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6 Past and present potential distribution of the Iberian *Abies* species: a

7 phytogeographic approach using fossil pollen data and species distribution

8 models

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10 Francisca Alba-Sánchez[1]*, José A. López-Sáez[2], Blas Benito-de Pando[1], Juan C. Linares[3],
11 Diego Nieto-Lugilde[1] and Lourdes López-Merino[2]

12

13 [1]Dpto. de Botánica, Facultad de Ciencias, Campus Universitario de Fuente Nueva, Universidad
14 de Granada, 18071 Granada, Spain
15 [2]GI Arqueobiología, Instituto de Historia, CCHS, CSIC, Albasanz 26-28, 28037 Madrid, Spain
16 [3]Dpto. Sistemas Físicos, Químicos y Naturales, Universidad Pablo de Olavide, Ctra. Utrera Km
17 1, 41013 Sevilla, Spain

18

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

22

ABSTRACT

Aim Quaternary palaeopalynological 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.

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

89   emblematic taxa, such as *Carpinus betulus* L., *Castanea sativa* Mill., *Fagus sylvatica* L.,

90   *Juglans regia* L. and evergreen oaks (*Quercus suber* L., *Quercus ilex* L. and *Quercus coccifera*

91   L.), have been reported for the most critical periods of the Pleistocene (Carrión & Sánchez-

92   Gómez, 1992; Carrión et al., 2003; Krebs et al., 2004; López de Heredia et al., 2007; López-

93   Merino et al., 2008). Nevertheless, in the case of *Abies*, given that fir species cannot be

94   distinguished in palynological analyses, previous studies related to their glacial refugia or past

95   distribution usually refer to the entire genus (Terhürne-Berson et al., 2004). So far, the fossil

96   records of *Abies* have been interpreted based on the presumption that the pollen grains of the

97   *Abies* morphotype documented in pollen sequences of south and south-eastern Spain refer to

98   *A. pinsapo* (Carrión et al., 2008; Cortés-Sánchez et al., 2008), whereas the pollen grains from

99   north and north-eastern Spain refer to *A. alba* populations (Huntley & Birks, 1983). However,

100   this geographic dichotomy lacks reliable ecological support.

101   The emerging field of species distribution models (SDMs) offers an independent

102   perspective on these questions. These models can be used to predict potential distributional

103   patterns for a given species and to assess the degree of ecological segregation among

104   different taxa (Guisan & Thuiller, 2005). An SDM represents an approximation of a species'

105   ecological niche in the environmental dimension being examined, translated into the

106   geographic space. Based on the environmental conditions of the sites of known occurrence,

107   these models constitute valuable tools for analytical biology (Peterson et al., 1999). Such

108   projections assume that a species is in equilibrium with its environmental requirements—that is,

109   its distribution is determined primarily by the environment, and not by other factors such as

110   competition or dispersal limitation. Similarly, under assumptions of niche conservatism

111   (Peterson, 2003), which have been extensively tested (Martínez-Meyer & Peterson, 2006).

112   SDMs can be projected onto palaeoclimate models to identify past potential distributions

113   (Martínez-Meyer et al., 2004).

114   The history of Iberian *Abies* species is poorly understood, in part because the

115   palaeopalynological approach has inherent biases and difficulties, due not only to the lack of

116   taxonomic precision discussed earlier, but also to limitations on inferring the timing and location

117   of refugia, restrictions on defining the spatial and temporal distribution range of different

118   species, and the failure to take into account that some taxa are underrepresented in the fossil

119   record. Consequently, the distribution of some species is probably underestimated.

120   Here, we propose the use of SDMs in conjunction with palaeoclimatic models as well

121   as fossil-pollen records for locating and describing Iberian *Abies* Quaternary refugia from the

122   last glacial maximum (LGM) to the present. The combination of these two approaches enables

123 far greater detail and accuracy in SDM applications used to predict potential Quaternary

124 refugia. In addition, this combination allows (1) the assignment of fossil records to *A. alba* or *A.*

125 *pinsapo* based on the predicted potential distribution patterns for the two species; (2) the

126 identification of environmental variables affecting their distribution; and (3) an evaluation of the

127 segregation between the two taxa.

128 We hypothesize that SDM and palaeorecords are closely correlated, suggesting that

129 the two approaches converge on similar inferences and that the two in tandem may offer

130 exciting new insights.

