the sites of known occurrence, these models constitute valuable tools for analytical biology (Peterson *et al.*, 1999). Such projections assume that a species is in equilibrium with its environmental requirements—that is, its distribution is determined primarily by the environment, and not by other factors such as competition or dispersal limitation. Similarly, under assumptions of niche conservatism (Peterson, 2003), which have been extensively tested (Martínez-Meyer & Peterson, 2006). SDMs can be projected onto palaeoclimate models to identify past potential distributions (Martínez-Meyer *et al.*, 2004).

The history of Iberian *Abies* species is poorly understood, in part because the palaeopalynological approach has inherent biases and difficulties, due not only to the lack of taxonomic precision discussed earlier, but also to limitations on inferring the timing and location of refugia, restrictions on defining the spatial and temporal distribution range of different species, and the failure to take into account that some taxa are under-represented in the fossil record. Consequently, the distribution of some species is probably underestimated.

Here, we propose the use of SDMs in conjunction with palaeoclimatic models as well as fossil-pollen records for locating and describing Iberian *Abies* Quaternary refugia from the last glacial maximum (LGM) to the present. The combination of these two approaches enables far greater detail and accuracy in SDM applications used to predict potential Quaternary refugia. In addition, this combination allows (1) the assignment of fossil records to *A. alba* or *A. pinsapo* based on the predicted potential distribution patterns for the two species; (2) the identification of environmental variables affecting their distribution; and (3) an evaluation of the segregation between the two taxa.

We hypothesize that SDM and palaeorecords are closely correlated, suggesting that the two approaches converge on similar inferences and that the two in tandem may offer exciting new insights.

## METHODS

### *Abies pinsapo* and *Abies alba* distribution models

In the present study, *A. pinsapo* and *A. alba* were modelled individually, first calibrating the model for their current distributions in relation to the present climate, and then applying it to the LGM and the Middle Holocene (Mid-Holocene) periods. This hindcasting process is often used to

estimate previous species distributions (e.g. Pearman *et al.*, 2008).

### Species records

The forest map of Spain (1 : 200,000) was the cartographic base for estimating the current range of *A. pinsapo* and *A. alba* (Ruiz de la Torre, 1990). *Abies pinsapo* is restricted to three populations on calcareous and serpentine substrates in the Baetic mountains, which occur from 900 to 1800 m a.s.l. in the Sierra de Grazalema (Cádiz), Sierra de las Nieves, and Sierra Bermeja (both in the province of Málaga). *Abies alba* occupies only the Pyrenees, reaching its south-western European and Iberian limit in Iraty (Navarra). The Coastal-Catalonian mountain Range constitutes its south-eastern limit in Spain. The largest *A. alba* stands are located in the province of Lleida (17,000 ha). In total, 524 records of *A. pinsapo* and 240 of *A. alba* were randomly sampled on the polygons corresponding to each of the species, ensuring a minimum distance of 400 m between points, in order to avoid sample autocorrelation effects. The dataset was randomly split, 75% of which were used to calibrate the algorithm, and 25% to evaluate the resulting SDMs.

### Environmental variables

Nine predictive variables were used as predictors to calibrate SDMs for each species, all of which had a spatial correlation degree lower than 0.75 (Pearson coefficient). Three of these represented resource gradients (*sensu* Austin *et al.*, 1984): annual precipitation (Pann), precipitation of the driest month (Pmin), and precipitation of the wettest month (Pmax). Three other variables refer to direct gradients: maximum temperature of the hottest month (Tmax), minimum temperature of the coldest month (Tmin), and annual temperature (Tann). The last three correspond to indirect gradients: slope, topographic exposure, and topographic wetness index (TWI). These latter three variables, derived from the digital elevation model (DEM), are capable of reproducing the physiological role of certain resources (Guisan & Zimmermann, 2000). Climate data for the present day (1950–1999) were drawn from the Digital Climatic Atlas of the Iberian Peninsula (Ninyerola *et al.*, 2005). The topographic data came from Shuttle Radar Topography Mission (SRTM) (<http://srtm.csi.cgiar.org/>) and were from 90 to 200 m [(5810 × 4600 cells, Universal Transverse Mercator (UTM) projection, European datum 1950 (ED50)]. The GRASS-GIS software (GRASS Development Team, 2008) was used to provide the geographical framework.

Current climate data from the Digital Climatic Atlas of the Iberian Peninsula database (Ninyerola *et al.*, 2005) were used as a basis for developing LGM (21 kyr BP) and Mid-Holocene (6 kyr BP) climate data. Two general atmospheric circulation models (GCM) were used to generate past climate scenarios for each period in order to avoid the uncertainty of using one alone: the Community Climate System Model [CCSM, <http://www.cesm.ucar.edu/>, (Kiehl & Gent, 2004)] and the Model for

Interdisciplinary Research on Climate [MIROC, ver. 3.2; <http://www.ccsr.u-tokyo.ac.jp/ehhtml/etopindex.shtml>]. The original GCM data were downloaded from the PMIP2 website (<http://www.pmip2.cnrs-gif.fr/>).

We then generated an anomaly map for each variable by subtracting values for the present, pre-industrial (PI) conditions (c. 1950), using the GCM-estimated LGM and Mid-Holocene values. The GCM data had a spatial resolution of 2.8°, or roughly 300 × 300 km. These anomaly maps were then interpolated to a 200-m resolution using the spline function in GRASS-GIS software with the tension option. Finally, the interpolated differences were added to the high-resolution current climate datasets from the Digital Climatic Atlas of the Iberian Peninsula to generate estimated climate maps at the LGM and the Mid-Holocene. This procedure had the dual advantage of producing data at a resolution relevant to the spatial scale of analysis, and of calibrating the downscaled LGM and Mid-Holocene climate data to actual observed climate conditions (Peterson & Nyári, 2008).

Comparison of the results of this GCM with climate reconstructions and other models show that the direction of climate change is in general correctly estimated in the PMIP2 models, although the degree of cooling in southern Europe is generally underestimated for the Middle Holocene (Brewer *et al.*, 2007) and LGM (Ramstein *et al.*, 2007). The LGM-simulated surface climate is colder and drier than PI conditions: global average annual surface temperature is a cooling of around 4.5 °C from PI conditions with amplification of this cooling at high latitudes (Otto-Bliesner *et al.*, 2006); similarly, the atmosphere is significantly drier with an around 18% decrease in precipitable water. The Middle Holocene simulations show a global annual cooling of < 0.1 °C compared to the PI simulation, and there are no differences in annual precipitation (Otto-Bliesner *et al.*, 2006; Braconnot *et al.*, 2007).

#### Modelling algorithm: MaxEnt

MAXENT (Maximum entropy modelling of species geographic distributions; Phillips *et al.*, 2006; Phillips & Dudik, 2008) is an algorithm specifically designed to calculate the potential geographic distribution of a species. It combines artificial intelligence (Machine Learning) and the Principle of Maximum Entropy (Jaynes, 1957), and thus, out of the wide range of possible modelling algorithms, provides one of the most accurate predictions (Elith *et al.*, 2006). MAXENT estimates the probability of the presence of any species, determining the maximum entropy distribution (the closest to uniformity) from a set of records of the presence of a taxon and from digital cartography of environmental variables, which influence the species distribution (Phillips *et al.*, 2006).

#### Model calibration and evaluation

A cumulative output format was chosen in order to determine the potential *Abies pinsapo* and *A. alba* distribution. This

output represents habitat suitability with continuous values [0, 100] (Phillips & Dudik, 2008). The algorithm parameters fixed to calibrate the SDMs were stricter than those recommended by Phillips *et al.* (2006). The SDMs were evaluated by the area under the ROC curve (AUC) test provided by the MAXENT software using a random data-splitting approach to establish an evaluation dataset (25% of the entire presence dataset) for *A. pinsapo* and *A. alba*.

Phillips *et al.* (2006), in a novel interpretation of AUC being applied only to presence-based algorithms, stated that 'AUC is the probability that a randomly chosen presence site is ranked above a random background site'. But the AUC method based on background points has a known weakness (Lobo *et al.*, 2008): the AUC scores are consistently higher for species with small ratios between the extent of occurrence and the entire extent of territory under study, as in the case of rare species such as *A. pinsapo*. Although there is ongoing discussion about the reliability of this measure of accuracy (see Peterson *et al.*, 2007; and Lobo *et al.*, 2008, for further details), this issue is beyond the scope of the present study.

#### Analysis of environmental requirements

The following analyses were also carried out for a comparative evaluation of the environmental requirements of *A. pinsapo* and *A. alba*: (1) principal-components analysis (PCA) over three groups of environmental variables (topography, temperature and rainfall); and (2) the Wilks test and Fisher discriminant analysis (Venables & Ripley, 2002) to analyse the differences between the two species in terms of ecological requirements. The analysis was performed on a random subsample of presences (*A. alba*,  $n = 33$ ; *A. pinsapo*,  $n = 44$ ). The R software environment (R Development Team, 2008) and its Rcmdr package (Fox *et al.*, 2007) were used for the statistical computing and graphics.

