

1 Yacine Kouba*¹, Concepción L. Alados¹ and Guillermo C. Bueno²

2

3 **Effects of abiotic and anthropogenic factors on the spatial distribution of *Quercus faginea***
4 **in the Spanish Central Pyrenees**

5

6 ¹Pyrenean Institute of Ecology (CSIC), Avda. Montañana 1005. P. O. Box 202, E- 50080 Zaragoza, Spain

7 ²Pyrenean Institute of Ecology (CSIC), Avda Rgmto Galicia s/n P. O. Box 64, Jaca E-22700, Huesca, Spain

8

9 *Corresponding author: Tel: +34 976 716034; fax: +34 976 716019; Email: yacine@ipe.csic.es;

10

11 **ABSTRACT**

12

13 Species distribution is usually explained by abiotic factors, particularly, climatic variables which
14 are often considered as the most important drivers of species distribution. Nevertheless, when
15 investigating the underlying causality in species distribution, the importance of those factors
16 together with the role of anthropogenic factors (land-use variables) must be considered.
17 Particularly in the Mediterranean basin where natural ecosystems underwent important
18 transformations due to anthropogenic pressure in the territory. In this work we studied the effects
19 of abiotic and anthropogenic factors on *Quercus faginea* distribution identifying the key factors
20 that shape its distribution in the Spanish Central Pyrenees. Data on presence-absence of *Q.*
21 *faginea* species, abiotic variables and anthropogenic variables were derived by GIS from digital
22 sources and aerial photographs. We used Bayesian model averaging to identify the key factors
23 that affect the spatial distribution of *Q. faginea*. ~~Then~~ Then we applied hierarchical partitioning
24 to estimate the relative importance of each key factor. In the Spanish Central Pyrenees, on a
25 broad scale, abiotic variables, i.e. climate and lithology, were identified as underlying factors that
26 shape the spatial distribution of *Q. faginea*. The presence of recently introduced plantations and
27 previous livestock pressure had a negative effect on *Q. faginea* distribution; which represent the
28 anthropogenic disturbance effect on this species. This study indicated that in this mountain area
29 and at our regional scale, although abiotic factors have a great importance in explaining the
30 underlying causality in *Q. faginea* distribution, anthropogenic factors can not be neglected.

31 **Keywords**

32 Species distribution models (SDM), explanatory models, Bayesian model averaging, hierarchical
33 partitioning, land use variables.

34

35 **Introduction**

36

37 The understanding of the factors that influence the distribution of species is of interest because
38 they enable us to estimate the drivers of species distribution across a study region. To model the
39 relationship between species and their environment, ecologists often use empirically based
40 statistical models (e.g. Coudun et al. 2006; Segurado and Araújo 2004; Thuiller et al. 2004).
41 Statistical models of species distribution (i.e. presence-absence of species) derive relationships
42 between the dependent variable and the values of a set of explanatory variables such as
43 temperature, slope or elevation. These techniques can be used for two purposes: (i) to explore the
44 underlying causality of species distribution (by examining the statistical significance of the
45 influence of explanatory variable upon the dependent variable) and/or (ii) prediction of the
46 distribution of species it self (by using the derived relationship between the dependent variable
47 and predictors to project the predicting map), but in many cases, statistical models are only used
48 to predict spatial distribution of species, while the explanation of the underlying causality tend to
49 be a secondary consideration. As a consequence, there is a few modeling studies which
50 addressed such purpose (e.g. Graham et al. 2004; Nally 2000).

51 Often, the spatial distribution of terrestrial species is studied with regard to abiotic variables only
52 (climatic variables), which are often the most important drivers of species distributions (Guisan
53 et al. 1995; Heegaard 2002; Lehmann et al. 2002). Moreover, human activities as well (e.g.
54 agricultural and livestock activities and reforestations) might influence the spatial distribution of
55 terrestrial species. Particularly, in the Mediterranean Basin which is recognized as one of the
56 Earth's biodiversity hotspot (Myers et al. 2000), human activities have played a fundamental role
57 in the fragmentation of communities and the loss of species (Maltez-Mouro et al. 2009). For
58 instance, the plantations made recently in the Spanish mountains have replaced the native forests
59 with faster growing species (Perry 1998); this fact has led to a reduction in the total ranges of
60 species and landscape diversity (Lasanta et al. 2009). In this sense, along with the influence of
61 abiotic factors, the anthropogenic disturbances must be considered when investigating the
62 underlying causality in species distribution.

63 The main objectives of this study were to explore and understand the effects of abiotic and
64 anthropogenic factors on *Q. faginea* forests in the Spanish Central Pyrenees. Our main question
65 was to determine the main factors that explain the occurrence of *Q. faginea* forests in the Spanish
66 Central Pyrenees.

67 *Q. faginea* was the subject of the study because it is sensitive to abiotic and anthropogenic
68 factors. It is a winter-deciduous tree that often does not exceed high-shrub stature because of

69 anthropogenic disturbances or environmental limitations (Maltez-Mouro et al. 2009). The *Q.*
70 *faginea* forest species is considered as an important structural component of native plant
71 communities in many mesic forests in Mediterranean environments (Rey Benayas et al. 2005)
72 holding a wide diversity of animal and plant communities, and thus is of great interest for
73 ecosystem conservation (Rey Benayas et al. 2005). Regardless of its huge importance as a
74 structural species of the ecosystems, and its important role as a fixative of rural populations,
75 providing several main resources to the rural populations (source of timber and acorn), *Q.*
76 *faginea* has not been much studied, compared to other species.

