

1 Alba-Sánchez F, López-Sáez JA, Benito de Pando B, Linares JC, Nieto-Lugilde D and López-
2 Merino L. 2010. Past and present potential distribution of the Iberian *Abies* species: A
3 phytogeographic approach using pollen data and species distribution models. Diversity and
4 Distributions 16 (2): 214- 228.

5

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

9

10 Francisca Alba-Sánchez^{1*}, José A. López-Sáez², Blas Benito-de Pando¹, Juan C. Linares³,
11 Diego Nieto-Lugilde¹ and Lourdes López-Merino²

12

13 ¹Dpto. de Botánica, Facultad de Ciencias, Campus Universitario de Fuente Nueva, Universidad
14 de Granada, 18071 Granada, Spain

15 ²GI Arqueobiología, Instituto de Historia, CCHS, CSIC, Albasanz 26-28, 28037 Madrid, Spain

16 ³Dpto. 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

23 **ABSTRACT**

24

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

33 **Location** The Iberian Peninsula.

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

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

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

54

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

56 INTRODUCTION

57

58 The geographical proximity of two *Abies* species in the Iberian Peninsula (*Abies alba* and *Abies*
59 *pinsapo*), with contrasting environmental requirements as well as different morphological traits
60 (Farjon & Rushforth, 1989), constitutes an unsolved biogeographic and palaeobotanic enigma.
61 Currently, *A. alba* is located exclusively in the Pyrenees mountain Range in the north-eastern
62 Iberian Peninsula (Costa Tenorio et al., 1997), which has a warm temperate climate with a
63 rainy and warm summer (Cfb Climate class: Köppen-Geiger climate classification by Kottek et
64 al., 2006). *Abies pinsapo* (Spanish populations) is found only in southern Spain, specifically in
65 the south-western Baetic mountain Range (Fig. 1), in a wet Mediterranean climate with a hot
66 and dry summer (see Csa climate class: Köppen–Geiger climate classification by Kottek et al.,
67 2006).

68 *Abies* is currently distributed around the Mediterranean basin with nine species and
69 one natural hybrid (Vidakovic, 1991). The age and timing of circum-Mediterranean *Abies*
70 speciation events as well as their subsequent migrations has been the subject of extensive
71 debate and analysis in the literature, with recent opinions indicating that the most important
72 speciation event took place during the Pliocene, when a regional drying trend led to geographic
73 isolation of drought-sensitive taxa (Hewitt, 1996; Willis & McElwain, 2002). According to
74 Krussmann (1972) and Farjon & Rushforth (1989), the successive migrations and
75 fragmentations would have favoured the differentiation of two *Abies* groups: (1) archaic firs,
76 represented by subsection Pinsapones Franco, with species having archaic morphological
77 features (indicating an earlier speciation) such as *Abies pinsapo*; and (2) modern firs,
78 represented by subsection Albae (Franco) Franco, these species having modern morphological
79 characteristics, indicating a later speciation, such as *A. alba*. These populations, restricted to
80 moist mountainous habitats during most of the Quaternary, would diverge to the current
81 diversity of related species (Linares, 2008).

82 Understanding Quaternary refuge distributions of species has been a core task in
83 historical biogeography for several reasons. For example, refugia based on biogeographic
84 evidence can guide palaeoenvironmental reconstructions, or accurate knowledge of
85 distributional responses to past climate change can provide an excellent calibration for
86 predictions of the consequences of present-day climate change (Waltari et al., 2007). In the
87 Iberian Peninsula, Quaternary refugia have been identified based on different types of historical
88 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 (Terhürme-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**

133

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

135

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*

142

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

156 *Environmental variables*

157

158 Nine predictive variables were used as predictors to calibrate SDMs for each species, all of
159 which had a spatial correlation degree lower than 0.75 (Pearson coefficient). Three of these
160 represented resource gradients (sensu Austin et al., 1984): annual precipitation (Pann),
161 precipitation of the driest month (Pmin), and precipitation of the wettest month (Pmax). Three
162 other variables refer to direct gradients: maximum temperature of the hottest month (Tmax),
163 minimum temperature of the coldest month (Tmin), and annual temperature (Tann). The last
164 three correspond to indirect gradients: slope, topographic exposure, and topographic wetness
165 index (TWI). These latter three variables, derived from the digital elevation model (DEM), are
166 capable of reproducing the physiological role of certain resources (Guisan & Zimmermann,
167 2000). Climate data for the present day (1950–1999) were drawn from the Digital Climatic Atlas
168 of the Iberian Peninsula (Ninyerola et al., 2005). The topographic data came from Shuttle
169 Radar Topography Mission (SRTM) (<http://srtm.csi.cgiar.org/>) and were from 90 to 200 m
170 [(5810 x 4600 cells, Universal Transverse Mercator (UTM) projection, European datum 1950
171 (ED50)]. The grass-gis software (GRASS Development Team, 2008) was used to provide the
172 geographical framework.

173 Current climate data from the Digital Climatic Atlas of the Iberian Peninsula database
174 (Ninyerola et al., 2005) were used as a basis for developing LGM (21 kyr BP) and Mid-
175 Holocene (6 kyr BP) climate data. Two general atmospheric circulation models (GCM) were
176 used to generate past climate scenarios for each period in order to avoid the uncertainty of
177 using one alone: the Community Climate System Model [CCSM, [http:// www.cesm.ucar.edu/](http://www.cesm.ucar.edu/),
178 (Kiehl & Gent, 2004)] and the Model for Interdisciplinary Research on Climate [miroc, ver. 3.2;
179 [http:// www.ccsr.u-tokyo.ac.jp/ehhtml/etopindex.shtml](http://www.ccsr.u-tokyo.ac.jp/ehhtml/etopindex.shtml)]. The original GCM data were downloaded
180 from the PMIP2 website ([http:// www.pmip2.cnrs-gif.fr/](http://www.pmip2.cnrs-gif.fr/)).

181 We then generated an anomaly map for each variable by subtracting values for the
182 present, pre-industrial (PI) conditions (c. 1950), using the GCM-estimated LGM and Mid-
183 Holocene values. The GCM data had a spatial resolution of 2.8°, or roughly 300 x 300 km.
184 These anomaly maps were then interpolated to a 200-m resolution using the spline function in
185 grass-gis software with the tension option. Finally, the interpolated differences were added to
186 the high-resolution current climate datasets from the Digital Climatic Atlas of the Iberian
187 Peninsula to generate estimated climate maps at the LGM and the Mid-Holocene. This
188 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).

201

202 *Modelling algorithm: MaxEnt*

203

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*

233

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

257 the *Abies* pollen curves were based on published diagrams, and the percentages were
258 recalculated when sufficient information was available, to compile a uniform and reliable body
259 of data. Pollen percentages are calculated using a pollen sum excluding fern spores and hydro-
260 hygrophyte taxa. Table 1 also indicates when the estimated chronology of a pollen sequence
261 overlaps the LGM (21 kyr BP) or Middle Holocene (6 kyr BP) periods. Spatial coincidences
262 between pollen records and potential distribution of *Abies* species was the criterion to assign
263 the fossil records to *A. alba* or *A. pinsapo*.