#### Fossil records of *Abies cf. pinsapo* and *Abies cf. alba* in the Iberian Peninsula

In relation to our review of all the fossil pollen sequences in the Iberian Peninsula (Spain and Portugal), Table 1 shows only the fossil evidence which includes *Abies* pollen. In Portugal, *Abies* pollen was completely absent from the pollen deposits analysed (e.g. Van der Knaap & van Leeuwen, 1994, 1995, 1997). These 35 selected sites are used to locate, geographically and temporally, *Abies* species refuges. Unfortunately, no palaeo-palynological studies have been performed to investigate the ranges currently inhabited by *A. pinsapo* (Fig. 1). The data for three sites (Padul, Navarrés and Roquetas de Mar) are included in the European Pollen Data (EPD), and the remaining data set are published but not included in EPD. The criterion for selecting a sequence was based on *Abies* pollen-percentage threshold values (occurrences of c. 1% or greater; see Iglesias, 1998 for supplementary information). The pollen data on *Abies cf. pinsapo*, even at the low threshold used here, probably

**Table 1** Pollen deposits indicating the code, site name, location (UTMx and UTMy), type of deposits, estimated chronology and bibliographic references.

Code	Site name	UTM x	UTM y	Site type	Estimated chronology (kyr BP)	6 kyr BP	21 kyr BP	References
1	Torreblanca	775227	4455047	Peatland	c. 6 and Late Holocene	Yes	No data	Dupré <i>et al.</i> (1994)
2	Navarrés	700392	4331106	Peatland	31–27	No	No	Carrión & van Geel (1999)
3	Les Malladetes	734653	4322087	Archaeological cave	c. 15–13	No data	No	Dupré (1980, 1988)
4	San Benito	670218	4305845	Lake	5–4 and 1.5–1.4	No	No data	Dupré <i>et al.</i> (1996)
5	Tossal de la Roca	736826	4297670	Archaeological rockshelter	c. 16–13 and 12–11.8	No data	No data	Cacho <i>et al.</i> (1983, 1995)
6	En Pardo	744816	4283668	Archaeological cave	Bölling/Allerod	No data	No	González Sampérez (1998)
7	Villena	681000	4276000	Lake	> 47 and c. 6	Yes	No	Yll <i>et al.</i> (2003)
8	Cucú	565515	4166070	Archaeological cave	c. 100–70	No data	No data	A. González-Ramón <i>et al.</i> (in preparation)
9	Las Ventanas	462694	4141062	Palaeontological cave	c. 10.7	No data	No data	Carrión <i>et al.</i> (2001)
10	Río Seco	469380	4102610	Lake	1.2–1.1	No data	No data	Esteban (1996)
11	Padul	446450	4096970	Peatland	c. 400–200, c. 120–110, c. 110–74, c. 60–30, c. 21–17, 11.9–10	No	Yes	Menéndez Amor & Florschütz (1962, 1964); Florschütz <i>et al.</i> (1971); Pons & Reille (1988); Valle <i>et al.</i> (2003)
12	Roquetas de Mar	536693	4072214	Marsh	c. 6 and Late Holocene	Yes	No data	Yll <i>et al.</i> (1994)
13	Zafarraya	399800	4090150	Archaeological cave	> 46	No data	No data	Lebreton <i>et al.</i> (2003)
14	Bajondillo	365140	4054550	Archaeological cave	c. 50–42, c. 40–38, c. 35–20, c. 13–11, 7.4–7.2, c. 4.2	Yes	Yes	López-Sáez <i>et al.</i> (2007); Cortés-Sánchez <i>et al.</i> (2008)
15	Gorham	288937	4001897	Archaeological cave	c. 19–16	No data	No	Finlayson <i>et al.</i> (2006)
16	A Pena Grande	120431	4806936	Archaeological rockshelter	Lateglacial	No	No data	Ramil Rego & Aira Rodríguez (1992)
17	Chan do Lamoso	133215	4826983	Peatland	c. 10–9	No	No data	Ramil Rego (1993)
18	Fervedes II	132731	4765568	Archaeological rockshelter	Lateglacial	No	No data	Ramil Rego & Aira Rodríguez (1992)
19	A Valiña	121014	4776451	Archaeological cave	c. 37–33	No data	No data	Fernández Rodríguez <i>et al.</i> (1993)
20	Kurtzia	502100	4805300	Peat sediments	Upper Pleistocene	No data	No data	Muñoz <i>et al.</i> (1990)
21	Morín	430084	4802975	Archaeological cave	c. 39–37	No data	No	Leroi-Gourhan (1971)
22	Rascaño	443552	4793773	Archaeological cave	Lateglacial	No data	No	Boyer-Klein (1980)
23	El Mirador	458063	4688701	Archaeological cave	c. 5.4–5	No	No data	Expósito <i>et al.</i> (2008)
24	Anzarán	596500	4802623	Marsh	Upper Pleistocene	No data	No	Edeso <i>et al.</i> (1989)
25	Tramacastilla	715103	4732997	Lake	Upper Pleistocene-Holocene	Yes	Yes	Montserrat (1992); González Sampérez <i>et al.</i> (2005)
26	Formigal	706794	4738638	Lake	LGM	No data	Yes	González Sampérez <i>et al.</i> (2005)
27	Las Ranas	704095	4743995	Lake	Upper Pleistocene-Holocene	Yes	Yes	Montserrat (1992)
28	El Portalet	712795	4741889	Peatland	Mid-Holocene	Yes	No	González Sampérez <i>et al.</i> (2006)
29	Llauset	805453	4728082	Lake	Mid-Holocene	Yes	No data	Montserrat & Vilaplana (1987)
30	La Feixa	899177	4712608	Peatland	Mid-Holocene	Yes	No data	Gómez Ortiz & Esteban Amat (1993)
31	Baños de Tredos	819778	4737028	Peatland	Mid-Holocene	Yes	No data	Bartley (1962)
32	Banyolas	975853	4680252	Lake	Lateglacial and Mid-Holocene	Yes	No	Pérez Obiol & Julià (1994)
33	La Palomera	963965	4677714	Archaeological cave	Late Holocene	No data	No data	Burjachs (1984)
34	Sobrestany	1006421	4676918	Lake	Mid-Holocene	Yes	No data	Parra <i>et al.</i> (2005)
35	Berguedà	908277	4683398	Palaeosoil	Mid-Holocene	Yes	No data	Pérez Obiol & Roure (1990)

Yes, presence of *Abies* pollen in pollen deposits during the Middle Holocene ( $\pm 500$  yr) or at the last glacial maximum (LGM) ( $\pm 500$  yr); No, absence of *Abies* pollen in pollen deposits during the Middle Holocene ( $\pm 500$  yr) or at the LGM ( $\pm 500$  yr); No data, no data are available.

underestimate the distribution of this tree, because it produces and spreads small amounts of pollen (Arista & Talavera, 1994). Then the *Abies* pollen curves were based on published diagrams, and the percentages were recalculated when sufficient information was available, to compile a uniform and reliable body of data. Pollen percentages are calculated using a pollen sum excluding fern spores and hydro-hygrophyte taxa. Table 1 also indicates when the estimated chronology of a pollen sequence overlaps the LGM (21 kyr BP) or Middle Holocene (6 kyr BP) periods. Spatial coincidences between pollen records and potential distribution of *Abies* species was the criterion to assign the fossil records to *A. alba* or *A. pinsapo*.

**RESULTS**

**Climate scenarios**

Table 2 shows the summarized values from the final interpolated models (CCSM and MIROC) and current climate data for the Iberian Peninsula. In addition, differences between values for the annual temperature (Tann) and temperature of the coldest month (Tmin) for the diverse climate scenarios are shown (see Fig. S1): at the LGM a cooling of 3 and 2.2 °C (Tann) and 2.5 and 1.9 °C (Tmin) (CCSM and MIROC simulation, respectively) was detected; while in the Middle Holocene, no significant anomalies were observed. Moreover, the surface temperature time course for the diverse climate scenarios with respect latitude (from Pyrenees to Straits of Gibraltar) (see Fig. S2) confirms an amplification of cooling at high latitudes during the LGM (see Otto-Bliesner *et al.*, 2006 for further information). Iberian model simulations show decreases from modern values of around 4 °C (near the Pyrenees) and 3 °C (near Gibraltar) for Tmin.

**Middle Holocene and LGM potential distributions of *Abies pinsapo* and *Abies alba***

The resulting SDMs provided high AUC scores [*A. pinsapo*: training data (0.999) and test data (0.998) and *A. alba*: training

data (0.996) and test data (0.992)] according to the evaluation test provided by the MAXENT software. This is a high AUC value, which demonstrates good model performance.