77

78 **Methods**

79

80 *Study area and species*

81

82 The study was conducted in the Spanish Central Pyrenees, between 42.49 N and 42.41 N and
83 between 0.32 W and 0.10 E (Fig. 1), which encompassed a wide elevation range (500-3000 m
84 a.s.l.). The 4394-km² area included about 325 villages and had clear rural character. In the area,
85 the climate is quite variable, with oceanic characteristics in the west and a Mediterranean
86 influence in the easternmost portion (Lasanta 2002). Mean annual rainfall is >800 mm year⁻¹ in
87 the lowest localities. This value is overcome in the rest of the area; above 1500 m the
88 precipitation is higher than 1500 (Vicente-Serrano et al. 2004). The intra annual variability is
89 very high, and the rain season extends from October to June. At the lowest elevations, mean
90 annual temperature varies between 9 °C and 11 °C and, at the highest elevations (>1500 m), it is
91 6 °C. The relief of the study area is placed in parallel bands with a NW-SE direction (Vicente-
92 Serrano et al. 2004). In the north part the Axial Pyrenees (2500-300 m of altitude). The next band
93 corresponds to Eocene flysch areas (800- 2200 m of altitude). The third band correspond to the
94 Ebro depression (400-800 m of altitude), forming a wide valley. The landscape is a mosaic of
95 natural and semi-natural forests, shrublands, grasslands, agricultural fields, and urban areas.

96 In the Central Pyrenees *Q. faginea* is considered as one of the most abundant species; it
97 occurs naturally, it is not artificially reforested. Its communities form a transition belt between
98 conifer-sclerophyllous forests of *Q. ilex* and *Pinus halepensis* and high mountain forests of *P.*
99 *sylvestris*, *P. nigra*, *Fagus sylvatica* and *Abies alba* (Jiménez et al. 1998; Loidi and Herrera
100 1990). The facility of hybridization of *Q. faginea* with other species of the same gender *Quercus*
101 (i.e. *Q. pubescens*) causes the existence of numerous hybridogenic populations in the study area

102 and many of individuals are difficult to identify (Himrane et al. 2004; Loidi and Herrera 1990),
103 so here we considered those hybrids (mainly *Q. subpyrenaica*) within *Q. faginea* species.

104

105 ***Species data***

106

107 The distribution map of *Q. faginea* in the Spanish Central Pyrenees was derived from the
108 Spanish National Forest Inventory map (IFN3; MMA 2007). In IFN3 map, 3 principal tree
109 species were considered for each patch and classified as first, second or third most dominant tree
110 specie, based on the estimation of the degree of their presence (explained in percentage) in that
111 patch. In this study, all patches where *Q. faginea* was the first, second or third dominant species,
112 were selected to build the distribution map of this species in the study area. Overall, the
113 percentage of presence of *Q. faginea* varied from 20% (in the patches where considered as third
114 dominant specie) to 90 % (in the patches where considered as first dominant specie). The derived
115 map was imported into a GIS for further processing; this process included edges of patches
116 correction and elimination for each patch of the areas where *Q. faginea* was absent. This action
117 was done by visual interpretation of the ortho-rectified, 0.5-m resolution aerial photographs
118 (1:30 000), obtained from the Spanish National Plan of Aerial Ortophotographs (IGN 2006). The
119 accuracy of the final map (96%) was quantified by sampling 200 random points and calculating
120 confusion matrices (Congalton 1991).

121 Data sampling was based on 20-m² grid layers that represented the entire dependent and
122 independent variables, within which 2000 pixels were chosen randomly (*Q. faginea* were
123 occurred in 900 samples) using the ArcGIS extension, Hawth's Analysis Tools 3. 27. The
124 distance of 400-m was considered as a minimum threshold in selecting sampling (see statistical
125 analysis section), thereby avoiding spatial-autocorrelation in data analysis (Legendre 1993). To
126 avoid non-representative sampling, each patch (polygon) of *Q. faginea* forests was represented
127 by a minimum of five records of occurrence.

128

129 ***Abiotic data***

130

131 The explanatory variables were chosen based on previous studies (Austin 2007; Guisan and
132 Zimmermann 2000; Purves et al. 2007). Our approach relies on the combination of abiotic
133 variables that might have a direct or indirect influence on *Q. faginea* species (Corcuera et al.
134 2004; Lansac et al. 1994; Mediavilla and Escudero 2004), and anthropogenic variables that
135 reflect the anthropogenic disturbances. Following Coudun et al. (2006), we selected abiotic

136 variables that have an influence on (1) biophysical processes (elevation, slope, aspect, terrain
137 curvature, and lithology), (2) frost conditions (number of frost days per year and mean monthly
138 minimum temperature), (3) drought (water balance and mean monthly maximum temperature).
139 We expected that most of the *Q. faginea* would occur at 600-900 m a.s.l., in areas that had a
140 sizable water balance, and characterized by moderate temperature, and a southern slope aspect.