264

265 **RESULTS**

266

267 **Climate scenarios**

268

269 Table 2 shows the summarized values from the final interpolated models (CCSM and MIROC)
270 and current climate data for the Iberian Peninsula. In addition, differences between values for
271 the annual temperature (Tann) and temperature of the coldest month (Tmin) for the diverse
272 climate scenarios are shown (see Fig. S1): at the LGM a cooling of 3 and 2.2 °C (Tann) and
273 2.5 and 1.9 °C (Tmin) (CCSM and MIROC simulation, respectively) was detected; while in the
274 Middle Holocene, no significant anomalies were observed. Moreover, the surface temperature
275 time course for the diverse climate scenarios with respect latitude (from Pyrenees to Straits of
276 Gibraltar) (see Fig. S2) confirms an amplification of cooling at high latitudes during the LGM
277 (see Otto-Bliesner et al., 2006 for further information). Iberian model simulations show
278 decreases from modern values of around 4 °C (near the Pyrenees) and 3 °C (near Gibraltar)
279 for Tmin.

280

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

282

283 The resulting SDMs provided high AUC scores [*A. pinsapo*: training data (0.999) and test data
284 (0.998) and *A. alba*: training data (0.996) and test data (0.992)] according to the evaluation test
285 provided by the Maxent software. This is a high AUC value, which demonstrates good model
286 performance.

287 Comparing the projection of present-day SDMs (Fig. 2) to Mid-Holocene (Fig. 3) and
288 LGM (Fig. 4) climates under both the CCSM and MIROC GCM climates models, we see that
289 the overall reconstructed distributions were not dramatically different at the LGM, but that

290 suitable areas were more fragmented and discontinuous than in the Middle Holocene and
291 present day. In particular, we observed reduced continuity of the species' potential distribution
292 area across the Pyrenees (*A. alba*) and Baetic mountain system (*A. pinsapo*) and a tendency to
293 persist during the LGM at lower altitudes than those they occupy now or which they occupied
294 during the Middle Holocene (see Figs S3–S7).

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

307 Table 3 shows a heuristic estimate of relative contributions of the environmental
308 variables to the MaxEnt model. The variables related to the seasonality of the Mediterranean
309 climate, both pluviometric (e.g. Pmax and Pmin) and thermometric variables (e.g. Tmax and
310 Tann) contribute greatly to explain the potential distribution of *A. pinsapo*, in addition to other
311 topographic variables (e.g. slope), which contribute to the potential model. Precipitation during
312 the driest month (Pmin), a highly significant feature in regions with Cfb Climate class, was the
313 most important variable to explain the *A. alba* distribution model. Also, Tann and Tmin play a
314 decisive part in this distribution model. Figure 5 illustrates a clear differentiation between the
315 ecological requirements of the two species, particularly on the axes referring to climatic
316 variables (temperature and rainfall), in contrast to the overlap of topographic characteristics
317 between the two habitats. The Fisher discriminant-analysis results ($k = 0.064$; $F = 86.828$; $P <$
318 0.0001) reinforced the hypothesis of segregation between the two taxa based on ecological
319 requirements. This analysis assigned the higher coefficients in the linear discrimination
320 equation (Table 4) to the Tmin (0.0926) and to the Tmax (0.0357).

321

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

323

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

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

347

348 **DISCUSSION**

349

350 **Model accuracy and prediction uncertainty**

351

352 The potential distribution models calibrated for *Abies pinsapo* and *A. alba* show high AUC
353 scores, according to the test provided by the modelling software (Phillips et al., 2006). Our
354 modelling approach relies on a robust method (Maxent) when dealing strictly with presence
355 data (Elith et al., 2006; Phillips et al., 2006). The resulting SDMs for *A. alba* and *A. pinsapo*
356 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 CO₂ concentrations (200 p.p.m. for CO₂; 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

458 CONCLUSIONS AND REQUIREMENTS FOR FURTHER RESEARCH

459

460 Our results confirm that SDMs projections can provide a useful complement to
461 palaeoecological studies, offering a less subjective and spatially explicit hypothesis concerning
462 the past geographic patterns of Iberian *Abies* species. Additionally, the pollen records provide
463 evidence for the existence of *Abies* populations in several locations corresponding to presumed
464 Pleistocene refugia. The integration of ecological-niche characteristics from known occurrences
465 of *Abies* species in conjunction with palaeoecological studies could constitute a suitable tool to
466 define proper areas in which to focus proactive conservation strategies. The results provide
467 evidence for the existence of several ecologically stable areas in the Pyrenees and Baetic
468 Range, where local conditions appear to have buffered the extreme effects of climate
469 variability, contributing to the long-time survival of *Abies* populations. This is especially
470 important to design future projections for *Abies* species under climate-change scenarios.

471

472 ACKNOWLEDGEMENTS

473

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

481

482 REFERENCES

483

- 484 Araújo, M.B. & Pearson, R.G. (2005) Equilibrium of species' distributions with climate. *Ecography*, 28,
485 693–695.
- 486 Arista, M. & Talavera, S. (1994) Pollen dispersal capacity and pollen viability of *Abies pinsapo* Boiss.
487 *Silvae Genetica*, 43, 155–158.
- 488 Austin, M.P., Cunningham, R.B. & Fleming, P.M. (1984) New approaches to direct gradient analysis
489 using environmental scalars and statistical curve-fitting procedures. *Vegetatio*, 55, 11–27.
- 490 Bartley, D.D. (1962) Pollen analysis of a small peat deposit at Baños de Tredos, near Viella in the
491 Central Pyrenees. *Pollen et Spores*, 4, 105–110.

492 Benito Garzón, M., Sánchez de Dios, R. & Sainz Ollero, H. (2007) Predictive modelling of tree species
493 distributions on the Iberian Peninsula during the Last Glacial Maximum and Mid-Holocene.
494 *Ecography*, 30, 120–134.

495 Boyer-Klein, A. (1980) Nouveaux résultats palynologiques de sites solutréens et magdaléniens
496 cantabriques. *Bulletin de la Société Préhistorique Française*, 77, 103–107.

497 Braconnot, P., Otto-Bliesner, B., Harrison, S. et al. (2007) Results of PMIP2 coupled simulations of the
498 Mid-Holocene and Last Glacial Maximum – Part 1: experiments and large-scale features.
499 *Climate of the Past*, 3(2), 261–277.

500 Brewer, S., Guiot, J. & Torre, F. (2007) Mid-Holocene climate change in Europe: a data-model
501 comparison. *Climate of the Past*, 3, 499–512.

502 Burjachs, F. (1984) Anàlisi polínica del poblat ibèric de La Palomera (La Garrotxa). *Revista de Girona*,
503 108, 38.