Comparing the projection of present-day SDMs (Fig. 2) to Mid-Holocene (Fig. 3) and LGM (Fig. 4) climates under both the CCSM and MIROC GCM climates models, we see that the overall reconstructed distributions were not dramatically different at the LGM, but that suitable areas were more fragmented and discontinuous than in the Middle Holocene and present day. In particular, we observed reduced continuity of the species' potential distribution area across the Pyrenees (*A. alba*) and Baetic mountain system (*A. pinsapo*) and a tendency to persist during the LGM at lower altitudes than those they occupy now or which they occupied during the Middle Holocene (see Figs S3–S7).

An expansion of these forests around 6000 yr BP is well reflected in our results. The warming and heavier precipitation (Table 2 and Fig. 3) had a great effect on *Abies* distribution, allowing their expansion from glacial refugia with a tendency to rise in altitude as well as in latitude. The potential distribution of *A. pinsapo* extended towards the nearest mountain ranges, to the south of the Iberian Peninsula, spreading to the southeastern end of the Baetic Range. Even the algorithm reveals several areas of potential distribution on the Mediterranean coast of the eastern Iberian Peninsula (Fig. 3; see also Fig. S4). In the Middle Holocene, *A. alba* displayed a larger and continuous potential distribution area compared with its LGM and existing distribution in the Pyrenees. Habitable areas were observed in Cantabrian Range, in which, today, there are no *A. alba* populations. In general, a tendency to rise in altitude was observed in both mountain systems. The model also shows suitable habitats in areas towards the inner Iberian Peninsula, in the Iberian mountain system.

Table 3 shows a heuristic estimate of relative contributions of the environmental variables to the MaxEnt model. The variables related to the seasonality of the Mediterranean climate, both pluviometric (e.g. Pmax and Pmin) and thermometric variables (e.g. Tmax and Tann) contribute greatly to explain the potential distribution of *A. pinsapo*, in addition to other topographic variables (e.g. slope), which

**Table 2** Value range for the different climate scenarios. Column 1 shows the present climate variables; columns 2 and 3 show past climate variables (in the Middle Holocene and the last glacial maximum, respectively) under two different general circulation model estimates (CCSM and MIROC).

	Present		6 kyr BP				21 kyr BP			
			MIROC		CCSM		MIROC		CCSM	
	Values range									
Tmax	14.4	38.7	13.9	38.0	14.4	38.7	12.5	36.7	10.9	35.4
Tann	-1.3	20.1	-1.6	19.0	-1.1	19.6	-3.2	17.5	-4.9	-17.3
Tmin	-14.6	11.0	-15.1	10.6	-14.6	11.0	-16.7	9.3	-18.3	9.8
Pmax	22	446	23	475	22.0	482	40	443	0	453
Pann	22	3206	274	3270	22.0	2856	81	2186	0	2150
Pmin	0	153	35	222	0	136	29	217	0	113

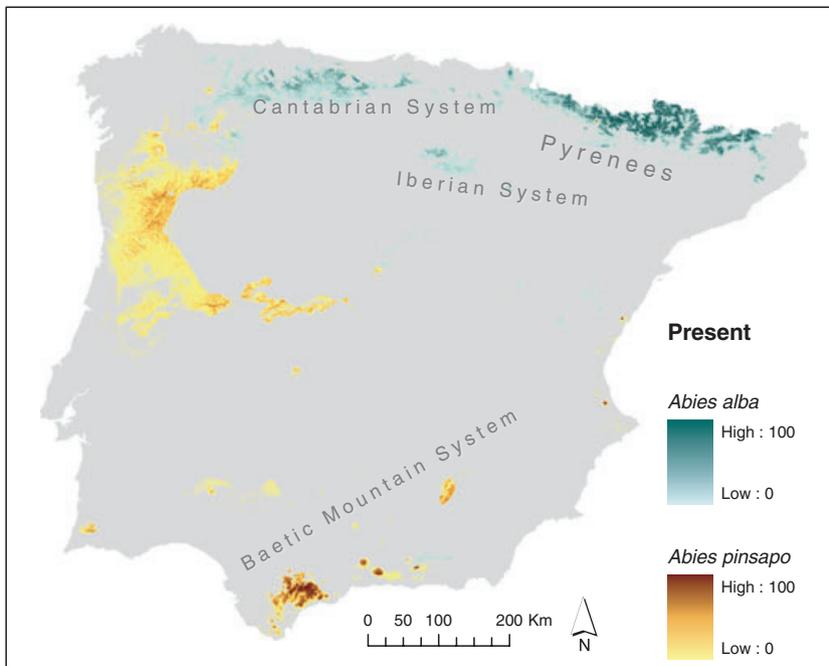


Figure 2 Potential distribution of *Abies pinsapo* and *Abies alba* at the present in relation to the current climate. Habitat suitability values are also shown.

contribute to the potential model. Precipitation during the driest month ( $P_{min}$ ), a highly significant feature in regions with Cfb Climate class, was the most important variable to explain the *A. alba* distribution model. Also,  $T_{ann}$  and  $T_{min}$  play a decisive part in this distribution model. Figure 5 illustrates a clear differentiation between the ecological requirements of the two species, particularly on the axes referring to climatic variables (temperature and rainfall), in contrast to the overlap of topographic characteristics between the two habitats. The Fisher discriminant-analysis results ( $\lambda = 0.064$ ;  $F = 86.828$ ;  $P < 0.0001$ ) reinforced the hypothesis of segregation between the two taxa based on ecological requirements. This analysis assigned the higher coefficients in the linear discrimination equation (Table 4) to the  $T_{min}$  (0.0926) and to the  $T_{max}$  (0.0357).

#### Fossil records of *Abies cf. pinsapo* and *Abies cf. alba* in the Iberian Peninsula

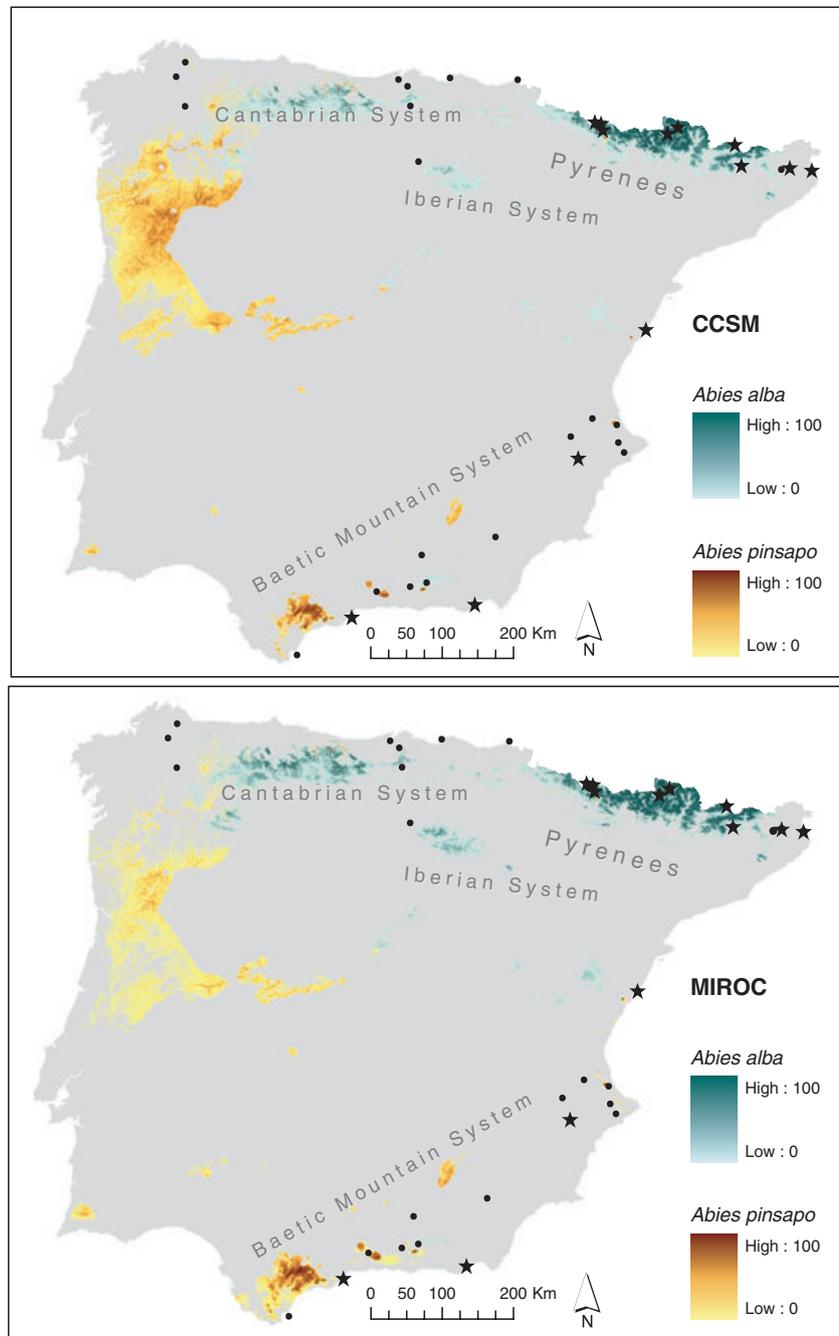
Based on the SDMs results (Figs 2-4), *Abies* pollen was classified as follows: *A. cf. pinsapo*, pollen deposits with codes that ranged from 1 to 15; *A. cf. alba*, pollen deposits with codes that ranged from 16 to 35 (Table 1). Spatial coincidences between pollen records and potential distribution of *Abies* species were found throughout the Baetic mountains, as well as the Pyrenees and Cantabrian Range (Figs 1-4 and Table 1). Unfortunately, at the LGM, few pollen sites were found that reflect the situation of *Abies* population in the Iberian Peninsula (Padul and Bajondillo sites in the south; Tramacastilla, Formigal and Las Ranas sites in the Pyrenees), for that reason the *Abies* refugia at this time is poorly understood based on palaeopolynological studies alone. In the Middle Holocene, more pollen sequences were found (four sites in the Baetic mountains and nine sites in the Pyrenees).