131

132 **METHODS**

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134 ***Abies pinsapo* and *Abies alba* distribution models**

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136 In the present study, *A. pinsapo* and *A. alba* were modelled individually, first calibrating the

137 model for their current distributions in relation to the present climate, and then applying it to the

138 LGM and the Middle Holocene (Mid-Holocene) periods. This hindcasting process is often used

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

140

141 *Species records*

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143 The forest map of Spain (1 : 200,000) was the cartographic base for estimating the current

144 range of *A. pinsapo* and *A. alba* (Ruiz de la Torre, 1990). Abies pinsapo is restricted to three

145 populations on calcareous and serpentine substrates in the Baetic mountains, which occur from

146 900 to 1800 m a.s.l. in the Sierra de Grazalema (Cádiz), Sierra de las Nieves, and Sierra

147 Bermeja (both in the province of Málaga). *Abies alba* occupies only the Pyrenees, reaching its

148 south-western European and Iberian limit in Iraty (Navarra). The Coastal-Catalonian mountain

149 Range constitutes its south-eastern limit in Spain. The largest *A. alba* stands are located in the

150 province of Lleida (17,000 ha). In total, 524 records of *A. pinsapo* and 240 of *A. alba* were

151 randomly sampled on the polygons corresponding to each of the species, ensuring a minimum

152 distance of 400 m between points, in order to avoid sample autocorrelation effects. The dataset

153 was randomly split, 75% of which were used to calibrate the algorithm, and 25% to evaluate the

154 resulting SDMs.

155

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 x 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.ccsm.ucar.edu/, (Kiehl & Gent, 2004)] and the Model for Interdisciplinary Research on Climate [miroc, ver. 3.2; http:// www.ccsr.u-tokyo.ac.jp/ehtml/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 x 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

189   of analysis, and of calibrating the downscaled LGM and Mid-Holocene climate data to actual

190   observed climate conditions (Peterson & Nyári, 2008).

191   Comparison of the results of this GCM with climate reconstructions and other models

192   show that the direction of climate change is in general correctly estimated in the PMIP2

193   models, although the degree of cooling in southern Europe is generally underestimated for the

194   Middle Holocene (Brewer et al., 2007) and LGM (Ramstein et al., 2007). The LGM-simulated

195   surface climate is colder and drier than PI conditions: global average annual surface

196   temperature is a cooling of around 4.5 °C from PI conditions with amplification of this cooling at

197   high latitudes (Otto-Bliesner et al., 2006); similarly, the atmosphere is significantly drier with an

198   around 18% decrease in precipitable water. The Middle Holocene simulations show a global

199   annual cooling of < 0.1 °C compared to the PI simulation, and there are no differences in

200   annual precipitation (Otto-Bliesner et al., 2006; Braconnot et al., 2007).

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202   *Modelling algorithm: MaxEnt*

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204   Maxent (Maximum entropy modelling of species geographic distributions; Phillips et al., 2006;

205   Phillips & Dudik, 2008) is an algorithm specifically designed to calculate the potential

206   geographic distribution of a species. It combines artificial intelligence (Machine Learning) and

207   the Principle of Maximum Entropy (Jaynes, 1957), and thus, out of the wide range of possible

208   modelling algorithms, provides one of the most accurate predictions (Elith et al., 2006). Maxent

209   estimates the probability of the presence of any species, determining the maximum entropy

210   distribution (the closest to uniformity) from a set of records of the presence of a taxon and from

211   digital cartography of environmental variables, which influence the species distribution (Phillips

212   et al., 2006).

213

214   *Model calibration and evaluation*

215

216   A cumulative output format was chosen in order to determine the potential *Abies pinsapo* and

217   *A. alba* distribution. This output represents habitat suitability with continuous values [0, 100]

218   (Phillips & Dudik, 2008). The algorithm parameters fixed to calibrate the SDMs were stricter

219   than those recommended by Phillips et al. (2006). The SDMs were evaluated by the area under

220   the ROC curve (AUC) test provided by the Maxent software using a random data-splitting

221   approach to establish an evaluation dataset (25% of the entire presence dataset) for *A. pinsapo*

222   and *A. alba*.

223   Phillips et al. (2006), in a novel interpretation of AUC being applied only to presence-

224   based algorithms, stated that '*AUC is the probability that a randomly chosen presence site is*

225   *ranked above a random background site*'. But the AUC method based on background points

226   has a known weakness (Lobo et al., 2008): the AUC scores are consistently higher for species

227   with small ratios between the extent of occurrence and the entire extent of territory under study,

228   as in the case of rare species such as *A. pinsapo*. Although there is ongoing discussion about

229   the reliability of this measure of accuracy (see Peterson et al., 2007; and Lobo et al., 2008, for

230   further details), this issue is beyond the scope of the present study.

231

232   *Analysis of environmental requirements*

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234   The following analyses were also carried out for a comparative evaluation of the environmental

235   requirements of *A. pinsapo* and *A. alba*: (1) principal-components analysis (PCA) over three

236   groups of environmental variables (topography, temperature and rainfall); and (2) the Wilks test

237   and Fisher discriminant analysis (Venables & Ripley, 2002) to analyse the differences between

238   the two species in terms of ecological requirements. The analysis was performed on a random

239   subsample of presences (*A. alba*, n = 33; *A. pinsapo*, n = 44). The R software environment (R

240   Development Team, 2008) and its Rcmdr package (Fox et al., 2007) were used for the

241   statistical computing and graphics.