141 The topographic variables, elevation (m.a.s.l), slope (degrees), aspect (north/south), and
142 terrain curvature (concavity/convexity), were derived from a Digital Elevation Model of Aragón
143 (CITA 2009) at 20-m resolution using ArcGIS 9.2 (ESR 2006). To obtain north/south orientation
144 the cosines of aspects were calculated. The data for climatic variables, obtained from the
145 Climatic Atlas of Aragon (DMA 2007) at 100-m resolution. These variables averaged over the
146 period 1971-2000 and included water balance (mm), number of frost days per year, and mean
147 monthly maximum and minimum temperatures (°C). The methodology used for the elaboration
148 of the climatic maps based essentially on the combination of local and global interpolation
149 methods. Likewise, a set of topographic (e.g. latitude, longitude, and insolation derived from the
150 Digital Elevation Model at 100-m resolution) and geographic variables (which quantified the
151 distance to rivers and Cantabrian Sea) were used as independent variables to explain the spatial
152 variability of the climatic factors. The following equation was used to predict the values of the
153 climatic variable in areas without information:

$$154 \quad z(x) = b_0 + b_1P_1 + b_2P_2 + \dots + b_nP_n$$

155 Where z is the predicted value in the point x , b_0, \dots, b_n are the coefficient of the regression, and
156 P_1, \dots, P_n are the values of the set of independent variables in the point x .

157 Furthermore, data regarding water balance was obtained subtracting the mean annually
158 precipitation by the potential evapo-transpiration. The later variable was calculated using
159 Hargreaves equation (Hargreaves 1975). In this study the climatic maps were downscaled from
160 the original grid (100-m² grid to a 20-m²) using nearest-neighborhood interpolation. The map of
161 lithology was derived from the geological map of Aragón (CITA 2007) and reclassified in 2
162 classes: flysch-limestones rocks and other types of rock.

163

164 ***Anthropogenic data (land-use variables)***

165

166 Several land use variables that might influence the spatial distribution of *Q. faginea* were used
167 in this study. First, the distance to the nearest village is used to account for human activities
168 concentrated around villages (i.e. agricultural practices), and to quantify the human influence on
169 *Q. faginea* forests in the study area. In addition, to determine whether *Q. faginea* was influenced

170 by the wood-harvesting associated with mining, we quantified the distance to the nearest mine.
171 Beside, to assess the extent to which livestock activities affected the spatial distribution of *Q.*
172 *faginea*, we included two explanatory variables: cost distance to pastures and cost distance to
173 livestock roads (see below). The extensive reforestation with pine plantations that has occurred
174 in the area within the last 50 year might have influenced the spatial distribution of *Q. faginea*;
175 therefore, the distance to the nearest pine plantation was included in the analyses. We expected
176 that *Q. faginea* would ~~be~~ occurs far from villages and mines, and rare near pastures and livestock
177 roads, but more common in older abandoned areas. In addition, we expected *Q. faginea* to be
178 affected negatively by pine plantations.

179 The map of villages was obtained from a map of settlements of Aragon (CHE 2009) and a
180 map of mines was derived from a map of CORINE Land Cover 2000 5th level project (IGN
181 2002). Raster layers were created based on the Euclidean distances to the nearest village and
182 mine within each pixel. Livestock variables (cost distance to pastures and cost distance to
183 livestock roads) were derived from a map of CORINE Land Cover 2000 5th level project (IGN
184 2002) and a livestock roads map of Aragón (DMA 2010) respectively. The Cost distance
185 function calculates the least accumulative cost for moving from each pixel to the source pixel (in
186 this case pasture or livestock road) using slope as cost layer. Cost distance raise with an
187 increasing of slope up to 35°; beyond that steepness, areas are essentially inaccessible (maximum
188 cost) to livestock. To identify a variable that best reflected the effect of pine plantations on *Q.*
189 *faginea* forests. First, the map of pine plantations (*P. sylvestris* and *P. nigra*) in the study area
190 was derived from Spanish National Forest Inventory map (IFN3; MMA 2007). Then, the
191 Euclidean distance to the nearest plantation was calculated for each pixel using ArcGIS 9.2 (ESR
192 2006).

193

194 ***Statistical analysis***

195

196 First, collinearity between all pairs of independent variables was investigated using Pearson's
197 correlation coefficient. The test of correlation indicated that several pairs of the explanatory
198 variables were strongly correlated ($r > 0.7$), so to solve this problem only the variables that was
199 thought most likely to be biologically important was used in the modeling (Graham 2003). The
200 final set of potential explanatory variables included: slope, aspect, terrain curvature, water
201 balance, number of frost days per year, distance to the nearest plantation, distance to the nearest
202 village, distance to the nearest mine, cost distance to livestock roads, and cost distance to
203 pastures. Spatial autocorrelation was tested for the *Q. faginea* distribution map (pixels of 20-m²)

204 here using the row-standardized Moran's I test (Cliff and Ord 1973). Spatial autocorrelation
205 decrease monotonically above a lag of fifteen map pixels (~300 m). Therefore, the distance of
206 400-m was considered as a minimum threshold in selecting sampling (Millington et al. 2007).

207 To model the *Q. faginea* responses to abiotic and anthropogenic factor we used Bayesian
208 model averaging (Madigan and Raftery 1994). BMA incorporates model selection and
209 parameters estimation uncertainties into inference and prediction (Hoeting et al. 1999; Raftery et
210 al. 1997), producing more accurate predictions than methods that select a single best model
211 (Thomson et al. 2007; Wintle et al. 2003). We used the function "bic.glm" in the "BMA"
212 package (Raftery et al. 2009) in R (R Development Core Team 2009), which performs BMA for
213 GLM (binomial error distribution and a logit link function). This function use Bayesian
214 Information Creterion (BIC) to compare models and "leaps and bounds" algorithm to identify the
215 most probable models (Raftery et al. 1997; Thomson et al. 2007). In the BMA approach the
216 posterior probability that a variable had a nonzero coefficient in the predictor model $\Pr(\beta_{vs} \neq 0)$
217 is used as a measure of the influence of that variable on the response. Explanatory variables with
218 high values of $\Pr(\beta_{vs} \neq 0)$ contributed most to model fit, whereas explanatory variables with low
219 values of $\Pr(\beta_{vs} \neq 0)$ were included only in less probable models (Nally et al. 2008; Thomson et
220 al. 2007). We considered explanatory variables that had values of $\Pr(\beta_{vs} \neq 0) > 0.75$ to be "key
221 factors," (Nally et al. 2008; Viallefont et al. 2001).