In general terms, during the Quaternary, pollen from *A. cf. pinsapo* appears throughout the entire Baetic mountains system, from Gibraltar (Gorham site) to Almería (Roquetas de Mar site), usually in coastal mountains. However, pollen records from Las Ventanas and Cucú sites suggest a certain expansion of *A. pinsapo* towards the inner zone (Table 1; Fig. 1). The most remarkable fossil evidence was found in the Prebaetic mountains (eastern Iberian Peninsula) (sites 1-7), areas far from the current distribution of *A. pinsapo* and of great interest for understanding the past distribution. Pollen studies indicated that *A. alba* inhabited mainly the Pyrenees Range during cool and dry periods, mainly at the foot of the mountain, as well as the rapid postglacial recovery towards surrounding areas. This suggests that this species held out in refuges in the Pyrenees area during the last ice age. In addition, pollen from *A. cf. alba* appears throughout the entire Cantabrian Range, from Galicia to the Basque Region, usually in coastal or pre-coastal areas (sites 16-22 and 24). Surprisingly, *Abies* pollen was also found towards the inner zone (site 23, located in the foothills of the Iberian mountain system).

## DISCUSSION

### Model accuracy and prediction uncertainty

The potential distribution models calibrated for *Abies pinsapo* and *A. alba* show high AUC scores, according to the test provided by the modelling software (Phillips et al., 2006). Our modelling approach relies on a robust method (MAXENT) when dealing strictly with presence data (Elith et al., 2006; Phillips et al., 2006). The resulting SDMs for *A. alba* and *A. pinsapo* should be among the best that can be achieved for our dataset (presence and environmental data). The overlap observed between the species' potential distribution and prior



**Figure 3** Potential distribution of *Abies pinsapo* and *Abies alba* during the Middle Holocene, under two different general circulation model (GCM) estimates (CCSM and MIROC). In addition, 35 pollen deposits are also shown. Presence of *Abies* pollen in pollen deposits during the Middle Holocene ( $\pm 500$  yr) is indicated with a star symbol.

presence of *Abies*—inferred from fossil pollen records—some way validates the model predictions made as well as the predictive ability of SDMs using hindcasting.

However, inconveniences arising from the palaeoclimatic scenarios could add uncertainty to the predictive models. For example, problems arising because of the appearance of non-analogous climate conditions when SDMs are projected across major climatic changes, especially those that occurred in the LGM, then modelling approaches will have unknown or unpredictable behaviour in predicting in those areas (Pearson *et al.*, 2006). An added complication may arise because the PMIP model data underestimated the drying and cooling

throughout the Mediterranean basin at the LGM (Ramstein *et al.*, 2007), and so the models presented could overestimate the *Abies* distribution during the LGM. In addition, according to the authors cited earlier, the spatial resolution of the PMIP models may be a supplementary difficulty, particularly in areas of complex topography such as the Iberian Peninsula. For the Pyrenees or the Baetic Range, the local climate can differ sharply from the climate simulated in the corresponding grid box of the models. Enhancing the models' resolution should improve the representation of a given region. However, it remains unclear whether the sensitivity of the models will be affected by changing their resolution.

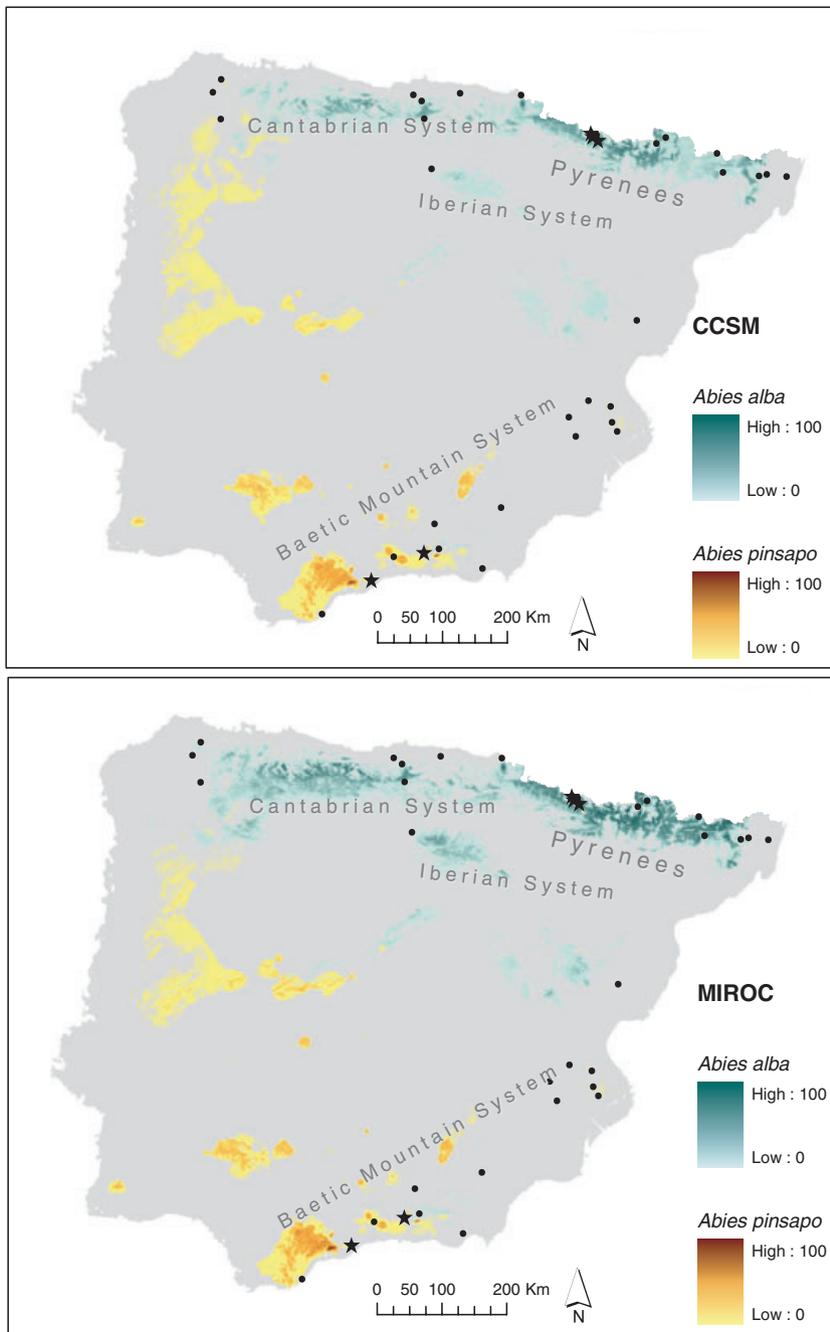


Figure 4 Potential distribution of *Abies pinsapo* and *Abies alba* at the last glacial maximum (LGM), under two general circulation model (GCM) estimates (CCSM and MIROC). In addition, 35 pollen deposits are also shown. Presence of *Abies* pollen in pollen deposits at the LGM ( $\pm 500$  yr) is indicated with a star symbol. The Iberian coastline during the LGM is displayed.

### Detecting suitable habitats based on SDMs and palaeorecords

In the present study, by integrating ecological-niche characteristics drawn from the environmental characteristics of known occurrences of *Abies* species and palaeoecological studies, we derived a more refined image of the distribution, discontinuities and segregation between Iberian *Abies* species. Some way, niche conservatism has been documented throughout the present-day distribution of Iberian *Abies* species (Figs 2-4), and it has been shown that at the LGM, the distribution area of *Abies* populations into several locations corresponding to presumed Pleistocene refugia (Table 1, Fig. 4

and Figs S6 & S7). The overlap noted between past *Abies* refugia—inferred from fossil pollen records—and the species’ potential distribution offers a new interpretation of the Quaternary distribution of the Iberian *Abies* species. According to Martínez-Meyer & Peterson (2006), from the standpoint of historical biology, our results propose that Quaternary distribution areas of some species could be inferred from present-day habitat characteristics, providing an additional tool for palaeobiogeography research.