504 Cacho, C., Fumanal, P., López García, P. & López, N. (1983) Contribution du Tossal de la Roca à la
505 chronostratigraphie du Paléolithique supérieur final dans la région de Valence. *Rivista di*
506 *Science Preistoriche*, 38, 69–90.

507 Cacho, C., Fumanal, M.P., López García, P., López-Sáez, J.A., Pérez, M., Martínez, R., Uzquiano, P.,
508 Aranz, A., Sánchez, A., Sevilla, P., Morales, A., Roselló, E., Garralda, M.D. & García, M.
509 (1995) El Tossal de la Roca (Vall d'Alcalà, Alicante). Reconstrucción paleoambiental y cultural
510 de la transición del Tardiglacial al Holoceno inicial. *Recerques del Museu d'Alcoi*, 4, 11–101.

511 Carrión, J.S. & Sánchez-Gómez, P. (1992) Palynological data in support of the survival of walnut
512 (*Juglans regia* L.) in the western Mediterranean during last glacial times. *Journal of*
513 *Biogeography*, 19, 623–630.

514 Carrión, J.S. & van Geel, B. (1999) Fine-resolution Upper Weichselian and Holocene palynological
515 record from Navarrés (Valencia, Spain) and a discussion about factors of Mediterranean forest
516 succession. *Review of Palaeobotany and Palynology*, 106, 209–236.

517 Carrión, J.S., Riquelme, J.A., Navarro, C. & Munuera, M. (2001) Pollen in hyaena coprolites reflects late
518 glacial landscape in southern Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology*,
519 176, 193–205.

520 Carrión, J.S., Yll, E.I., Walker, M.J., Legaz, A.J., Chaín, C. & López, A. (2003) Glacial refugia of
521 temperate, Mediterranean and Ibero-North African flora in south-eastern Spain: new evidence
522 from cave pollen at two Neanderthal man sites. *Global Ecology & Biogeography*, 12, 119–129.

523 Carrión, J.S., Finlayson, C., Fernández, S., Finlayson, G., Allué, E., López-Sáez, J.A., López García, P.,
524 Gil-Romera, G., Bailey, G. & González-Sampériz, P. (2008) A coastal reservoir of biodiversity
525 for Upper Pleistocene human populations: palaeoecological investigations in Gorham's Cave
526 (Gibraltar) in the context of the Iberian Peninsula. *Quaternary Science Reviews*, 27, 2118–
527 2135.

- 528 Cortés-Sánchez, M., Morales-Muñiz, A., Simón-Vallejo, M.D., Bergadá-Zapata, M.M., Delgado-Huertas,
529 A., López-García, P., López-Sáez, J.A., Lozano-Francisco, M.C., Riquelme-Cantal, J.A.,
530 Roselló-Izquierdo, E., Sánchez-Marco, A. & Vera-Peláez, J.L. (2008) Paleoenvironmental and
531 cultural dynamics of the coast of Málaga (Andalucía, Spain) during the Upper Pleistocene and
532 early Holocene. *Quaternary Science Reviews*, 27, 2176–2193.
- 533 Costa Tenorio, M., Morla Juaristi, C. & Sáinz Ollero, H. (1997) Los bosques ibéricos. Una interpretación
534 geobotánica. Editorial Planeta, Barcelona.
- 535 Dupré, M. (1980) Análisis polínico de sedimentos arqueológicos de la Cueva de Les Malladetes (Barx,
536 Valencia). *Cuadernos de Geografía*, 26, 1–22.
- 537 Dupré, M. (1988) Palinología y paleoambiente. Nuevos datos españoles. Referencias. Diputación
538 Provincial de Valencia, Valencia.
- 539 Dupré, M., Pérez Obiol, R. & Roure, J.M. (1994) Análisis polínico del sondeo TU de la turbera de
540 Torrelblanca Castellón, España). *Trabajos de Palinología Básica y Aplicada. X Simposio de*
541 *Palinología* (ed. by I. Mateu, M. Dupré, J. Güemes and M.E. Burgaz), pp. 165–174. Universitat
542 de València, València.
- 543 Dupré, M., Fumanal, M.P., Martínez, J., Pérez Obiol, R., Roure, J.M. & Usera, J. (1996) The Laguna de
544 San Benito (Valencia, Spain): palaeoenvironmental reconstruction of an endorheic system.
545 *Quaternaire*, 7, 177–186.
- 546 Edeso, J.M., Ugarte, F.M. & Peñalba, M.C. (1989) El depósito detrítico pleistoceno (estuarino-fluvial) de
547 Anzarán (Irún, estuario del Bidasoa): caracterización geomorfológica y palinológica. *Actas de*
548 *la 2ª Reunión del Cuaternario Ibérico*, pp. 16–17. AEQUA-GTPEQ, Madrid.
- 549 Elith, J., Graham, C.H., Anderson, R.P. et al. (2006) Novel methods improve prediction of species'
550 distributions from occurrence data. *Ecography*, 29, 129–151.
- 551 Esteban, A. (1996) Evolución del paisaje nevadense durante los últimos 1.500 años a partir del análisis
552 polínico de borreguiles. 1ª Conferencia Internacional Sierra Nevada, pp. 251–273. Universidad
553 de Granada, Granada.
- 554 Expósito, I., Yll, R. & Burjachs, F. (2008) Paleoambiente del Neolítico de la Meseta Norte Ibérica a
555 partir del registro palinológico de un depósito de origen antropozoógeno (Cueva de El Mirador,
556 Sierra de Atapuerca, Burgos). *Proceedings XVI international APLE symposium of palynology*,
557 pp.77. Universitat de les Illes Balears, Palma de Mallorca.
- 558 Farjon, A. & Rushforth, K.D. (1989) A classification of *Abies* Miller (Pinaceae). *Notes of the Royal*
559 *Botanic Garden Edinburgh*, 46, 59–79.
- 560 Fernández Rodríguez, C., Ramil Rego, P., Martínez Cortizas, A., Rey Salgado, J.M. & Peña Villamide,
561 P. (1993) La cueva de A Valiña (Castroverde, Lugo): Aproximación estratigráfica,
562 paleobotánica y paleontológica al Paleolítico superior inicial de Galicia. *Estudios sobre*
563 *Cuaternario. Medios sedimentarios. Cambios Ambientales. Hábitat humano* (ed. By M.P.
564 Fumanal and J. Bernabeu), pp. 159–177. Universitat de València, València.

565 Finlayson, C., Giles Pachecho, F., Rodríguez Vidal, J. et al. (2006) Late survival of Neanderthals at the
566 southernmost extreme of Europe. *Nature*, 443, 850–853.

567 Florschütz, F., Menéndez Amor, J. & Wijmstra, T.A. (1971) Palynology of a thick Quaternary succession
568 in Southern Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 10, 233–264.