222 Because more than one key factor was identified in our analysis, we performed the
223 hierarchical partitioning (HP) to determine relative importance of each key factor (Nally et al.
224 2008). Here we used the HP to estimate the "independent" contribution of each "key factor" to
225 the total variance explained by the model (Chevan and Sutherland 1991; Nally et al. 2008). We
226 used the "hier.part" package for R (Walsh and Nally 2008). Log-Likelihood goodness of fit
227 measure was used. A logistic model is most appropriate here as the dependent variable is binary
228 (presence vs. absence). Note that the hierarchical partitioning, as currently implemented in the
229 "hier.part" package, depends on monotonic relationship between the response and the
230 explanatory variables (Luoto et al. 2006). To improve the linearity of relationship between key
231 factors and response variable, these variables were log-transformed (Heikkinen et al. 2005)
232 except for litology which is a dummy variable.

233

234 **Results**

235

236 *Identifying "key factors"*

237

238 BMA identified most influential factors that affected the distribution of *Q. faginea* in the Spanish
239 Central Pyrenees. Among the 11 explanatory variables included in the model, the following six
240 were identified as key factors, i.e. variables that had a $\text{Pr}(\beta_{vs} \neq 0) > 0.75$: three abiotic variables
241 (lithology, slope, and water balance) and three anthropogenic variables (cost distance to pastures,
242 cost distance to the livestock roads and distance to the nearest plantation). BMA suggested that
243 aspect, terrain curvature, number of frost days per year, distance to the nearest village and
244 distance to the nearest mine were unimportant in explaining the *Q. faginea* probability of
245 occurrence [$\text{Pr}(\beta_{vs} \neq 0) < 0.25$].

246 All identified key factors had high probability of inclusion in the final model, with [$\text{Pr}(\beta_{vs}$
247 $\neq 0) > 0.94$], indicating strong relationships with occurrence of *Q. faginea* in the model-building
248 data. Water balance and cost distance to the livestock roads had negative effect on *Q. faginea*
249 occurrence, as the posterior means (PM+SD) for the coefficients associated with each variable
250 were negative (Table 1), which means that the probability of occurrence of *Q. faginea* increase
251 with a decreasing of water balance values, and in zones near livestock roads and were accessible
252 to livestock. Slope, lithology, distance to the nearest plantation, and cost distance to pastures had a
253 positive effect in *Q. faginea* occurrence (Table 1), indicating that the probability of *Q. faginea*
254 occurrence increase with increasing slope values (the cross tabulation between slope and *Q.*
255 *faginea* distribution maps reflected that most ($> 90\%$) of the areas occupied by *Q. faginea* had a
256 slope angle of 5-30°, with the majority between 10° and 15°), also indicating a higher probability
257 of *Q. faginea* occurrence, in lithological zones formed by flysch-limestone rocks which are
258 located away from introduced plantations than in other zones. Finally, this result indicate that the
259 probability of occurrence increase with an increasing of cost distance to pastures, which means
260 that there is more probability to find *Q. faginea* in inaccessible areas from pastures lands to
261 livestock, than in other areas.

262

263 ***Independent explained variance***

264

265 In HP, the key factors had different independent contributions in the total explained variance.
266 This method suggests that the abiotic factors together explained more than 66% of the total
267 independent variance, which reflect the importance of those factors on the distribution of *Q.*
268 *faginea*. Interestingly, water balance had a highest independent contribution (33.36%), lithology
269 (17.02%) was the second most important variable followed by slope (16.36%). The
270 anthropogenic factors explained almost 34% of the total independent variance, a great part was
271 explained by distance to the nearest plantation (14.20%) and cost distance to pastures (10.74%),

272 these 2 variables had a negative effect on *Q. faginea* occurrence therefore reflect the
273 anthropogenic disturbance. ~~east~~-Cost distance to livestock roads (8.30%) had clearly lowest
274 independent contribution of all key factors.