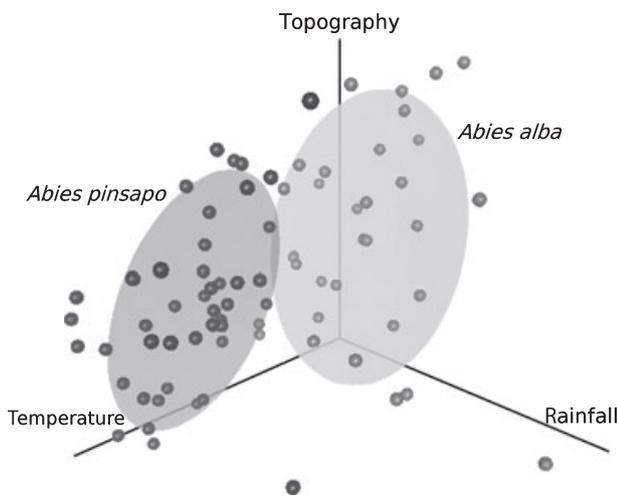
The results presented here could constitute further evidence for the conservation of climatic and topographic dimensions of ecological niches over moderate periods of time, despite strong

**Table 3** Relative contributions of the environmental variables to the MaxEnt model.

<i>Abies pinsapo</i>		<i>Abies alba</i>	
Variable	Percent contribution (%)	Variable	Percent contribution (%)
Pmax	40.3	Pmin	38.9
Pmin	23.6	Tann	33.8
Tmax	18.6	Tmin	16.2
Slope	9.1	Slope	4.0
Tann	4.9	Pmax	2.9
Tmin	2.6	TWI	2.1
TWI	0.6	Tmax	1.4
Topographic exposure	0.2	Pann	0.4
Pann	0.1	Topographic exposure	0.3

Pann (annual precipitation); Pmin (precipitation of the driest month); Pmax (precipitation of the wettest month); Tmax (maximum temperature of the hottest month), Tmin (minimum temperature of the coldest month); Tann (annual temperature); TWI (topographic wetness index).

climatic and environmental changes. The agreement between past and present-day *Abies* refuge data could be explained by relative climate stasis in the refuge areas and revolves around the importance of their local intrinsic properties. As suggested by the palaeopalynological and palaeoclimatic studies (see Tzedakis *et al.*, 2002 and reference therein), factors that currently lead to high precipitation in some mountain areas of the Mediterranean basin (essentially, orographic uplift of air charged with moisture from the nearby coasts) also operated during the LGM, moderating the impact of regional aridity on tree populations. The palynological data (Table 1) provide



**Figure 5** Presence records of *Abies alba* and *Abies pinsapo* with respect to three axes (obtained by principal-components analysis), representing the different groups of environmental variables (topography, temperature and rainfall).

**Table 4** Linear discriminant coefficients.

Predictor	Coefficients
Tmin	0.092661
Tmax	0.035758
TWI	0.003944
Topographic exposure	0.003694
Slope	0.002549
Pann	0.000590
Pmax	-0.002087
Pmin	-0.016655
Tann	-0.106213

Pann (annual precipitation); Tmax (maximum temperature of the hottest month); Tann (annual temperature); Tmin (minimum temperature of the coldest month); TWI (topographic wetness index).

evidence for the existence of an ecologically stable area where local conditions appear to have buffered the extreme effects of Quaternary climate variability, contributing to the survival of residual *Abies* populations.

At the LGM, the combined effects of reduced annual precipitation and winter temperatures throughout the Iberian Peninsula (see Table 2) with a shorter growing season and also lower atmospheric CO<sub>2</sub> concentrations (200 p.p.m. for CO<sub>2</sub>; see Braconnot *et al.*, 2007), which led to *Abies* population contraction and fragmentation (Fig. 4 and Figs S6–S7), but these events were not severe enough to cause their total elimination. One idea bolstering this assumption is that a gradual southward attenuation of the North Atlantic climate signal probably occurred at the LGM, as suggested by the Iberian climatic simulations (Fig. S2). Topography is also a critical factor, which determines the extent to which populations can shift altitudinally in response to climate change (Tzedakis, 1993; Tzedakis *et al.*, 2002), seeking to evade extirpation. At the LGM, both the Pyrenees and Baetic Range provided the sufficient topographical variability to supply a number of microhabitats suitable for survival. A trend to persist during the LGM at lower altitudes as well as reduced continuity of the species' potential distributional area throughout the Pyrenees (*A. alba*) and Baetic Range (*A. pinsapo*) were found in this study (Fig. 4 and Figs S6 & S7).

In the Middle Holocene, a significant expansion of *Abies* populations is well reflected in our results by two approaches. During this period, *Abies pinsapo* and *A. alba* displayed a larger and continuous potential distribution area compared with its LGM and current distribution in the Pyrenees or Baetic Range, respectively (see Figs 1 & 3). The increased precipitation and the warming (Table 2 and Figs S1 & S2) allowed the spread of *Abies* throughout Iberian mountains since the last glacial period. A trend to rise in altitude to avoid the warming was observed in both *Abies* species. The occupation area, as well as its altitudinal range in the mountains, has a very similar feature to present-day potential distribution. Comparing the three projections—present-day SDM, Mid-Holocene SDM and LGM SDM—we see that the overall reconstructed distributions

did not significantly differ, indicating a high degree of evolutionary stasis in the *Abies* climatic requirements (see Svenning, 2003 and references therein).

Previous studies (Terhürne-Berson *et al.*, 2004; Muller *et al.*, 2007) suggest that the southern Iberian Peninsula was probably a refuge for *A. pinsapo*. The increasing availability of pollen sequences, and the fact that such taxa as *A. pinsapo* are under-represented in the fossil record, strengthens the assumption of a wider distribution of *A. pinsapo* forests throughout the Baetic Range (including the Prebaetic zone, in eastern Iberia). In addition, some authors (such as Reille & Lowe, 1993) considered it unlikely that the Pyrenees or the Iberian Peninsula were refugia during the LMG. However, Terhürne-Berson *et al.* (2004), Muller *et al.* (2007) and Liepelt *et al.* (2009) reconstructed the location of the last glacial refugia and postglacial spread of *Abies* throughout Europe, confirming the long-lasting refuge areas. The SDMs as well as the fossil evidence suggest a wider Quaternary distribution, which would have extended across the Pyrenees Range and the Cantabrian mountain system and even reached the Iberian mountain system, in an intermediate geographic position. Previous studies based on SDM confirm the presence of *A. alba* during the LGM in the Pyrenees (Benito Garzón *et al.*, 2007).

### ***Abies pinsapo* and *Abies alba* ecological segregation**

*Abies alba* and *A. pinsapo* niches differ significantly in climatic-niche dimensions (Fig. 5), pointing to an early evolutionary divergence of the two species. The ecological segregation suggests that the two species remained geographically isolated throughout their Quaternary history, although we do not reject the hypothesis that Quaternary contact may have existed between *A. alba* and *A. pinsapo* populations in eastern Iberia (Figs 3 & 4). Geographical overlap among *Abies* species seems to have been common during the glacial periods (Scaltsoyianes *et al.*, 1999).

SDMs yielded two well-differentiated potential ranges for the Iberian *Abies* species: the *A. pinsapo* range presents in Baetic-Prebaetic mountains in a Mediterranean climate; and the *A. alba* range, along the north Atlantic coast and the north-eastern Iberian, in temperate mountainous areas (Figs 2–4). According to Araújo & Pearson (2005) and Pearson (2006), the previously mentioned overlap provides useful information on the ecological conditions that allowed some populations of *A. pinsapo* and *A. alba* to survive until the present and indicates that the two species have independent biogeographical dynamics.

### **CONCLUSIONS AND REQUIREMENTS FOR FURTHER RESEARCH**

Our results confirm that SDMs projections can provide a useful complement to palaeoecological studies, offering a less subjective and spatially explicit hypothesis concerning the past geographic patterns of Iberian *Abies* species. Additionally, the

pollen records provide evidence for the existence of *Abies* populations in several locations corresponding to presumed Pleistocene refugia. The integration of ecological-niche characteristics from known occurrences of *Abies* species in conjunction with palaeoecological studies could constitute a suitable tool to define proper areas in which to focus proactive conservation strategies. The results provide evidence for the existence of several ecologically stable areas in the Pyrenees and Baetic Range, where local conditions appear to have buffered the extreme effects of climate variability, contributing to the long-time survival of *Abies* populations. This is especially important to design future projections for *Abies* species under climate-change scenarios.

### **ACKNOWLEDGEMENTS**

This study was funded by a Technology Research Consolider Programme for the evaluation and conservation of Cultural Heritage -TCP-CSD2007-00058; by the Andalusian Innovation, Science, and Industry Regional Ministry (RNM 1067 project), and by the National Plan of the Spanish Government (HAR2008-06477-C03-03/HIST project). We also thank H.P. Linder for constructive comments and discussion of the Iberian *Abies* species history. We appreciate the helpful observations of A. Guisan, J.C. Svenning, and two anonymous reviewers on a previous version of this article.