242

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

244

245   In relation to our review of all the fossil pollen sequences in the Iberian Peninsula (Spain and

246   Portugal), Table 1 shows only the fossil evidence which includes *Abies* pollen. In Portugal,

247   *Abies* pollen was completely absent from the pollen deposits analysed (e.g. Van der Knaap &

248   van Leeuwen, 1994, 1995, 1997). These 35 selected sites are used to locate, geographically

249   and temporally, *Abies* species refuges. Unfortunately, no palaeopalynological studies have

250   been performed to investigate the ranges currently inhabited by *A. pinsapo* (Fig. 1). The data

251   for three sites (Padul, Navarrés and Roquetas de Mar) are included in the European Pollen

252   Data (EPD), and the remaining data set are published but not included in EPD. The criterion for

253   selecting a sequence was based on *Abies* pollen-percentage threshold values (occurrences of

254   c. 1% or greater; see Iglesias, 1998 for supplementary information). The pollen data on *Abies*

255   cf. *pinsapo*, even at the low threshold used here, probably underestimate the distribution of this

256   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 contribute to the potential model. Precipitation during the driest month (Pmin), a highly significant feature in regions with Cfb Climate class, was the most important variable to explain the *A. alba* distribution model. Also, Tann and Tmin 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 (k = 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 Tmin (0.0926) and to the Tmax (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 palaeopalynological 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

357   data). The overlap observed between the species' potential distribution and prior presence of

358   *Abies*—inferred from fossil pollen records—some way validates the model predictions made as

359   well as the predictive ability of SDMs using hindcasting.

360   However, inconveniences arising from the palaeoclimatic scenarios could add

361   uncertainty to the predictive models. For example, problems arising because of the appearance

362   of non-analogous climate conditions when SDMs are projected across major climatic changes,

363   especially those that occurred in the LGM, then modelling approaches will have unknown or

364   unpredictable behaviour in predicting in those areas (Pearson et al., 2006). An added

365   complication may arise because the PMIP model data underestimated the drying and cooling

366   throughout the Mediterranean basin at the LGM (Ramstein et al., 2007), and so the models

367   presented could overestimate the *Abies* distribution during the LGM. In addition, according to

368   the authors cited earlier, the spatial resolution of the PMIP models may be a supplementary

369   difficulty, particularly in areas of complex topography such as the Iberian Peninsula. For the

370   Pyrenees or the Baetic Range, the local climate can differ sharply from the climate simulated in

371   the corresponding grid box of the models. Enhancing the models' resolution should improve the

372   representation of a given region. However, it remains unclear whether the sensitivity of the

373   models will be affected by changing their resolution.

374

375   **Detecting suitable habitats based on SDMs and palaeorecords**

376

377   In the present study, by integrating ecological-niche characteristics drawn from the

378   environmental characteristics of known occurrences of *Abies* species and palaeoecological

379   studies, we derived a more refined image of the distribution, discontinuities and segregation

380   between Iberian *Abies* species. Some way, niche conservatism has been documented

381   throughout the present-day distribution of Iberian *Abies* species (Figs 2-4), and it has been

382   shown that at the LGM, the distribution area of *Abies* populations into several locations

383   corresponding to presumed Pleistocene refugia (Table 1, Fig. 4 and Figs S6 & S7). The overlap

384   noted between past *Abies* refugia—inferred from fossil pollen records—and the species'

385   potential distribution offers a new interpretation of the Quaternary distribution of the Iberian

386   *Abies* species. According to Martínez-Meyer & Peterson (2006), from the standpoint of

387   historical biology, our results propose that Quaternary distribution areas of some species could

388   be inferred from present-day habitat characteristics, providing an additional tool for

389   palaeobiogeography research.

390   The results presented here could constitute further evidence for the conservation of

391   climatic and topographic dimensions of ecological niches over moderate periods of time,

392   despite strong climatic and environmental changes. The agreement between past and present-

393   day *Abies* refuge data could be explained by relative climate stasis in the refuge areas and

394   revolves around the importance of their local intrinsic properties. As suggested by the

395   palaeopalynological and palaeoclimatic studies (see Tzedakis et al., 2002 and reference

396   therein), factors that currently lead to high precipitation in some mountain areas of the

397   Mediterranean basin (essentially, orographic uplift of air charged with moisture from the nearby

398   coasts) also operated during the LGM, moderating the impact of regional aridity on tree

399   populations. The palynological data (Table 1) provide evidence for the existence of an

400   ecologically stable area where local conditions appear to have buffered the extreme effects of