569 Fox, J., Ash, M., Boye, T., Calza, S., Chang, A., Grosjean, P., Heiberger, R., Kerns, G.J., Lancelot, R.,
570 Lesnoff, M., Messad, S., Maechler, M., Putler, D., Ristic, M. & Wolf, P. (2007) Rcmdr: R
571 Commander. R package version 1,3–9. Available at:
572 <http://socserv.socsci.mcmaster.ca/jfox/Misc/Rcmdr/>

573 Gómez Ortiz, A. & Esteban Amat, A. (1993) Análisis polínico de la turbera de La Feixa (La Màniga,
574 Cerdanya, 2.150 m). Evolución del paisaje. Estudios sobre Cuaternario, medios sedimentarios,
575 cambios ambientales, hábitat humano (ed. By M.P. Fumanal and J. Bernabeu) pp. 185–190.
576 Universitat de València, València.

577 González Sampérez, P. (1998) Estudio palinológico de la Cueva de En Pardo (Planes, Alicante).
578 Primeros resultados. *Cuaternario y Geomorfología*, 12, 45–61.

579 González Sampérez, P., Valero Gracés, B.L., Carrión, J.S., Peña-Monné, J.L., García-Ruiz, J.M. &
580 Martí-Bono, C. (2005) Glacial and Lateglacial vegetation in northeastern Spain: new data and
581 a review. *Quaternary International*, 140–141, 4–20.

582 González Sampérez, P., Valero Gracés, B.L., Moreno, A., Jalut, G., García Ruiz, J.M., Martí Bono, C.,
583 Delgado Huertas, A., Navas, A., Otto, T. & Dedoubat, J.J. (2006) Climate variability in the
584 Spanish Pyrenees during the last 30,000 yr revealed by the El Portalet sequence. *Quaternary*
585 *Research*, 66, 38–52.

586 GRASS Development Team (2008) Geographic resources analysis support system (GRASS) software,
587 version 6.3.0. Available at: <http://grass.osgeo.org>.

588 Guisan, A. & Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat
589 models. *Ecology Letters*, 8, 993–1009.

590 Guisan, A. & Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological*
591 *Modelling*, 135, 147–186.

592 Hewitt, G.M. (1996) Some genetic consequences of ice ages, and their role in divergence and
593 speciation. *Biological Journal of the Linnean Society*, 58, 247–276.

594 Huntley, B. & Birks, H.J.B. (1983) An atlas of past and present pollen maps for Europe. Cambridge
595 University Press, Cambridge.

596 Iglesias, M. (1998) Relation végétation-pluie pollinique actuelle phytomasse epigée pérenne dans les
597 steppes du Sud-Est de l'Espagne et du Nord-Est du Maroc. PhD Thesis, University of Paul
598 Sabatier-Toulouse III, Toulouse.

599 Jaynes, E.T. (1957) Information theory and statistical mechanics. *Physical Review*, 106, 620–630.

600 Kiehl, J.T. & Gent, P.R. (2004) The community climate system model, version 2. *Journal of Climate*, 17,
601 3666–3682.

602 Kottek, M., Grieser, J., Beck, C., Rudolf, B. & Rubel, F. (2006) World Map of the Koppen-Geiger climate
603 classification updated. *Meteorologische Zeitschrift*, 15, 259–263.

604 Krebs, P., Conedera, M., Pradella, M., Torriani, D., Felber, M. & Tinner, W. (2004) Quaternary refugia of
605 the sweet chestnut (*Castanea sativa* Mill.): an extended palynological approach. *Vegetation*
606 *History and Archaeobotany*, 13, 145–160.

607 Krussmann, G. (1972) *Handbuch der Nadelgehölze*. Parey, Berlin.

608 Lebreton, V., Renault-Miskovsky, J., Carrión, J.S. & Dupré, M. (2003) Estudio palinológico del
609 sedimento de la Cueva del Boquete de Zafarraya. El Pleistoceno Superior de la Cueva de El
610 Boquete de Zafarraya (ed. by C. Barroso), pp. 149–160. Junta de Andalucía, Sevilla.

611 Leroi-Gourhan, A. (1971) Análisis polínico. Cueva Morín (ed. by J. González Echegaray and L.G.
612 Freeman), pp. 359–364. Patronato Cuevas Prehistóricas de la Provincia de Santander,
613 Santander.

614 Liepelt, S., Cheddadi, R., de Beaulieu, J.-L., Fady, B., Gömöry, D., Hussendörfer, E., Konner, M., Litt,
615 T., Longauer, R., Terhuime-Berson, R. & Ziegenhagen, B. (2009) Postglacial range expansion
616 and its genetic imprints in *Abies alba* (Mill.) – A synthesis from palaeobotanic and genetic data.
617 *Review of Palaeobotany and Palynology*, 153, 139–149.

618 Linares, J.C. (2008) Efectos del cambio global sobre la dinámica poblacional y la ecofisiología de
619 bosques relictos de *Abies pinsapo* Boiss. PhD Thesis, University of Jaén, Jaén.

620 Lobo, J.M., Jiménez-Valverde, A. & Real, R. (2008) AUC: a misleading measure of the performance of
621 predictive distribution models. *Global Ecology and Biogeography*, 17, 145–151.

622 López de Heredia, U., Carrión, J.S., Jiménez, P., Collada, C. & Gil, L. (2007) Molecular and
623 palaeoecological evidence for multiple glacial refugia for evergreen oaks on the Iberian
624 Peninsula. *Journal of Biogeography*, 34, 1505–1517.

625 López-Merino, L., López-Sáez, J.A., Ruiz Zapata, M.B. & Gil García, M.J. (2008) Reconstructing the
626 history of beech (*Fagus sylvatica* L.) in the north-western Iberian Range (Spain): from Late-
627 Glacial refugia to the Holocene anthropic-induced forests. *Review of Palaeobotany and*
628 *Palynology*, 152, 58–65.

629 López-Sáez, J.A., López-García, P. & Cortés-Sánchez, M. (2007) Paleovegetación del Cuaternario
630 reciente: Estudio arqueopalinológico. Cueva Bajondillo (Torremolinos). Secuencia
631 cronocultural y paleoambiental del Cuaternario reciente en la Bahía de Málaga (ed. by M.
632 Cortés-Sánchez) pp. 139–156. Diputación de Málaga, Junta de Andalucía, Universidad de
633 Málaga, Fundación Cueva de Nerja y Fundación Obra Social de Unicaja, Málaga.

634 Martínez-Meyer, E. & Peterson, A.T. (2006) Conservatism of ecological niche characteristics in North
635 American plant species over the Pleistocene-to-Recent transition. *Journal of Biogeography*, 33,
636 1779–1789.