### **REFERENCES**

- Araújo, M.B. & Pearson, R.G. (2005) Equilibrium of species' distributions with climate. *Ecography*, **28**, 693–695.
- Arista, M. & Talavera, S. (1994) Pollen dispersal capacity and pollen viability of *Abies pinsapo* Boiss. *Silvae Genetica*, **43**, 155–158.
- Austin, M.P., Cunningham, R.B. & Fleming, P.M. (1984) New approaches to direct gradient analysis using environmental scalars and statistical curve-fitting procedures. *Vegetatio*, **55**, 11–27.
- Bartley, D.D. (1962) Pollen analysis of a small peat deposit at Baños de Tredos, near Viella in the Central Pyrenees. *Pollen et Spores*, **4**, 105–110.
- Benito Garzón, M., Sánchez de Dios, R. & Sainz Ollero, H. (2007) Predictive modelling of tree species distributions on the Iberian Peninsula during the Last Glacial Maximum and Mid-Holocene. *Ecography*, **30**, 120–134.
- Boyer-Klein, A. (1980) Nouveaux résultats palynologiques de sites solutréens et magdaléniens cantabriques. *Bulletin de la Société Préhistorique Française*, **77**, 103–107.
- Braconnot, P., Otto-Bliesner, B., Harrison, S. *et al.* (2007) Results of PMIP2 coupled simulations of the Mid-Holocene and Last Glacial Maximum – Part 1: experiments and large-scale features. *Climate of the Past*, **3**(2), 261–277.
- Brewer, S., Guiot, J. & Torre, F. (2007) Mid-Holocene climate change in Europe: a data-model comparison. *Climate of the Past*, **3**, 499–512.

- Burjachs, F. (1984) Anàlisi polínica del poblat ibèric de La Palomera (La Garrotxa). *Revista de Girona*, **108**, 38.
- Cacho, C., Fumanal, P., López García, P. & López, N. (1983) Contribution du Tossal de la Roca à la chronostratigraphie du Paléolithique supérieur final dans la région de Valence. *Rivista di Science Preistoriche*, **38**, 69–90.
- Cacho, C., Fumanal, M.P., López García, P., López-Sáez, J.A., Pérez, M., Martínez, R., Uzquiano, P., Arnanz, A., Sánchez, A., Sevilla, P., Morales, A., Roselló, E., Garralda, M.D. & García, M. (1995) El Tossal de la Roca (Vall d'Alcalà, Alicante). Reconstrucción paleoambiental y cultural de la transición del Tardiglacial al Holoceno inicial. *Recerques del Museu d'Alcoi*, **4**, 11–101.
- Carrión, J.S. & Sánchez-Gómez, P. (1992) Palynological data in support of the survival of walnut (*Juglans regia* L.) in the western Mediterranean during last glacial times. *Journal of Biogeography*, **19**, 623–630.
- Carrión, J.S. & van Geel, B. (1999) Fine-resolution Upper Weichselian and Holocene palynological record from Navarrés (Valencia, Spain) and a discussion about factors of Mediterranean forest succession. *Review of Palaeobotany and Palynology*, **106**, 209–236.
- Carrión, J.S., Riquelme, J.A., Navarro, C. & Munuera, M. (2001) Pollen in hyaena coprolites reflects late glacial landscape in southern Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **176**, 193–205.
- Carrión, J.S., Yll, E.I., Walker, M.J., Legaz, A.J., Chaín, C. & López, A. (2003) Glacial refugia of temperate, Mediterranean and Ibero-North African flora in south-eastern Spain: new evidence from cave pollen at two Neanderthal man sites. *Global Ecology & Biogeography*, **12**, 119–129.
- Carrión, J.S., Finlayson, C., Fernández, S., Finlayson, G., Allué, E., López-Sáez, J.A., López García, P., Gil-Romera, G., Bailey, G. & González-Sampériz, P. (2008) A coastal reservoir of biodiversity for Upper Pleistocene human populations: palaeoecological investigations in Gorham's Cave (Gibraltar) in the context of the Iberian Peninsula. *Quaternary Science Reviews*, **27**, 2118–2135.
- Cortés-Sánchez, M., Morales-Muñiz, A., Simón-Vallejo, M.D., Bergadà-Zapata, M.M., Delgado-Huertas, A., López-García, P., López-Sáez, J.A., Lozano-Francisco, M.C., Riquelme-Cantal, J.A., Roselló-Izquierdo, E., Sánchez-Marco, A. & Vera-Peláez, J.L. (2008) Paleoenvironmental and cultural dynamics of the coast of Málaga (Andalusia, Spain) during the Upper Pleistocene and early Holocene. *Quaternary Science Reviews*, **27**, 2176–2193.
- Costa Tenorio, M., Morla Juaristi, C. & Sáinz Ollero, H. (1997) *Los bosques ibéricos. Una interpretación geobotánica*. Editorial Planeta, Barcelona.
- Dupré, M. (1980) Anàlisi polínica de sediments arqueològics de la Cueva de Les Malladetes (Barx, Valencia). *Cuadernos de Geografía*, **26**, 1–22.
- Dupré, M. (1988) *Palinología y paleoambiente. Nuevos datos españoles. Referencias*. Diputación Provincial de Valencia, Valencia.
- Dupré, M., Pérez Obiol, R. & Roure, J.M. (1994) Anàlisi polínica del sondeo TU de la turbera de Torreblanca (Castellón, España). *Trabajos de Palinología Básica y Aplicada. X Simposio de Palinología* (ed. by I. Mateu, M. Dupré, J. Güemes and M.E. Burgaz), pp. 165–174. Universitat de València, València.
- Dupré, M., Fumanal, M.P., Martínez, J., Pérez Obiol, R., Roure, J.M. & Usera, J. (1996) The Laguna de San Benito (Valencia, Spain): palaeoenvironmental reconstruction of an endorheic system. *Quaternaire*, **7**, 177–186.
- Edeso, J.M., Ugarte, F.M. & Peñalba, M.C. (1989) El depósito detrítico pleistoceno (estuarino-fluvial) de Anzarán (Irún, estuario del Bidasoa): caracterización geomorfológica y palinológica. *Actas de la 2ª Reunión del Cuaternario Ibérico*, pp. 16–17. AEQUA-GTPEQ, Madrid.
- Elith, J., Graham, C.H., Anderson, R.P. *et al.* (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, **29**, 129–151.
- Esteban, A. (1996) Evolución del paisaje nevadense durante los últimos 1.500 años a partir del análisis polínico de borreguiles. *1ª Conferencia Internacional Sierra Nevada*, pp. 251–273. Universidad de Granada, Granada.
- Expósito, I., Yll, R. & Burjachs, F. (2008) Paleambiente del Neolítico de la Meseta Norte Ibérica a partir del registro palinológico de un depósito de origen antropozógeno (Cueva de El Mirador, Sierra de Atapuerca, Burgos). *Proceedings XVI international APLE symposium of palynology*, pp.77. Universitat de les Illes Balears, Palma de Mallorca.
- Farjon, A. & Rushforth, K.D. (1989) A classification of *Abies* Miller (Pinaceae). *Notes of the Royal Botanic Garden Edinburgh*, **46**, 59–79.
- Fernández Rodríguez, C., Ramil Rego, P., Martínez Cortizas, A., Rey Salgado, J.M. & Peña Villamide, P. (1993) La cueva de A Valiña (Castroverde, Lugo): Aproximación estratigráfica, paleobotánica y paleontológica al Paleolítico superior inicial de Galicia. *Estudios sobre Cuaternario. Medios sedimentarios. Cambios Ambientales. Hábitat humano* (ed. by M.P. Fumanal and J. Bernabeu), pp. 159–177. Universitat de València, València.
- Finlayson, C., Giles Pachecho, F., Rodríguez Vidal, J. *et al.* (2006) Late survival of Neanderthals at the southernmost extreme of Europe. *Nature*, **443**, 850–853.
- Florschütz, F., Menéndez Amor, J. & Wijmstra, T.A. (1971) Palynology of a thick Quaternary succession in Southern Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **10**, 233–264.
- Fox, J., Ash, M., Boye, T., Calza, S., Chang, A., Grosjean, P., Heiberger, R., Kerns, G.J., Lancelot, R., Lesnoff, M., Messad, S., Maechler, M., Putler, D., Ristic, M. & Wolf, P. (2007) *Rcmdr: R Commander. R package version 1.3–9*. Available at: <http://socserv.socsci.mcmaster.ca/jfox/Misc/Rcmdr/>
- Gómez Ortiz, A. & Esteban Amat, A. (1993) Anàlisi polínica de la turbera de La Feixa (La Màniga, Cerdanya, 2.150 m). Evolución del paisaje. *Estudios sobre Cuaternario, medios sedimentarios, cambios ambientales, hábitat humano* (ed. by M.P. Fumanal and J. Bernabeu) pp. 185–190. Universitat de València, València.