401   Quaternary climate variability, contributing to the survival of residual *Abies* populations.

402   At the LGM, the combined effects of reduced annual precipitation and winter

403   temperatures throughout the Iberian Peninsula (see Table 2) with a shorter growing season

404   and also lower atmospheric CO_2 concentrations (200 p.p.m. for CO_2; see Braconnot et al.,

405   2007), which led to *Abies* population contraction and fragmentation (Fig. 4 and Figs S6-S7), but

406   these events were not severe enough to cause their total elimination. One idea bolstering this

407   assumption is that a gradual southward attenuation of the North Atlantic climate signal probably

408   occurred at the LGM, as suggested by the Iberian climatic simulations (Fig. S2). Topography is

409   also a critical factor, which determines the extent to which populations can shift altitudinally in

410   response to climate change (Tzedakis, 1993; Tzedakis et al., 2002), seeking to evade

411   extirpation. At the LGM, both the Pyrenees and Baetic Range provided the sufficient

412   topographical variability to supply a number of microhabitats suitable for survival. A trend to

413   persist during the LGM at lower altitudes as well as reduced continuity of the species' potential

414   distributional area throughout the Pyrenees (*A. alba*) and Baetic Range (*A. pinsapo*) were

415   found in this study (Fig. 4 and Figs S6 & S7).

416   In the Middle Holocene, a significant expansion of *Abies* populations is well reflected in

417   our results by two approaches. During this period, *Abies pinsapo* and *A. alba* displayed a larger

418   and continuous potential distribution area compared with its LGM and current distribution in the

419   Pyrenees or Baetic Range, respectively (see Figs 1 & 3). The increased precipitation and the

420   warming (Table 2 and Figs S1 & S2) allowed the spread of *Abies* throughout Iberian mountains

421   since the last glacial period. A trend to rise in altitude to avoid the warming was observed in

422   both *Abies* species. The occupation area, as well as its altitudinal range in the mountains, has

423   a very similar feature to present-day potential distribution. Comparing the three projections—

424 present-day SDM, Mid-Holocene SDM and LGM SDM—we see that the overall reconstructed

425 distributions did not significantly differ, indicating a high degree of evolutionary stasis in the

426 *Abies* climatic requirements (see Svenning, 2003 and references therein).

427   Previous studies (Terhürne-Berson et al., 2004; Muller et al., 2007) suggest that the

428 southern Iberian Peninsula was probably a refuge for *A. pinsapo*. The increasing availability of

429 pollen sequences, and the fact that such taxa as *A. pinsapo* are underrepresented in the fossil

430 record, strengthens the assumption of a wider distribution of *A. pinsapo* forests throughout the

431 Baetic Range (including the Prebaetic zone, in eastern Iberia). In addition, some authors (such

432 as Reille & Lowe, 1993) considered it unlikely that the Pyrenees or the Iberian Peninsula were

433 refugia during the LMG. However, Terhürne-Berson et al. (2004), Muller et al. (2007) and

434 Liepelt et al. (2009) reconstructed the location of the last glacial refugia and postglacial spread

435 of *Abies* throughout Europe, confirming the long-lasting refuge areas. The SDMs as well as the

436 fossil evidence suggest a wider Quaternary distribution, which would have extended across the

437 Pyrenees Range and the Cantabrian mountain system and even reached the Iberian mountain

438 system, in an intermediate geographic position. Previous studies based on SDM confirm the

439 presence of *A. alba* during the LGM in the Pyrenees (Benito Garzón et al., 2007).

440

441 ***Abies pinsapo* and *Abies alba* ecological segregation**

442

443 *Abies alba* and *A. pinsapo* niches differ significantly in climatic-niche dimensions (Fig. 5),

444 pointing to an early evolutionary divergence of the two species. The ecological segregation

445 suggests that the two species remained geographically isolated throughout their Quaternary

446 history, although we do not reject the hypothesis that Quaternary contact may have existed

447 between *A. alba* and *A. pinsapo* populations in eastern Iberia (Figs 3 & 4). Geographical

448 overlap among *Abies* species seems to have been common during the glacial periods

449 (Scaltsoyiannes et al., 1999).

450   SDMs yielded two well-differentiated potential ranges for the Iberian *Abies* species: the

451 *A. pinsapo* range presents in Baetic-Prebaetic mountains in a Mediterranean climate; and the

452 *A. alba* range, along the north Atlantic coast and the northeastern Iberian, in temperate

453 mountainous areas (Figs 2–4). According to Araújo & Pearson (2005) and Pearson (2006), the

454 previously mentioned overlap provides useful information on the ecological conditions that

455 allowed some populations of *A. pinsapo* and *A. alba* to survive until the present and indicates

456 that the two species have independent biogeographical dynamics.

457

14

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.