275

276 **Discussion**

277

278 *Effects of abiotic factors*

279

280 The spatial distribution of *Q. faginea* in the Spanish Central Pyrenees was explained in great part
281 by the abiotic factors; particularly, climate, lithology and slope. Changes in precipitation and soil
282 water recharge can have a significant effect on the establishment of *Q. faginea* plants (Corcuera
283 et al. 2004) and an increase in the soil water recharge favors the growth of *Q. faginea*. Moreover,
284 our study indicated that water balance had a negative relationship with the occurrence of *Q.*
285 *faginea*, due to the particularity of the Central Pyrenees, where water balance becomes positive
286 with the increased elevation while the temperature, on the other hand, is characterized by very
287 low values in winter (elevation, water balance, and mean monthly minimum temperatures were
288 strongly correlated). The cross tabulation between elevation and *Q. faginea* distribution maps
289 reflected that in the Central Pyrenees all the areas occupied by this species were located between
290 450 m and 1500 m of altitude. The species does not raise the high elevated lands (situated above
291 1500 m of altitude) because of freezing temperatures that inhibit the establishment and growth of
292 seedlings. As in our study, Sánchez de Dios et al. (2006) found that *Q. faginea* forests in the
293 Iberian Peninsula were associated to continental areas with low precipitation. The phenological
294 pattern of *Q. faginea* in northeastern Spain is similar to those of species that have deep roots and
295 can access deep water reserves (Pilar and Gabriel 1998). Our study showed that the presence of
296 *Q. faginea* is associated with areas that are characterized lithologically by flysch-limestone rocks
297 and are rich in calcium carbonate, which generates calcareous soils that are suited to the
298 establishment and growth of this species (Ceballos and Torre 1979; Jiménez et al. 1998). In
299 addition, the probability of *Q. faginea* presence increased with an increase in slope due to the
300 competition from agricultural activities. The traditional management has been maintained for
301 centuries, based on an integral use of land resources. This fact implies important
302 transformations in natural space. The *Q. faginea* forest located in low slopes was cut and the
303 lands used for cereal cultivation (Lasanta 1989), which restricted this species to poor soils and
304 stony hillsides, this result reflected that the occupation of shallow slope by *Q. faginea* is not a
305 natural process, but is a result of the anthropogenic disturbance.

306

307 ***The importance of anthropogenic factors***

308

309 This study reflected that anthropogenic factors play a second role in affecting the spatial
310 distribution of *Q. faginea*, and act as restrictive factors that inhibit its spatial extension.
311 Particularly, livestock grazing and introduced plantations had negative effects on *Q. faginea*
312 distribution representing the anthropogenic disturbances. The probability of *Q. faginea*
313 occurrence decrease in areas close to pine plantations, this result is in agreement with some
314 recent studies (Echeverria et al. 2006; Teixido et al.), which suggested that native forests can be
315 severely affected by the presence of introduced species, particularly, those that are characterized
316 as fast growing and having dispersal abilities. In the Central Pyrenees, *Q. faginea* forests were
317 extensively deforested to increase the amount of arable land, especially for the cultivation of
318 cereals (Lasanta 1989). Most of those lands were abandoned after a few decades of exploitation.
319 During the ultimate 50 year, some of the abandoned lands were reforested with pine plantations
320 by the Spanish forestry service in order to restore the ecological diversity lost through
321 agricultural intensification (Amo et al. 2007), while the remainder has undergone natural re-
322 vegetation, i.e. secondary succession (see below). The introduced plantations spread to the
323 detriment of *Q. faginea* and other species (Amo et al. 2007) and currently, occupy areas that
324 were occupied by native *Q. faginea* forests before. In addition, our results showed that *Q.*
325 *faginea* probability of occurrence decreased in areas close to pastures and were essentially
326 accessible to livestock. In areas that are subject to livestock overgrazing, the regeneration of tree
327 populations is practically impossible (Barbero et al. 1990). Livestock eliminates seedlings, which
328 diminishes recruitment and, consequently, hinders species regeneration (Cierjacks and Hensen
329 2004). At some areas of the Central Pyrenees, the *Q. faginea* forests were used directly as
330 “dehesas” system (Barbero et al. 1990; Montserrat 1990), i.e., a silvo-pastoral system with sparse
331 *Q. faginea* and perennial grass layers. Likewise, the *Q. faginea* forests located between 1200-
332 1600 m a.s.l. were cut down, and summer livestock pastures were created (Lasanta et al. 2005),
333 which has relegated this species to areas that have poor soils and stony hillsides. Furthermore,
334 the *Q. faginea* forests were overexploited for the production of firewood used as source of
335 combustible during that period. In contrast, the occurrence of *Q. faginea* seemed to be favored in
336 areas near livestock roads and of facile accessibility to livestock, although this variable had a
337 weaker effect (low independent explained variance). This fact is probably associated with the
338 high acorn production near livestock roads, as consequence of silvicultural practices (thinning,
339 pruning) applied by forestry service alongside the livestock roads, which maintain the health of

340 *Q. faginea* stands closed to livestock roads. The BMA approach suggested that distance to the
341 nearest village did not affect the occurrence of *Q. faginea*, which might be because of rural
342 exodus campaigned by the abandonment of croplands. Since the early 20th C., a significant
343 progressive decrease in anthropogenic pressure has occurred. Under those circumstances, the
344 exploitation of the land has been more concentrated spatially, and other areas have experienced a
345 reduction in extensive use and an increase in the abandonment of many croplands (Lasanta et al.
346 2000). In abandoned agricultural fields, secondary succession is a natural process in which
347 progressively mature and stable vegetation develops (Gallego et al. 2004; Tatoni et al. 2004). In
348 the Central Pyrenees, secondary succession is well known (Molinillo et al. 1997; Montserrat
349 1990), and the first plants of *Q. faginea* appear in abandoned fields about 100 year after
350 abandonment (Montserrat 1990), which explains why recently abandoned fields are not
351 colonized by *Q. faginea* despite the recent reduction in anthropomorphic pressure in the region
352 (Lasanta and Vicente-Serrano 2006).

353

354 **Conclusion**

355

356 This study has demonstrated that abiotic variables were the main underlying factors that shape
357 the distribution of *Q. faginea* in the Spanish Central Pyrenees. The spatial distribution of this
358 species is determined by abiotic factors operating on a broad scale, i.e. lithology and climate.
359 The anthropogenic factors, particularly the recent addition of plantations and previous livestock
360 pressure, affected negatively the distribution of *Q. faginea* in the study area.