- González Sampérez, P. (1998) Estudio palinológico de la Cueva de En Pardo (Planes, Alicante). Primeros resultados. *Cuaternario y Geomorfología*, **12**, 45–61.
- González Sampérez, P., Valero Garcés, B.L., Carrión, J.S., Peña-Monné, J.L., García-Ruiz, J.M. & Martí-Bono, C. (2005) Glacial and Lateglacial vegetation in northeastern Spain: new data and a review. *Quaternary International*, **140–141**, 4–20.
- González Sampérez, P., Valero Garcés, B.L., Moreno, A., Jalut, G., García Ruiz, J.M., Martí Bono, C., Delgado Huertas, A., Navas, A., Otto, T. & Dedoubat, J.J. (2006) Climate variability in the Spanish Pyrenees during the last 30,000 yr revealed by the El Portalet sequence. *Quaternary Research*, **66**, 38–52.
- GRASS Development Team (2008) *Geographic resources analysis support system (GRASS) software, version 6.3.0*. Available at: <http://grass.osgeo.org>.
- Guisan, A. & Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, **8**, 993–1009.
- Guisan, A. & Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling*, **135**, 147–186.
- Hewitt, G.M. (1996) Some genetic consequences of ice ages, and their role in divergence and speciation. *Biological Journal of the Linnean Society*, **58**, 247–276.
- Huntley, B. & Birks, H.J.B. (1983) *An atlas of past and present pollen maps for Europe*. Cambridge University Press, Cambridge.
- Iglesias, M. (1998) Relation végétation-pluie pollinique actuelle phytomasse épigée pérenne dans les steppes du Sud-Est de l'Espagne et du Nord-Est du Maroc. PhD Thesis, University of Paul Sabatier-Toulouse III, Toulouse.
- Jaynes, E.T. (1957) Information theory and statistical mechanics. *Physical Review*, **106**, 620–630.
- Kiehl, J.T. & Gent, P.R. (2004) The community climate system model, version 2. *Journal of Climate*, **17**, 3666–3682.
- Kottek, M., Grieser, J., Beck, C., Rudolf, B. & Rubel, F. (2006) World Map of the Köppen-Geiger climate classification updated. *Meteorologische Zeitschrift*, **15**, 259–263.
- Krebs, P., Conedera, M., Pradella, M., Torriani, D., Felber, M. & Tinner, W. (2004) Quaternary refugia of the sweet chestnut (*Castanea sativa* Mill.): an extended palynological approach. *Vegetation History and Archaeobotany*, **13**, 145–160.
- Krussmann, G. (1972) *Handbuch der Nadelgehölze*. Parey, Berlin.
- Lebreton, V., Renault-Miskovsky, J., Carrión, J.S. & Dupré, M. (2003) Estudio palinológico del sedimento de la Cueva del Boquete de Zafarraya. *El Pleistoceno Superior de la Cueva de El Boquete de Zafarraya* (ed. by C. Barroso), pp. 149–160. Junta de Andalucía, Sevilla.
- Leroi-Gourhan, A. (1971) Análisis polínico. *Cueva Morín* (ed. by J. González Echegaray and L.G. Freeman), pp. 359–364. Patronato Cuevas Prehistóricas de la Provincia de Santander, Santander.
- Liepelt, S., Cheddadi, R., de Beaulieu, J.-L., Fady, B., Gömöry, D., Hussendörfer, E., Konner, M., Litt, T., Longauer, R., Terhürne-Berson, R. & Ziegenhagen, B. (2009) Postglacial range expansion and its genetic imprints in *Abies alba* (Mill.) – A synthesis from palaeobotanic and genetic data. *Review of Palaeobotany and Palynology*, **153**, 139–149.
- Linares, J.C. (2008) *Efectos del cambio global sobre la dinámica poblacional y la ecofisiología de bosques relictos de Abies pinsapo Boiss.* PhD Thesis, University of Jaén, Jaén.
- Lobo, J.M., Jiménez-Valverde, A. & Real, R. (2008) AUC: a misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography*, **17**, 145–151.
- López de Heredia, U., Carrión, J.S., Jiménez, P., Collada, C. & Gil, L. (2007) Molecular and palaeoecological evidence for multiple glacial refugia for evergreen oaks on the Iberian Peninsula. *Journal of Biogeography*, **34**, 1505–1517.
- López-Merino, L., López-Sáez, J.A., Ruiz Zapata, M.B. & Gil García, M.J. (2008) Reconstructing the history of beech (*Fagus sylvatica* L.) in the north-western Iberian Range (Spain): from Late-Glacial refugia to the Holocene anthropic-induced forests. *Review of Palaeobotany and Palynology*, **152**, 58–65.
- López-Sáez, J.A., López-García, P. & Cortés-Sánchez, M. (2007) Paleovegetación del Cuaternario reciente: Estudio arqueopalinológico. *Cueva Bajondillo (Torremolinos). Secuencia cronocultural y paleoambiental del Cuaternario reciente en la Bahía de Málaga* (ed. by M. Cortés-Sánchez) pp. 139–156. Diputación de Málaga, Junta de Andalucía, Universidad de Málaga, Fundación Cueva de Nerja y Fundación Obra Social de Unicaja, Málaga.
- Martínez-Meyer, E. & Peterson, A.T. (2006) Conservatism of ecological niche characteristics in North American plant species over the Pleistocene-to-Recent transition. *Journal of Biogeography*, **33**, 1779–1789.
- Martínez-Meyer, E., Peterson, A.T. & Hargrove, W.W. (2004) Ecological niches as stable distributional constraints on mammal species, with implications for Pleistocene extinctions and climate change projections for biodiversity. *Global Ecology and Biogeography*, **13**, 305–314.
- Menéndez Amor, J. & Florschütz, F. (1962) Un aspect de la végétation en Espagne méridionale durant la dernière glaciation et l'Holocène. *Geologie en Mijnbouw*, **41**, 131–134.
- Menéndez Amor, J. & Florschütz, F. (1964) Results of the preliminary palynological investigation of samples from a 50 m boring in southern Spain. *Boletín de la Real Sociedad Española de Historia Natural (sección Geología)*, **62**, 251–255.
- Montserrat, J. (1992) *Evolución glacial y postglacial del clima y la vegetación en la vertiente sur del Pirineo: Estudio palinológico*. Monografías del Instituto Pirenaico de Ecología 6. Instituto Pirenaico de Ecología, CSIC, Zaragoza.
- Montserrat, J. & Vilaplana, J.M. (1987) The paleoclimatic records of the Upper Pleistocene and Holocene in the Llauset Valley (Central Southern Pyrenees). *Pirineos*, **129**, 107–113.
- Muller, S.D., Nakagawa, T., de Beaulieu, J.-L., Court-Picon, M., Carcaillet, C., Miramont, C., Roiron, P., Bouterlin, C., Ali, A.A. & Bruneton, E. (2007) Post-glacial migration of silver fir (*Abies alba* Mill.) in the south-western Alps. *Journal of Biogeography*, **37**, 876–899.