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744 **Tables**

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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	4465047	Peatland	c. 6 and Late Holocene	Yes	No data	Dupré et al. (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 et al. (1996)
5	Tossal de la Roca	736826	4297670	Archaeological rockshelter	c. 16–13 and 12–11.8	No data	No data	Cacho et al. (1983, 1995)
6	En Pardo	744816	4283668	Archaeological cave	Bölling/Alerod	No data	No	González Sampériz (1998)
7	Villena	681000	4276000	Lake	> 47 and c. 6	Yes	No	Yll et al. (2003)
8	Cucú	565515	4166070	Archaeological cave	c. 100–70	No data	No data	A. González-Ramón et al. (in preparation)
9	Las Ventanas	462694	4141062	Palaeontological cave	c. 10.7	No data	No data	Carrión et al. (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 et al (1971); Pons & Reille (1988); Valle et al. (2003)
12	Roquetas de Mar	536693	4072214	Marsh	c. 6 and Late Holocene	Yes	No data	Yll et al. (1994)
13	Zafarraya	399800	4090150	Archaeological cave	> 46	No data	No data	Lebreton et al. (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 et al (2007); Cortés-Sánchez et al. (2008)
15	Gorham	288937	4001897	Archaeological cave	c. 19–16	No data	No	Finlayson et al. (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	4763568	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 et al. (1993)
20	Kurtzia	502100	4805300	Peat sediments	Upper Pleistocene	No data	No data	Muñoz et al. (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 et al. (2008)
24	Anzarán	596500	4802623	Marsh	Upper Pleistocene	No data	No	Edeso et al. (1989)
25	Tramacastilla	715103	4732997	Lake	Upper Pleistocene-Holocene	Yes	Yes	Montserrat (1992); González Sampériz et al. (2005)
26	Formigal	706794	4738638	Lake	LGM	No data	Yes	González Sampériz et al. (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 Sampériz et al. (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 & Juliá (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 et al. (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 (± 500 yr) or at the last glacial maximum (LGM) (± 500 yr); No, absence of *Abies* pollen in pollen deposits during the Middle Holocene (± 500 yr) or at the LGM (± 500 yr); No data, no data are available.

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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		Values range		Values range		Values range		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

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

Abies pinsapo		Abies alba	
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).

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).

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752 **Figure captions**

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754 **Figure 1.** Current *Abies* distribution in the Iberian Peninsula: *Abies pinsapo* in the Baetic

755 Range and *Abies alba* in the Pyrenees Range. Pollen deposits with the code indication are

756 shown (see complementary information in Table 1).

757

758 **Figure 2.** Potential distribution of *Abies pinsapo* and *Abies alba* at the present in relation to the

759 current climate. Habitat suitability values are also shown.

760

761 **Figure 3.** Potential distribution of *Abies pinsapo* and *Abies alba* during the Middle Holocene,

762 under two different general circulation model (GCM) estimates (CCSM and MIROC). In

763 addition, 35 pollen deposits are also shown. Presence of *Abies* pollen in pollen deposits during

764 the Middle Holocene (± 500 yr) is indicated with a star symbol.

765

766 **Figure 4.** Potential distribution of *Abies pinsapo* and *Abies alba* at the last glacial maximum

767 (LGM), under two general circulation model (GCM) estimates (CCSM and MIROC). In addition,

768 35 pollen deposits are also shown. Presence of *Abies* pollen in pollen deposits at the LGM (±

769 500 yr) is indicated with a star symbol. The Iberian coastline during the LGM is displayed.

770

771 **Figure 5.** Presence records of *Abies alba* and *Abies pinsapo* with respect to three axes

772 (obtained by principal-components analysis), representing the different groups of environmental