- 637 Martínez-Meyer, E., Peterson, A.T. & Hargrove, W.W. (2004) Ecological niches as stable distributional
638 constraints on mammal species, with implications for Pleistocene extinctions and climate
639 change projections for biodiversity. *Global Ecology and Biogeography*, 13, 305–314.
- 640 Menéndez Amor, J. & Florschütz, F. (1962) Un aspect de la végétation en Espagne méridionale durant
641 la dernière glaciation et l'Holocène. *Geologie en Mijnbouw*, 41, 131–134.
- 642 Menéndez Amor, J. & Florschütz, F. (1964) Results of the preliminary palynological investigation of
643 samples from a 50 m boring in southern Spain. *Boletín de la Real Sociedad Española de
644 Historia Natural (sección Geología)*, 62, 251–255.
- 645 Montserrat, J. (1992) Evolución glacial y postglacial del clima y la vegetación en la vertiente sur del
646 Pirineo: Estudio palinológico. *Monografías del Instituto Pirenaico de Ecología* 6. Instituto
647 Pirenaico de Ecología, CSIC, Zaragoza.
- 648 Montserrat, J. & Vilaplana, J.M. (1987) The paleoclimatic records of the Upper Pleistocene and
649 Holocene in the Llauset Valley (Central Southern Pyrenees). *Pirineos*, 129, 107–113.
- 650 Muller, S.D., Nakagawa, T., de Beaulieu, J.-L., Court-Picon, M., Carcaillet, C., Miramont, C., Roiron, P.,
651 Boutherin, C., Ali, A.A. & Bruneton, E. (2007) Post-glacial migration of silver fir (*Abies alba* Mill.)
652 in the south-western Alps. *Journal of Biogeography*, 37, 876–899.
- 653 Muñoz, M., Sánchez Goñi, M.F. & Ugarte, F.M. (1990) El entorno geo-ambiental del yacimiento
654 arqueológico de Kurtzia. *Sopela-Barrika. Costa occidental de Bizkaia. Munibe*, 41, 107–115.
- 655 Ninyerola, M., Pons, X. & Roure, J.M. (2005) Atlas Climático Digital de la Península Ibérica.
656 Metodología y aplicaciones en bioclimatología y geobotánica. Universidad Autónoma de
657 Barcelona, Bellaterra. Available at: <http://opengis.uab.es>.
- 658 Otto-Bliesner, B.L., Brady, E.C., Clauzet, G., Tomas, R., Levis, S. & Kothavala, Z. (2006) Last glacial
659 maximum and holocene climate in CCSM3. *Journal of Climate*, 19, 2526–2544.
- 660 Parra, I., Van Campo, E. & Otto, T. (2005) Análisis palinológico y radiométrico del sondeo Sobrestany.
661 Nueve milenios de historia natural e impactos humanos sobre la vegetación del Alt Empordà.
662 *Empuriès*, 54, 33–44.
- 663 Pearman, P.B., Randin, C.F., Broennimann, O., Vittoz, P., Knaap, W.O., Engler, R., Lay, G.L.,
664 Zimmermann, N.E. & Guisan, A. (2008) Prediction of plant species distributions across six
665 millennia. *Ecology Letters*, 11, 357–369.
- 666 Pearson, R.G. (2006) Climate change and the migration capacity of species. *Trends in Ecology &
667 Evolution*, 21, 111–113.
- 668 Pearson, R.G., Thuiller, W., Araujo, M.B., Martínez-Meyer, E., Brotons, L., McClean, C., Miles, L.,
669 Segurado, P., Dawson, T.P. & Lees, D.C. (2006) Model-based uncertainty in species range
670 prediction. *Journal of Biogeography*, 33, 1704–1711.
- 671 Pérez Obiol, R. & Julià, R. (1994) Climatic change on the Iberian Peninsula recorded in a 30,000-Yr
672 pollen record from Lake Banyoles. *Quaternary Research*, 41, 91–98.

673 Pérez Obiol, R. & Roure, J.M. (1990) Evidència de la regressió recent des les avetoses a partir de les
674 anàlisis pol.líniques. *Orsis*, 5, 5–11.

675 Peterson, A.T. (2003) Predicting the geography of species' invasions via ecological niche modeling. *The*
676 *Quarterly Review of Biology*, 78, 419–433.

677 Peterson, A.T. & Nyári, Á.S. (2008) Ecological niche conservatism and Pleistocene refugia in the
678 thrush-like mourner, *Schiffornis* Sp., in the Neotropics. *Evolution*, 62, 173–183.

679 Peterson, A.T., Soberón, J. & Sánchez-Cordero, V. (1999) Conservatism of ecological niches in
680 evolutionary time. *Science*, 285, 1265–1267.

681 Peterson, A.T., Papes, M. & Eaton, M. (2007) Transferability and model evaluation in ecological niche
682 modeling: a comparison of GARP and Maxent. *Ecography*, 30, 550–560.

683 Phillips, S.J. & Dudík, M. (2008) Modeling of species distributions with Maxent: new extensions and a
684 comprehensive evaluation. *Ecography*, 31, 161–175.

685 Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006) Maximum entropy modeling of species
686 geographic distributions. *Ecological Modelling*, 190, 231–259.

687 Pons, A. & Reille, M. (1988) The Holocene and upper Pleistocene pollen record from Padul (Granada,
688 Spain): a new study. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 35, 145–214.

689 R Development Team (2008) The R project for statistical computing, R version 2.8.1. Available at:
690 <http://www.r-project.org>.

691 Ramil Rego, P. (1993) Evolución climática e historia de la vegetación durante el Pleistoceno Superior y
692 el Holoceno en las regiones montañosas del Noroeste Ibérico. La evolución del paisaje en las
693 montañas del entorno de los Caminos Jacobeos (ed. by A. Pérez Alberti, L. Guitián Rivera and
694 P. Ramil Rego), pp. 25–60. Xunta de Galicia, A Coruña.

695 Ramil Rego, P. & Aira Rodríguez, M.J. (1992) Contribución al conocimiento de la vegetación
696 Tardiglaciaria y Holocena en el extremo norte de la Terra Cha' (Galicia, España). *Nova Acta*
697 *Científica Compostelana (Biología)*, 3, 49–58.

698 Ramstein, G., Kageyama, M., Guiot, J., Wu, H., Hély, C., Krinner, G. & Brewer, S. (2007) How cold was
699 Europe at the Last Glacial Maximum? A synthesis of the progress achieved since the first
700 PMIP model-data comparison. *Climate of the Past*, 3, 331–339.

701 Reille, M. & Lowe, J.J. (1993) A re-evaluation of the vegetation history of the eastern Pyrénées (France)
702 from the end of the glacial to the present. *Quaternary Science Reviews*, 12, 47–77.

703 Ruiz de la Torre, J. (1990) Mapa Forestal de España. ICONAM. A.P.A., Madrid.

704 Scaltsoyiannes, A., Tsaktsira, M. & Drouzas, A.D. (1999) Allozyme differentiation in the Mediterranean
705 firs (*Abies*, Pinaceae). A first comparative study with phylogenetic implications. *Plant*
706 *Systematics and Evolution*, 216, 289–307.

707 Svenning, J.C. (2003) Deterministic Plio-Pleistocene extinctions in the European cool-temperate tree
708 flora. *Ecology Letters*, 6, 646–653.