361 Much attention has been focused on the role of abiotic variables as drivers of terrestrial tree
362 species distribution. However, our study exemplified how anthropomorphic changes in land use
363 could affect the distribution of terrestrial tree species, especially in the Mediterranean region
364 where natural ecosystems underwent a large modification caused by changes in the
365 anthropomorphic use of land.

366

367 **Acknowledgments** The Spanish CICYT CGL2008-00655/BOS Project supported this research
368 financially. The first author was also supported through IAMZ-CIHEAM and AECID grants
369 given by the International Centre for Advanced Mediterranean Agronomic Studies and The
370 Spanish Agency for International Cooperation and Development, respectively. We would like to
371 thank MacWhirter for improving the English. We are also grateful to the reviewers of the
372 manuscript for their valuable comments.

373

374 **References**

- 375 Amo L, López P, Martín J (2007) Natural oak forest vs. ancient pine plantations: lizard
376 microhabitat use may explain the effects of ancient reforestations on distribution and
377 conservation of Iberian lizards. *Biodivers Conserv* 16: 3409-3422
- 378 Austin M (2007) Species distribution models and ecological theory: A critical assessment and
379 some possible new approaches. *Ecol Model* 200: 1-19
- 380 Barbero M, Bonin G, Loisel R, Quézel P (1990) Changes and disturbances of forest ecosystems
381 caused by human activities in the western part of the mediterranean basin. *Plant Ecol* 87:
382 151-173
- 383 Ceballos L, Torre JRd (1979) Árboles y arbustos de la España peninsular. ETSIM, Madrid
- 384 CHE (2009) Mapa de núcleos de población 1:50 000. Confederación Hidrográfica del Ebro,
385 Zaragoza, Spain. <http://www.chebro.es/>. Accessed December 2009
- 386 Chevan A, Sutherland M (1991) Hierarchical partitioning. *Am Stat* 45: 90-96
- 387 Cierjacks A, Hensen I (2004) Variation of stand structure and regeneration of Mediterranean
388 holm oak along a grazing intensity gradient. *Plant Ecol* 173: 215-223.
- 389 CITA (2007) Mapa geológico de la comunidad autónoma de Aragón 1:50 000. Centro de
390 Información Territorial de Aragón, Gobierno de Aragón, Zaragoza, Spain.
391 <http://sitar.aragon.es/>. Accessed December 2009
- 392 CITA (2009) Modelo Digital del Terrino de la comunidad autónoma de Aragón. Centro de
393 Información Territorial de Aragón, Gobierno de Aragón, Zaragoza, Spain.
394 <http://sitar.aragon.es/>. Accessed December 2009
- 395 Cliff A, Ord J (1973) Spatial autocorrelation. Pion Press, London
- 396 Congalton RG (1991) A review of assessing the accuracy of classifications of remotely sensed
397 data. *Remote Sens Environ* 37: 35-46
- 398 Corcuera L, Camarero J, Gil-Pelegrin E (2004) Effects of a severe drought on growth and wood
399 anatomical properties of *Quercus faginea*. *IAWA J* 25: 185-204
- 400 Coudun C, Gégout JC, Piedallu C, Rameau JC (2006) Soil nutritional factors improve models of
401 plant species distribution: an illustration with *Acer campestre* (L.) in France. *J Biogeogr*
402 33: 1750-1763
- 403 DMA (2007) Atlas Climático de Aragón. Departamento de Medio Ambiente, Gobierno de
404 Aragón, Zaragoza, Spain.
- 405 DMA (2010) Mapa de vías pecuarias de la comunidad autónoma de Aragón 1:50 000.
406 Departamento de Medioambiente, Gobierno de Aragón, Zaragoza, Spain

- 407 Echeverria C, Coomes D, Salas J, Rey-Benayas JM, Lara A, Newton A (2006) Rapid
408 deforestation and fragmentation of Chilean Temperate Forests. *Biol Conserv* 130: 481-
409 494
- 410 ESRI (2006) ArcGIS Help (9.2). Environmental Systems Research Institute, Inc., New York, USA
- 411 Gallego FJB, Mora RMG, Novo FG (2004) Vegetation dynamics of mediterranean shrublands in
412 former cultural landscape at grazalema mountains, south Spain. *Plant Ecol* 172: 83-94
- 413 Graham CH, Ron SR, Santos JC, Schneider CJ, Moritz C (2004) Integrating phylogenetics and
414 environmental niche models to explore speciation mechanisms dendrobatid frogs.
415 *Evolution* 58: 1781-1793
- 416 Graham MH (2003) Confronting multicollinearity in ecological multiple regression. *Ecology* 84:
417 2809-2815
- 418 Guisan A, Theurillat J, Spichiger R (1995) Effects of climate change on alpine plant diversity
419 and distribution: the modeling and monitoring perspectives. In: Guisan, A., Holten, J.I.,
420 Spichiger, R., Tessier, L. (Eds.), *Potential Ecol. Impacts of Climate Change in the Alps*
421 *and Fennoscandian Mountains*, Conservatoire et Jardin Botaniques de Genève, vol. 8.
422 Switzerland, hors-série, pp 129-135
- 423 Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. *Ecol*
424 *Model* 135: 147-186
- 425 Hargreaves GH (1975) Moisture availability and crop production. *Trans. Am. Soc. Agric. Eng*
426 18: 980-984
- 427 Heegaard E (2002) A model of alpine species distribution in relation to snowmelt time and
428 altitude. *J Veg Sci* 13: 493-504
- 429 Heikkinen RK, Luoto M, Kuussaari M, Pöyry J (2005) New insights into butterfly-environment
430 relationships using partitioning methods. *Proc R Soc B: Biol Sci* 272: 2203-2210
- 431 Himrane H, Camarero JJ, Gil-Pelegrín E (2004) Morphological and ecophysiological variation of
432 the hybrid oak *Quercus subpyrenaica* (*Q. faginea* × *Q. pubescens*). *Trees-Struct Funct*
433 18: 566-575
- 434 Hoeting JA, Madigan D, Raftery AE, Volinsky CT (1999) Bayesian model averaging: A tutorial.
435 *Stat Sci* 14: 382-401
- 436 IGN (2002) Corine 2000: descripción de la nomenclatura del Corine Land Cover al nivel 5°.
437 Actualización 2000. Instituto Geográfico Nacional, Centro Nacional de Información
438 Geográfica, Ministerio de Fomento, Madrid, Spain
- 439 IGN (2006) Plan Nacional de Ortofotografía Aérea 1: 30 000. Instituto Geográfico Nacional,
440 Centro Nacional de Información Geográfica, Ministerio de Fomento, Madrid, Spain