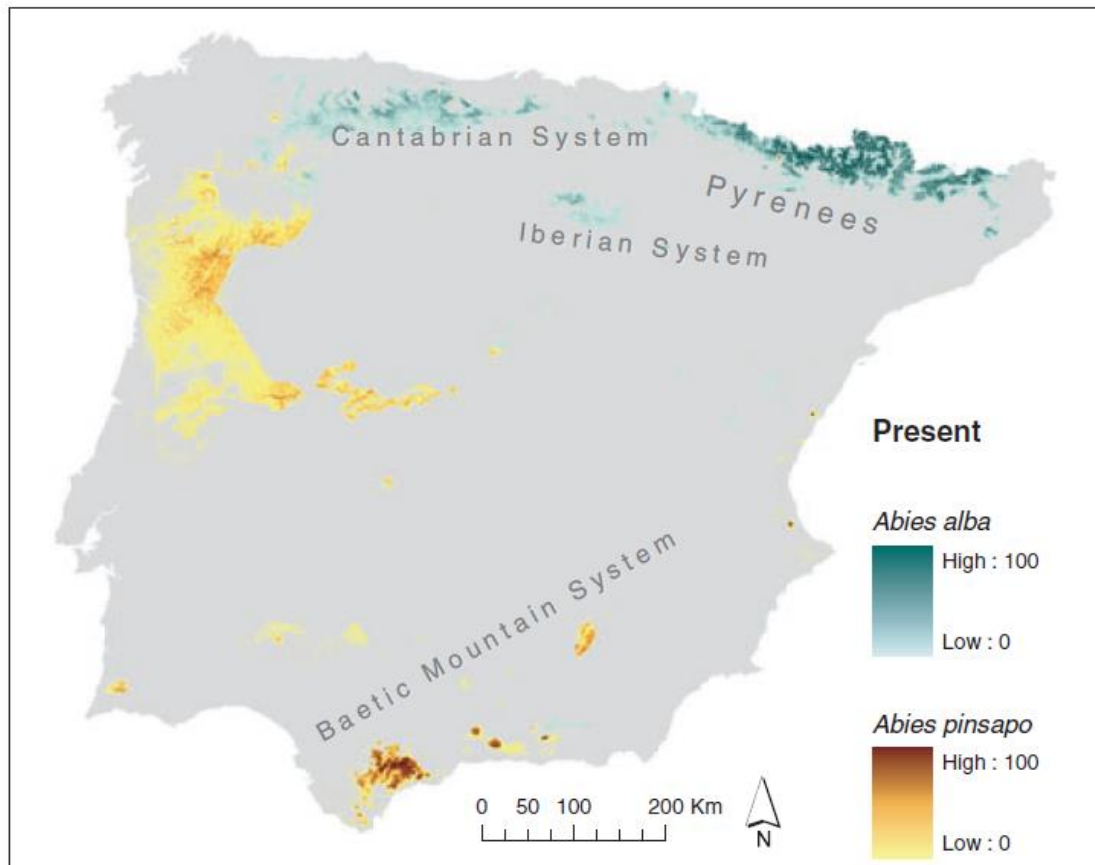773 variables (topography, temperature and rainfall).
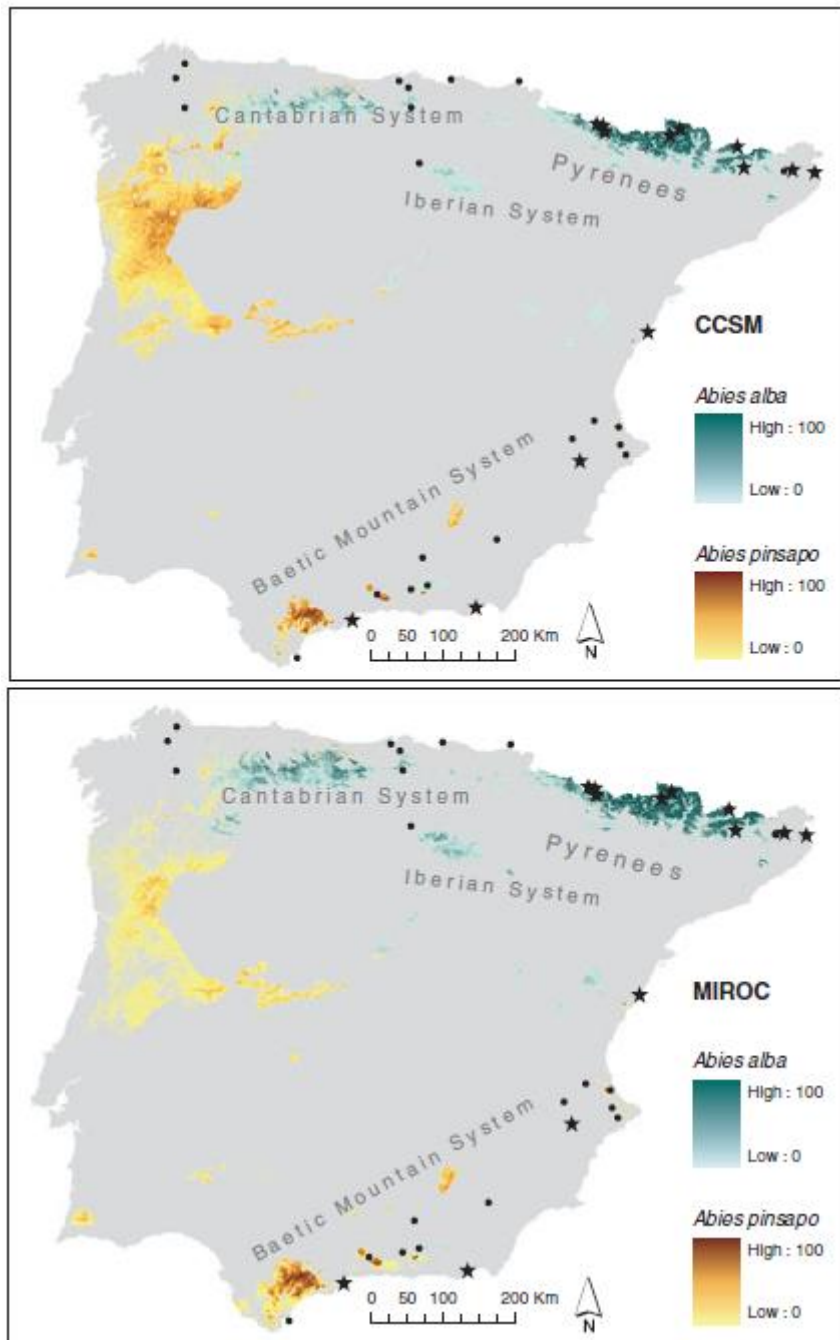