- 709 Terhürne-Berson, R., Litt, T. & Cheddadi, R. (2004) The spread of *Abies* throughout Europe since the
710 last glacial period: combined macrofossil and pollen data. *Vegetation History and*
711 *Archaeobotany*, 13, 257–268.
- 712 Tzedakis, P.C. (1993) Long-term tree populations in northwest Greece through multiple Quaternary
713 climatic cycles. *Nature*, 364, 437–440.
- 714 Tzedakis, P.C., Lawson, I.T., Frogley, M.R., Hewitt, G.M. & Preece, R.C. (2002) Buffered tree
715 population changes in a Quaternary refugium: evolutionary implications. *Science*, 297, 2044–
716 2047.
- 717 Valle, M., Rivas, M.R., Lucini, M., Ortiz, J.E. & Torres, T. (2003) Interpretación paleoecológica y
718 paleoclimática del tramo superior de la turbera de Padul (Granada, España). *Polen*, 13, 85–
719 95.
- 720 Van der Knaap, W.O. & van Leeuwen, J.F.N. (1994) Holocene vegetation, human impact, and climatic
721 change in Serra da Estrela, Portugal. *Dissertationes Botanicae*, 234, 497–535.
- 722 Van der Knaap, W.O. & van Leeuwen, J.F.N. (1995) Holocene vegetation and degradation as
723 responses to climatic change and human activity in the Serra da Estrela, Portugal. *Review of*
724 *Palaeobotany and Palynology*, 89, 153–211.
- 725 Van der Knaap, W.O. & van Leeuwen, J.F.N. (1997) Late Glacial and early Holocene vegetation
726 succession, altitudinal vegetation zonation, and climatic change in the Serra da Estrela,
727 Portugal. *Review of Palaeobotany and Palynology*, 97, 239–285.
- 728 Venables, W.N. & Ripley, B.D. (2002) *Modern applied statistics with S*, 4th edn. Springer-Verlag, New
729 York.
- 730 Vidakovic, M. (1991) *Conifers, morphology and variation*. Zdravko Zidovec, Zagreb.
- 731 Waltari, E., Hijmans, R.J., Peterson, A.T., Nyári, Á.S., Perkins, S.L. & Guralnick, R.P. (2007) Locating
732 Pleistocene Refugia: comparing phylogeographic and ecological Niche model predictions.
733 *PLoS ONE*, 2, e563.
- 734 Willis, K.J. & McElwain, J.C. (2002) *The evolution of plants*. Oxford University Press, New York.
- 735 Yll, R., Roure, J.M., Pantaleón, J. & Pérez Obiol, R. (1994) Análisis polínico de una secuencia
736 holocénica en Roquetas de Mar (Almería). *Trabajos de Palinología Básica y Aplicada*. X
737 Simposio de Palinología (ed. by I. Mateu, M. Dupré, J. Guñemes and M.E. Burgaz), pp. 189–
738 198. Universitat de València, València.
- 739 Yll, R., Carrión, J.S., Pantaleón, J., Dupré, M., La Roca, N., Roure, J.M. & Pérez-Obiol, R. (2003)
740 Palinología del Cuaternario reciente en la Laguna de Villena (Alicante, España). *Anales de*
741 *Biología*, 25, 65–72.
- 742
- 743

Table 1 Pollen deposits indicating the code, site name, location (UTMx and UTM y), 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	Navarés	700992	4351106	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/Alerod	No data	No	González Sampérix (1998)
7	Villena	681000	4276000	Lake	> 47 and c. 6	Yes	No	Yli <i>et al.</i> (2003)
8	Cuadé	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	Eteban (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 & Florinchi (1962, 1964); Florinchi <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	Yli <i>et al.</i> (1994)
13	Zafarraya	399800	4090150	Archaeological cave	> 46	No data	No data	Ielbreton <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-Sánchez <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 Lameiro	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	Mafios <i>et al.</i> (1990)
21	Morín	430084	4802975	Archaeological cave	c. 39–37	No data	No	Lesni-Gouffan (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	Anarín	596500	4802623	Marsh	Upper Pleistocene	No data	No	Edeso <i>et al.</i> (1989)
25	Tramacastilla	715103	4732997	Lake	Upper Pleistocene-Holocene	Yes	Yes	Montsernat (1992); González Sampérix <i>et al.</i> (2005)
26	Formigal	706794	4738638	Lake	LGM	No data	Yes	González Sampérix <i>et al.</i> (2005)
27	Las Ranas	704095	4743995	Lake	Upper Pleistocene-Holocene	Yes	Yes	Montsernat (1992)
28	El Portalet	712795	4741889	Peatland	Mid-Holocene	Yes	No	González Sampérix <i>et al.</i> (2006)
29	Llanset	805453	4728082	Lake	Mid-Holocene	Yes	No data	Montsernat & Vilaplana (1987)
30	La Feixa	899177	4712608	Peatland	Mid-Holocene	Yes	No data	Gómez Ortiz & Eteban Amat (1993)
31	Baños de Tredos	819778	4737028	Peatland	Mid-Holocene	Yes	No data	Bardley (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 <i>et al.</i> (2005)
35	Beguadà	908277	4683398	Palaeosol	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.

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

748

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).

749

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).

750

751

752 **Figure captions**

753

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

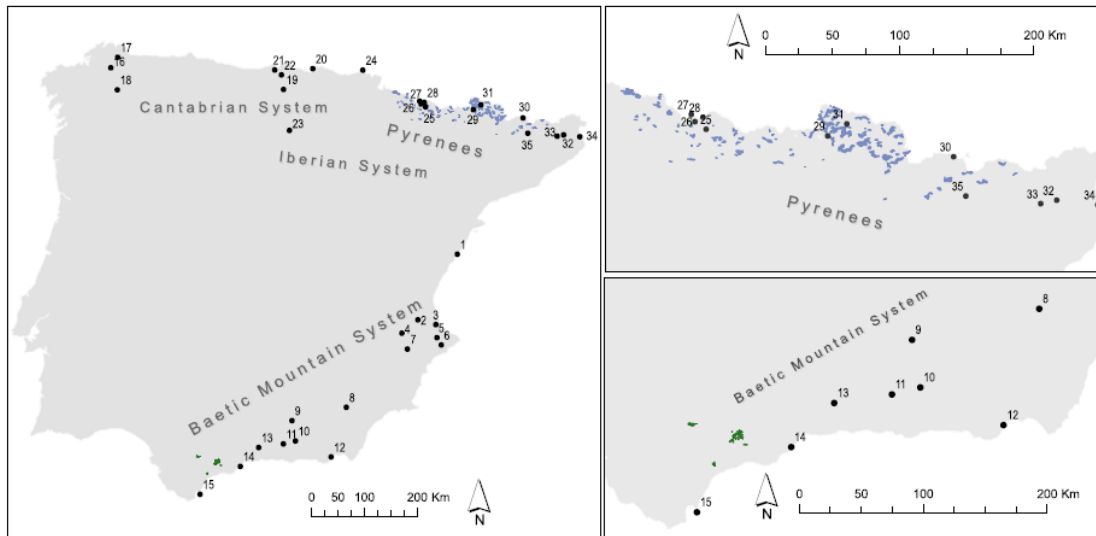
766 **Figure 4.** Potential distribution of *Abies pinsapo* and *Abies alba* at the last glacial maximum
767 (LGM), under two general circulation model (GCM) estimates (CCSM and MIROC). In addition,
768 35 pollen deposits are also shown. Presence of *Abies* pollen in pollen deposits at the LGM (\pm
769 500 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).