- 441 Jiménez MPS, Fernández PMD, Albertos SM, Sánchez LG (1998) Regiones de procedencia de
442 *Quercus pyrenaica* Willd. *Quercus faginea* Lam. *Quercus canariensis* Willd. OAPN,
443 Madrid
- 444 Lansac AR, Zaballos JP, Martin A (1994) Seasonal water potential changes and proline
445 accumulation in mediterranean shrubland species. *Vegetatio* 113: 141-154
- 446 Lasanta T. 1989. Evolución reciente de la agricultura de montaña. Geoforma Edición, Logroño
- 447 Lasanta T (2002) Los sistemas de gestión en el Pirineo Central español durante el siglo XX: del
448 aprovechamiento global de los recursos a la descoordinación espacial en los usos del
449 suelo. *Ager* 2: 173-195
- 450 Lasanta T, Arnáez J, Errea MP, Ortigosa L, Ruiz-Flaño P (2009) Mountain pastures,
451 environmental degradation, and landscape remediation: the example of a Mediterranean
452 policy initiative. *Appl Geogr* 29: 308-319
- 453 Lasanta T, Vicente-Serrano S (2006) Factores en la variabilidad espacial de los cambios de
454 cubierta vegetal en el Pirineo. *Cuad Invest Geogr* 32: 57-80
- 455 Lasanta T, Vicente-Serrano S, Cuadrat J (2000) Marginación productiva y la recuperación de la
456 cubierta vegetal en el Pirineo: un caso de estudio en el valle de Borau. *Bol AGE* 29: 5-28
- 457 Lasanta T, Vicente-Serrano S, Guadrat J (2005) Spatial temporal variability of the plant
458 landscape in the mediterranean highlands due to the abandonment of traditional land
459 uses: a study of the Spanish Central Pyrenees. *Appl. Geogr* 25: 47-65
- 460 Legendre P (1993) Spatial Autocorrelation: Trouble or New Paradigm? *Ecology* 74: 1659-1673.
- 461 Lehmann A, Leathwick JR, Overton JM (2002) Assessing New Zealand fern diversity from
462 spatial predictions of species assemblages. *Biodivers Conserv* 11: 2217-2238
- 463 Loidi J, Herrera M (1990) The *Quereus pubescens* and *Quereus faginea* forests in the Basque
464 Country (Spain): distribution and typology in relation to climatic factors. *Plant Ecol* 90:
465 81-92
- 466 Luoto M, Heikkinen RK, Pöyry J, Saarinen K (2006) Determinants of the biogeographical
467 distribution of butterflies in boreal regions. *J Biogeogr* 33: 1764-1778
- 468 Madigan D, Raftery AE (1994) Model selection and accounting for model uncertainty in
469 graphical models using occam's window. *J Am Stat Assoc* 89: 1535-1546
- 470 Maltez-Mouro S, García L, Freitas H (2009) Influence of forest structure and environmental
471 variables on recruit survival and performance of two Mediterranean tree species (*Quercus*
472 *faginea* L. and *Q. suber* Lam.). *Eur J For Res* 128: 27-36
- 473 Mediavilla S, Escudero A (2004) Stomatal responses to drought of mature trees and seedlings of
474 two co-occurring Mediterranean oaks. *For Ecol Manag* 187: 281-294