- Muñoz, M., Sánchez Goñi, M.F. & Ugarte, F.M. (1990) El entorno geo-ambiental del yacimiento arqueológico de Kurtzia. Sopela-Barrika. Costa occidental de Bizkaia. *Munibe*, **41**, 107–115.
- Ninyerola, M., Pons, X. & Roure, J.M. (2005) *Atlas Climático Digital de la Península Ibérica. Metodología y aplicaciones en bioclimatología y geobotánica*. Universidad Autónoma de Barcelona, Bellaterra. Available at: <http://opengis.uab.es>.
- Otto-Bliessner, B.L., Brady, E.C., Clauzet, G., Tomas, R., Levis, S. & Kothavala, Z. (2006) Last glacial maximum and holocene climate in CCSM3. *Journal of Climate*, **19**, 2526–2544.
- Parra, I., Van Campo, E. & Otto, T. (2005) Análisis palinológico y radiométrico del sondeo Sobrestany. Nueve milenios de historia natural e impactos humanos sobre la vegetación del Alt Empordà. *Empuriès*, **54**, 33–44.
- Pearman, P.B., Randin, C.F., Broennimann, O., Vittoz, P., Knaap, W.O., Engler, R., Lay, G.L., Zimmermann, N.E. & Guisan, A. (2008) Prediction of plant species distributions across six millennia. *Ecology Letters*, **11**, 357–369.
- Pearson, R.G. (2006) Climate change and the migration capacity of species. *Trends in Ecology & Evolution*, **21**, 111–113.
- Pearson, R.G., Thuiller, W., Araujo, M.B., Martinez-Meyer, E., Brotons, L., McClean, C., Miles, L., Segurado, P., Dawson, T.P. & Lees, D.C. (2006) Model-based uncertainty in species range prediction. *Journal of Biogeography*, **33**, 1704–1711.
- Pérez Obiol, R. & Julià, R. (1994) Climatic change on the Iberian Peninsula recorded in a 30,000-Yr pollen record from Lake Banyoles. *Quaternary Research*, **41**, 91–98.
- Pérez Obiol, R. & Roure, J.M. (1990) Evidència de la regressió recent des les avetoses a partir de les anàlisis pol·líniques. *Osis*, **5**, 5–11.
- Peterson, A.T. (2003) Predicting the geography of species' invasions via ecological niche modeling. *The Quarterly Review of Biology*, **78**, 419–433.
- Peterson, A.T. & Nyári, Á.S. (2008) Ecological niche conservatism and Pleistocene refugia in the thrush-like mourner, *Schiffornis* Sp., in the Neotropics. *Evolution*, **62**, 173–183.
- Peterson, A.T., Soberón, J. & Sánchez-Cordero, V. (1999) Conservatism of ecological niches in evolutionary time. *Science*, **285**, 1265–1267.
- Peterson, A.T., Papes, M. & Eaton, M. (2007) Transferability and model evaluation in ecological niche modeling: a comparison of GARP and Maxent. *Ecography*, **30**, 550–560.
- Phillips, S.J. & Dudík, M. (2008) Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography*, **31**, 161–175.
- Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, **190**, 231–259.
- Pons, A. & Reille, M. (1988) The Holocene and upper Pleistocene pollen record from Padul (Granada, Spain): a new study. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **35**, 145–214.
- R Development Team (2008) *The R project for statistical computing, R version 2.8.1*. Available at: <http://www.r-project.org>.
- Ramil Rego, P. (1993) Evolución climática e historia de la vegetación durante el Pleistoceno Superior y el Holoceno en las regiones montañosas del Noroeste Ibérico. *La evolución del paisaje en las montañas del entorno de los Caminos Jacobeos* (ed. by A. Pérez Alberti, L. Guitián Rivera and P. Ramil Rego), pp. 25–60. Xunta de Galicia, A Coruña.
- Ramil Rego, P. & Aira Rodríguez, M.J. (1992) Contribución al conocimiento de la vegetación Tardiglacial y Holocena en el extremo norte de la Terra Chá (Galicia, España). *Nova Acta Científica Compostelana (Biología)*, **3**, 49–58.
- Ramstein, G., Kageyama, M., Guiot, J., Wu, H., Hély, C., Krinner, G. & Brewer, S. (2007) How cold was Europe at the Last Glacial Maximum? A synthesis of the progress achieved since the first PMIP model-data comparison. *Climate of the Past*, **3**, 331–339.
- Reille, M. & Lowe, J.J. (1993) A re-evaluation of the vegetation history of the eastern Pyrénées (France) from the end of the glacial to the present. *Quaternary Science Reviews*, **12**, 47–77.
- Ruiz de la Torre, J. (1990) *Mapa Forestal de España*. ICONA-M.A.P.A., Madrid.
- Scaltsioyianes, A., Tsaktsira, M. & Drouzas, A.D. (1999) Allozyme differentiation in the Mediterranean firs (*Abies*, Pinaceae). A first comparative study with phylogenetic implications. *Plant Systematics and Evolution*, **216**, 289–307.
- Svenning, J.C. (2003) Deterministic Plio-Pleistocene extinctions in the European cool-temperate tree flora. *Ecology Letters*, **6**, 646–653.
- Terhürne-Berson, R., Litt, T. & Cheddadi, R. (2004) The spread of *Abies* throughout Europe since the last glacial period: combined macrofossil and pollen data. *Vegetation History and Archaeobotany*, **13**, 257–268.
- Tzedakis, P.C. (1993) Long-term tree populations in northwest Greece through multiple Quaternary climatic cycles. *Nature*, **364**, 437–440.
- Tzedakis, P.C., Lawson, I.T., Frogley, M.R., Hewitt, G.M. & Preece, R.C. (2002) Buffered tree population changes in a Quaternary refugium: evolutionary implications. *Science*, **297**, 2044–2047.
- Valle, M., Rivas, M.R., Lucini, M., Ortiz, J.E. & Torres, T. (2003) Interpretación paleoecológica y paleoclimática del tramo superior de la turbera de Padul (Granada, España). *Polen*, **13**, 85–95.
- Van der Knaap, W.O. & van Leeuwen, J.F.N. (1994) Holocene vegetation, human impact, and climatic change in Serra da Estrela, Portugal. *Dissertationes Botanicae*, **234**, 497–535.
- Van der Knaap, W.O. & van Leeuwen, J.F.N. (1995) Holocene vegetation and degradation as responses to climatic change and human activity in the Serra da Estrela, Portugal. *Review of Palaeobotany and Palynology*, **89**, 153–211.
- Van der Knaap, W.O. & van Leeuwen, J.F.N. (1997) Late Glacial and early Holocene vegetation succession, altitudinal vegetation zonation, and climatic change in the Serra da Estrela, Portugal. *Review of Palaeobotany and Palynology*, **97**, 239–285.
- Venables, W.N. & Ripley, B.D. (2002) *Modern applied statistics with S*, 4th edn. Springer-Verlag, New York.

- Vidakovic, M. (1991) *Conifers, morphology and variation*. Zdravko Zidovec, Zagreb.
- Waltari, E., Hijmans, R.J., Peterson, A.T., Nyári, Á.S., Perkins, S.L. & Guralnick, R.P. (2007) Locating Pleistocene Refugia: comparing phylogeographic and ecological Niche model predictions. *PLoS ONE*, **2**, e563.
- Willis, K.J. & McElwain, J.C. (2002) *The evolution of plants*. Oxford University Press, New York.
- Yll, R., Roure, J.M., Pantaleón, J. & Pérez Obiol, R. (1994) Análisis polínico de una secuencia holocénica en Roquetas de Mar (Almería). *Trabajos de Palinología Básica y Aplicada. X Simposio de Palinología* (ed. by I. Mateu, M. Dupré, J. Güemes and M.E. Burgaz), pp. 189–198. Universitat de València, València.
- Yll, R., Carrión, J.S., Pantaleón, J., Dupré, M., La Roca, N., Roure, J.M. & Pérez-Obiol, R. (2003) Palinología del Cuaternario reciente en la Laguna de Villena (Alicante, España). *Anales de Biología*, **25**, 65–72.

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Figure S1** Additional information concerning temperature in the different climate scenarios is shown. Boxplot (the bottom and top of the box are the lower and upper quartiles, respectively; and the band near the middle of the box is the median) with whiskers from minimum to maximum; in addition the mean of the data are indicated. The diagram display the variation between Tmin and Tann during the three periods—present, Middle Holocene and LGM—the two latter under two general circulation model estimates (CCSM and MIROC). Tmin (minimum temperature of the coldest month); Tann (annual temperature).

**Figure S2** Additional information concerning temperature values in the different climate scenarios is shown. The diagram displays the variation of the Tmin and Tann in relation with latitude (from Pyrenees to Straits of Gibraltar) during three periods—present, the Middle Holocene and LGM—the two latter under two GCM model estimates (CCSM and MIROC). The temperature trend displays a reduction of cooling at low latitudes during LGM and vice-versa. Tmin (minimum temperature of the coldest month); Tann (annual temperature).

**Figure S3** Additional information concerning the potential distribution of *Abies pinsapo* and *A. alba* at the present. Pollen deposits with the code indication are shown.

**Figure S4** Additional information concerning the potential distribution of *Abies pinsapo* during the Middle Holocene under two GCM estimates (CCSM and MIROC). Pollen deposits with the code indication are shown. Presence of *Abies* pollen in pollen deposits during the Middle Holocene ( $\pm 500$  yr) is indicated with a star symbol.

**Figure S5** Additional information concerning the potential distribution of *Abies alba* during the Middle Holocene under two GCM estimates (CCSM and MIROC). Pollen deposits with the code indication are shown. Presence of *Abies* pollen in pollen deposits during the Middle Holocene ( $\pm 500$  yr) is indicated with a star symbol.

**Figure S6** Additional information concerning the potential distribution of *Abies pinsapo* at the LGM under two GCM estimates (CCSM and MIROC). Pollen deposits with the code indication are shown. Presence of *Abies* pollen in pollen deposits at the LGM ( $\pm 500$  yr) is indicated with a star symbol.

**Figure S7** Additional information about the potential distribution of *Abies alba* at the LGM under two GCM estimates (CCSM and MIROC). Pollen deposits with the code indication are shown. Presence of *Abies* pollen in pollen deposits at the LGM ( $\pm 500$  yr) is indicated with a star symbol.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

## BIOSKETCH

**Research Team (UGR-CSIC-UPO)** leads projects on the evolution of Mediterranean vegetation during the Quaternary period in Western Europe. The postglacial recolonization and the dynamics of mountain plants in the Iberian Peninsula are also studied. In the field of computer sciences, the group is proficient in spatial analysis techniques, such as GIS, the remote sensing, or artificial intelligence (Machine Learning) that allow to development species distribution models (SDMs).

Author contributions: J.A.L.S. and F.A.S. conceived the ideas; J.A.L.S. and L.L.M. collected data; B.B.P. and D.N.L. analysed the data; and F.A.S., J.A.L.S. and J.C.L. led the writing. (<http://www.ih.csic.es/grupos/arqueobio.html>).

---

Editor: H. Linder