774

775 Figure 1

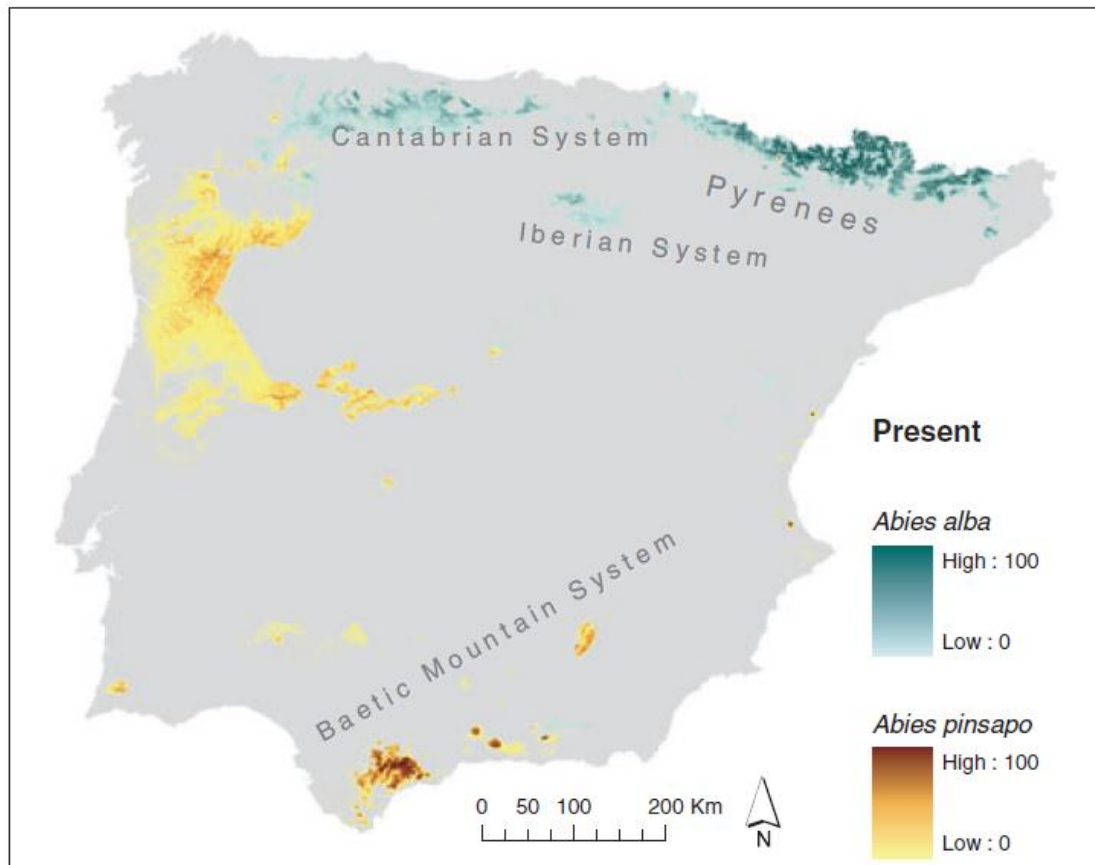


776

777

778

779 Figure 2

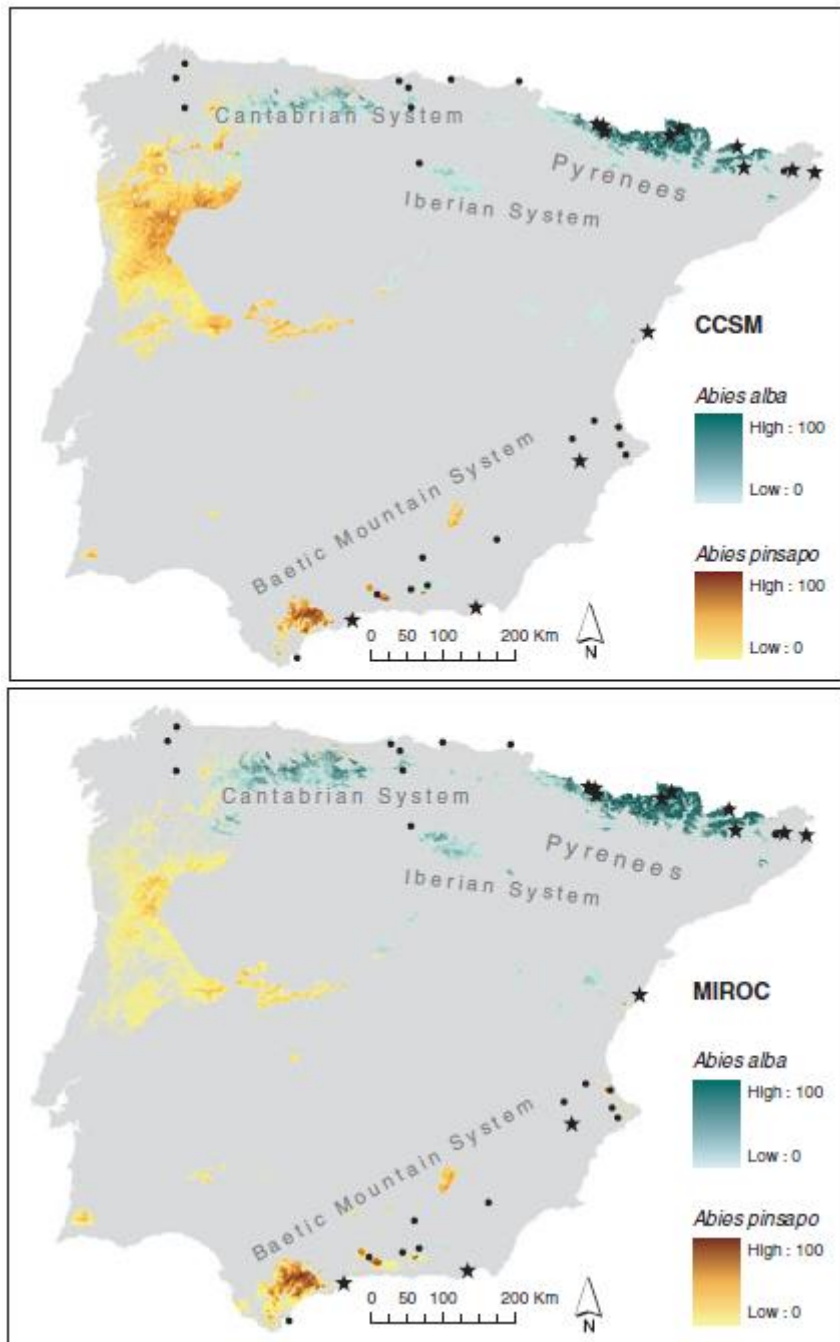


780

781

782

783 Figure 3