- 475 Millington J, Perry G, Romero-Calcerrada R (2007) Regression techniques for examining land
476 use/cover change: a case study of a mediterranean landscape. *Ecosystems* 10: 562-578
- 477 MMA (2007) Tercer inventario forestal nacional (IFN3) 1:50 000. Ministerio de Medio
478 Ambiente y Medio Rural y Marino, Madrid, Spain
- 479 Molinillo M, Lasanta T, García-Ruiz JM (1997) Managing mountainous degraded landscapes
480 after farmland abandonment in the Central Spanish Pyrenees. *Environ Manag* 21: 587-
481 598
- 482 Montserrat G (1990) Estudio de la colonización vegetal de los campos abandonados del valle de
483 Aísa (Jaca, Huesca), Informe del proyecto LUCDEME: Erosión y colonización vegetal
484 en campos abandonados, 77p, Jaca
- 485 Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity
486 hotspots for conservation priorities. *Nature* 403: 853-858
- 487 Nally RM (2000) Regression and model-building in conservation biology, biogeography and
488 ecology: The distinction between – and reconciliation of – ‘predictive’ and ‘explanatory’
489 models. *Biodivers Conserv* 9: 655-671
- 490 Nally RM, Vries LD, Thomson JR (2008) Are replanted floodplain forests in southeastern
491 Australia providing bird biodiversity benefits? *Restor Ecol* 18: 85-94
- 492 Perry DA (1998) Landscape pattern and forest pest. *Northwest Environ. J.* 4: 213-228
- 493 Pilar CD, Gabriel MM (1998) Phenological pattern of fifteen Mediterranean phanerophytes
494 from shape *Quercus ilex* communities of NE-Spain. *Plant Ecology* 139: 103-112
- 495 Purves DW, Zavala MA, Ogle K, Prieto F, Benayas JMR (2007) Environmental heterogeneity,
496 bird-mediated directed dispersal, and oak woodland dynamics in mediterranean Spain.
497 *Ecol Monogr* 77: 77-97
- 498 Raftery AE, Madigan D, Hoeting JA (1997) Bayesian model averaging for linear regression
499 models. *J Ame Stat Assoc* 92: 179-191
- 500 Raftery E, Hoeting J, Volinsky C, Painter I, Yeung K (2009) BMA: Bayesian model averaging.
501 R package version 3.12. <http://CRAN.R-project.org/package=BMA>
- 502 R Development Core Team (2009) R: A language and environment for statistical
503 computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-
504 900051-07-0, URL <http://www.R-project.org>
- 505 Rey Benayas JM, Navarro J, Espigares T, Nicolau JM, Zavala MA (2005) Effects of artificial
506 shading and weed mowing in reforestation of Mediterranean abandoned cropland with
507 contrasting *Quercus* species. *For Ecol Manag* 212: 302-314

508 Sánchez de Dios R, Benito-Garzón M, Sainz-Ollero H (2006) Hybrid zones between two
509 european oaks: a plant community approach. *Plant Ecol* 187: 109-125

510 Segurado P, Araújo MB (2004) An evaluation of methods for modelling species distributions. *J*
511 *Biogeogr* 31: 1555-1568.

512 Tatoni T, Médail F, Roche P, Barbero M (2004) The impact of changes in land use on ecological
513 patterns in Provence (Mediterranean France). In: Mazzoleni, S., Di Pasquale, G., Di
514 Martino, P.,ego, F. and Mulligan, M., Editors, *Recent dynamics of Mediterranean*
515 *vegetation and landscape*, John Wiley and Sons, London (2004), pp 107-120

516 Teixido AL, Quintanilla LG, Carreño F, Gutiérrez D (2010) Impacts of changes in land use and
517 fragmentation patterns on Atlantic coastal forests in northern Spain. *J Environ Manag* 91:
518 879-886

519 Thomson JR, Nally RM, Fleishman E, Horrocks G (2007) Predicting bird species distributions in
520 reconstructed landscapes. *Conserv Biol* 21: 752-766

521 Thuiller W, Araújo MB, Lavorel S (2004) Do we need land-cover data to model species
522 distributions in Europe? *J Biogeogr* 31: 353-361

523 Viallefont V, Raftery AE, Richardson S (2001) Variable selection and bayesian model averaging
524 in case-control studies. *Stat Med* 20: 3215-3230

525 Vicente-Serrano SM, Lasanta T, Romo A (2004) Analysis of spatial and temporal evolution of
526 vegetation cover in the Spanish Central Pyrenees: role of human management. *Environ*
527 *Manag* 34: 802-818

528 Walsh C, Nally RM (2008) hier.part: Hierarchical partitioning. R package version 1.0-3

529 Wintle BA, McCarthy MA, Volinsky CT, Kavanagh RP (2003) The use of bayesian model
530 averaging to better represent uncertainty in ecological models. *Conserv Biol* 17: 1579-
531 1590

532

533

534

535

536

537

538

539

540

541 **Table 1** This table contains the explanatory variables introduced in the BMA (Variables), posterior
 542 probability that a variable had a nonzero coefficient $\Pr(\beta_{vs} \neq 0)$, posterior means and standard deviation
 543 (PM+SD) for the coefficients associated with each variable, and independent explained variance (%I) for
 544 the explanatory variables with $\Pr(\beta_{vs} \neq 0) > 0.75$ (key factors, bold) is explained as a percentage of the
 545 total explained variance for the full model.

546 .

Variables	Pr ($\beta_{vs} \neq 0$)	PM+ SD	%I
Lithology	100%	0.632±0.190	17.023
Aspect	24.5%	-0.001±0.018	0
Slope	100%	0.324±0.031	16.361
Curvature	01.3%	0.001±0.015	0
Water balance	100%	-0.354±0.000	33.363
Number of frosts days	05.0%	0.003±0.001	0
Cost distance to pastures	100%	0.014±0.000	10.741
Cost distance to the livestock roads	100%	-0.017±0.000	08.302
Distance to the nearest mine	11.7%	-0.001±0.000	0
Distance to the nearest village	03.8%	-0.002±0.000	0
Distance to the nearest plantation	94.5%	0.159±0.172	14.207

547

548

549

550

551

552

553

554

555

556

557

558

559

560

561

562

563

564

565

566

567 **Figure1.** (a) The Central Pyrenees, north of the Aragon Autonomous Community, northeastern Spain. (b) Digital
568 Elevation Model of the study area, grey scale indicates the elevation range (m) above sea level. White patches
569 represent the *Q. faginea* distribution.

570
571
572
573
574
575