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775   Figure 1
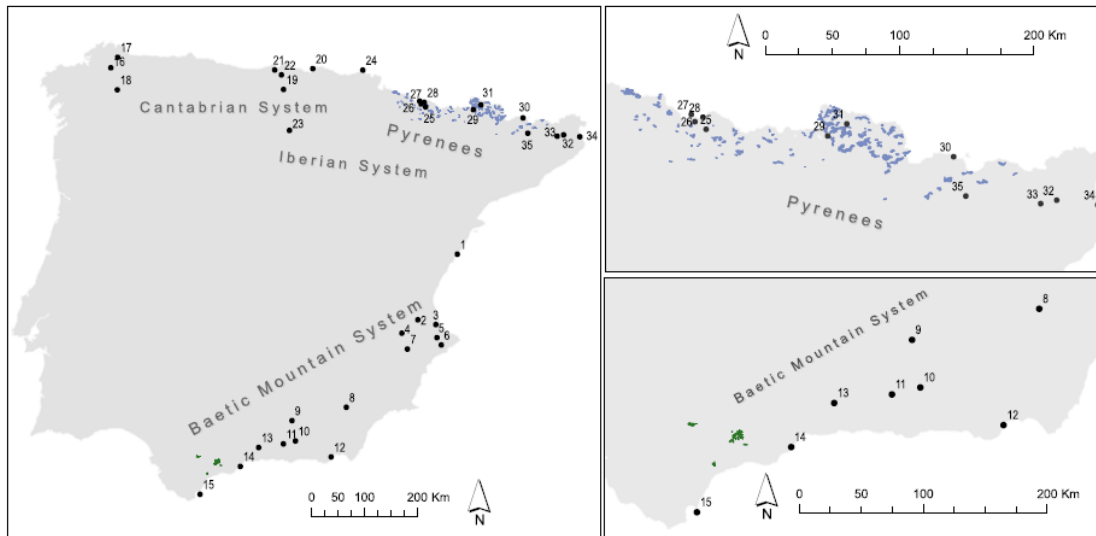
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