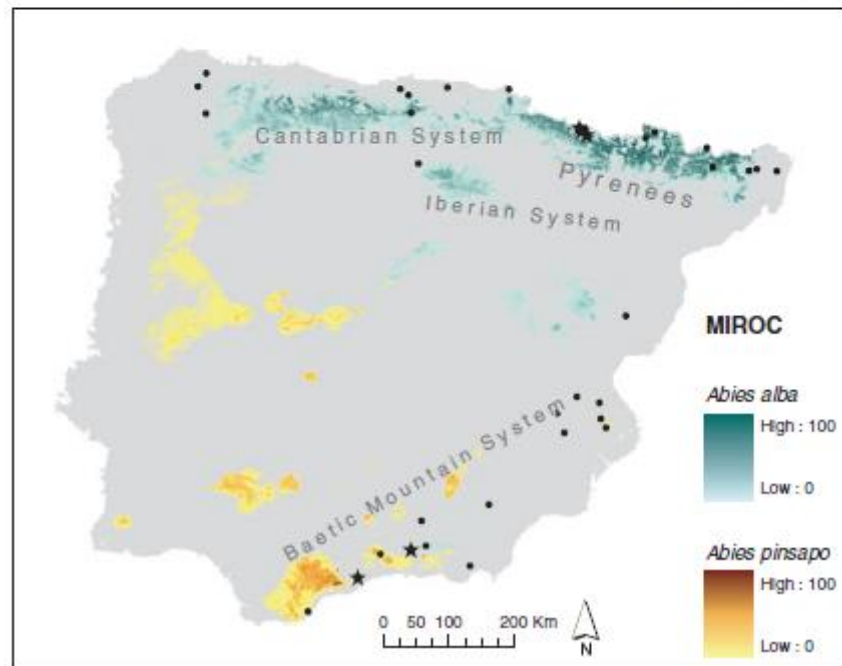
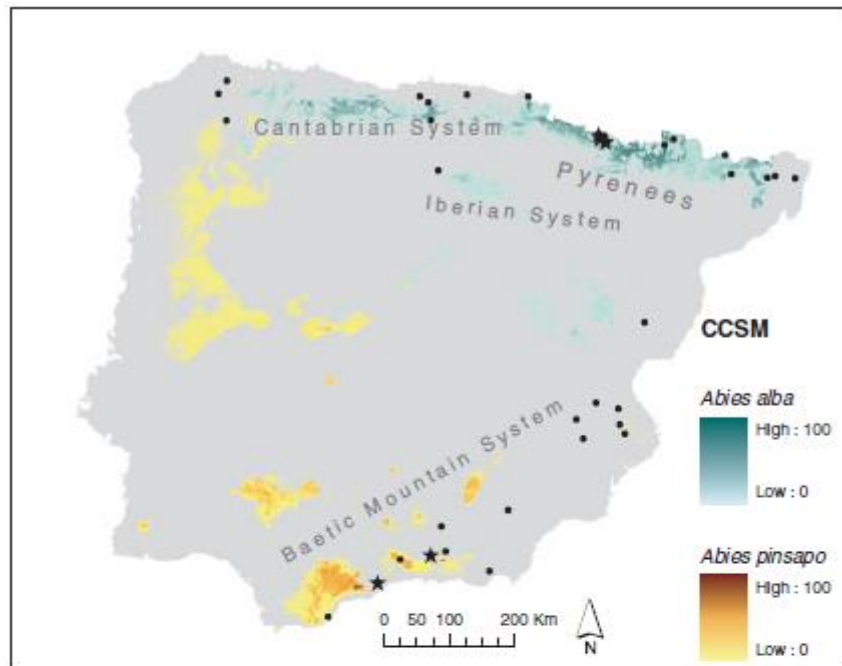


784

785

786

787 Figure 4

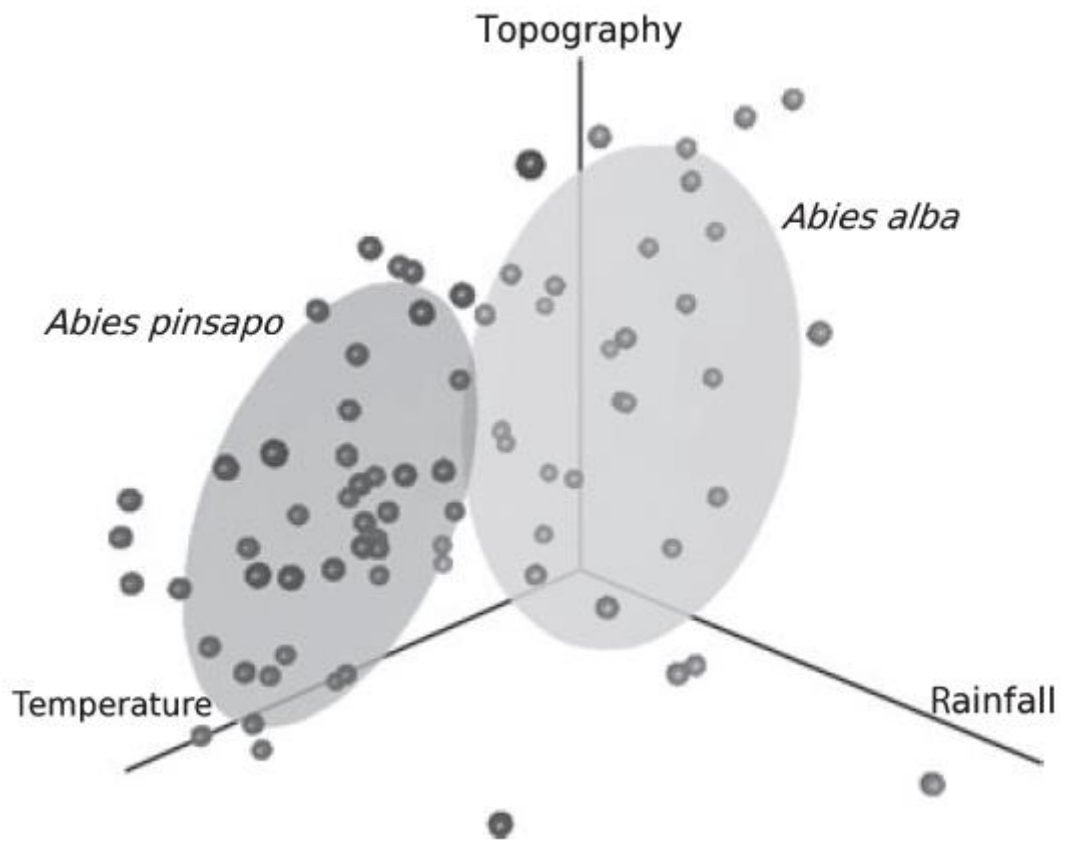


788

789

790

791 Figure 5



792

793

794