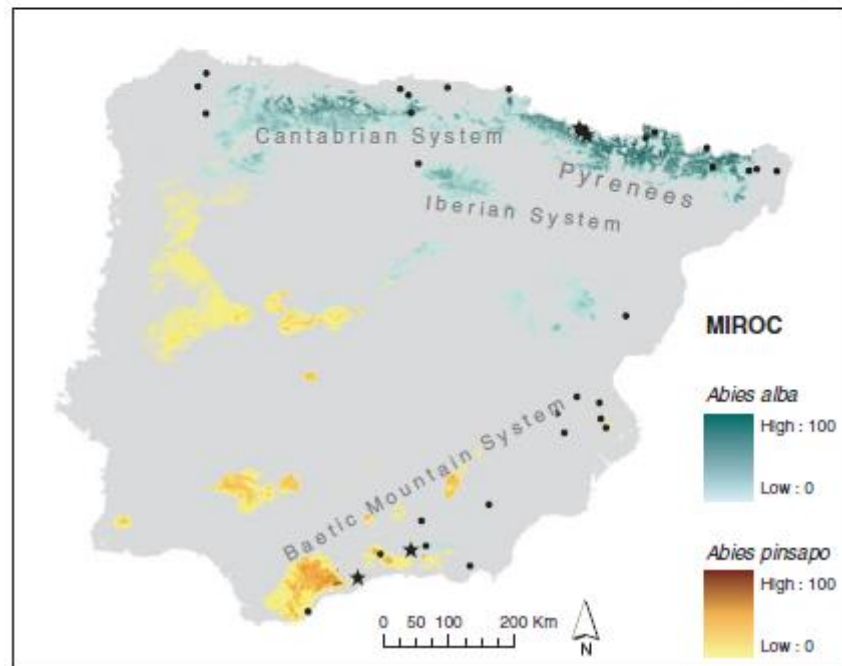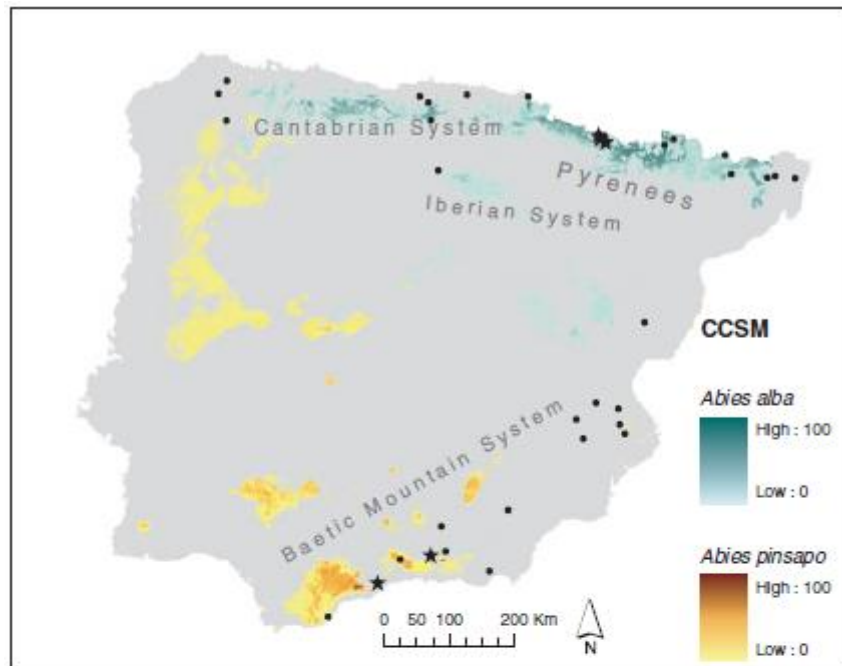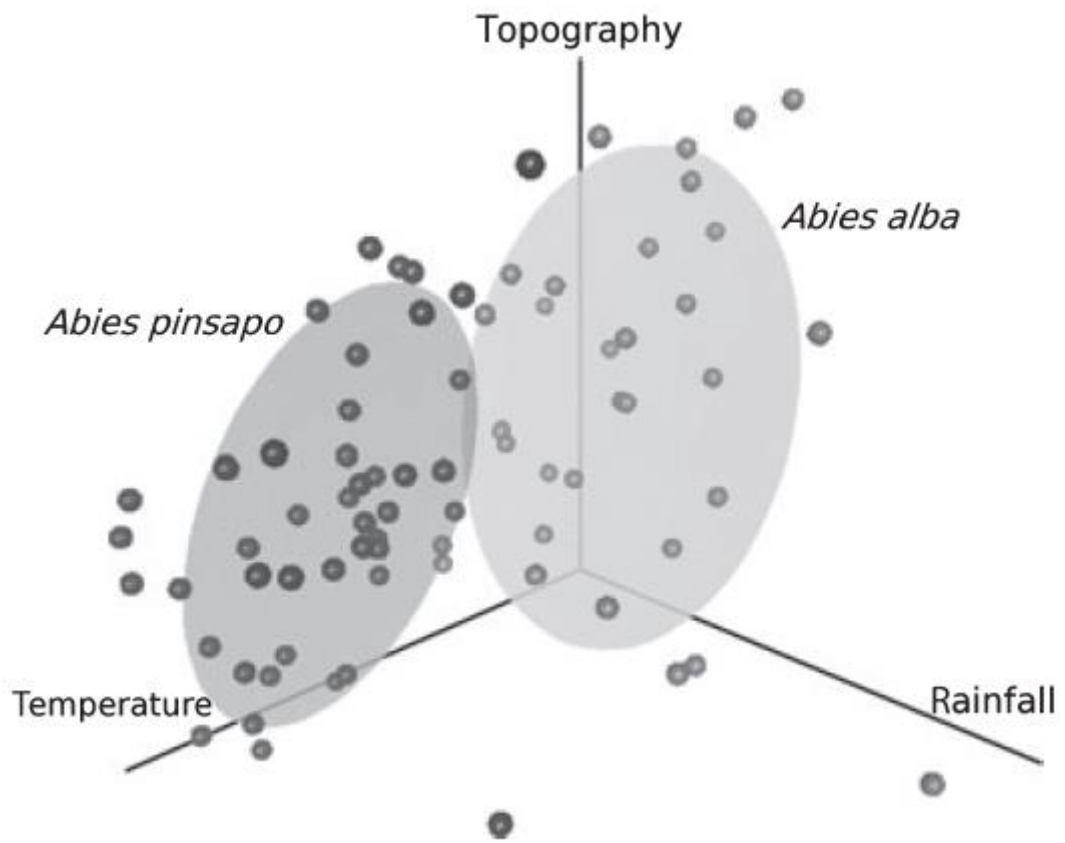

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