Recruitment patterns of four tree species along elevation gradients in Mediterranean mountains: not only climate matters

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Abstract

Evidence of tree regeneration failure of some species in the Iberian Peninsula forests warns us about the impact that the global change may exert on the preservation of Mediterranean forests, such as we know them. Predictions agree about an exacerbation of the summer drought there, acknowledged as the main limiting factor for the recruits' survival. On the other hand, many studies have also proved the relevant role that local heterogeneity has over the spatial distribution of forest species recruitment by providing safe sites. Therefore, to unravel how climate interacts with local factors over juveniles' performance seems crucial for the design of successful management strategies that allow facing the global warming. Here, we surveyed the natural recruitment of four dominant tree species in seven mountainous regions in the Iberian Peninsula, along entire elevational ranges as surrogates of their climatic ranges. Two of them have alpine and temperate distributions with populations at their rear edge in the Spanish mountains: *Fagus sylvatica* and *Pinus uncinata*; and the other two have a genuine Mediterranean distribution: *Quercus ilex* and *P. nigra*. Our main goal was to analyze for each species the effect of climate, local factors (*i. e.* light availability, stand structure and ground cover) and the interactions among them to identify the main drivers leading the regeneration process, assessed in terms of presence, abundance and mean annual growth of juveniles. The results showed different environmental factors determining the recruitment patterns of each species. Nevertheless, they highlighted the pervasive role exerted by both climate and fine scale factors, particularly the co-occurring vegetation on recruits' abundance, and the light availability on their growth. Moreover, we found some interactions among annual mean temperature and local factors, suggesting that climate and local heterogeneity act hierarchically, *i. e.* the local conditions may mitigate or exacerbate the impact of climate on juveniles. These results advocate for further research to increase our knowledge on the complex net of

42   interactions among factors involved in recruitment at different scales, which in turn should be

43   taken into account and incorporated in forthcoming management strategies.

44   **Key words:** climatic gradient; forest regeneration; juvenile distribution; juvenile performance;

45   local heterogeneity; Mediterranean forests.

46   **Abbreviations:** S1: seedlings, from one to five years; S2: saplings, over five years. ZIP: Zero-

47   Inflated Poisson distribution.

48

1. Introduction

The Mediterranean Basin is one of the most vulnerable areas for biodiversity loss due to climate warming (Bakkenes et al., 2002; Thuiller et al., 2005). Predictions agree that increasing aridity and temperature, and more frequent extreme climatic events will occur there (Giorgi and Lionello, 2008; Nogués-Bravo et al., 2008). Therefore, since summer drought is acknowledged as the main limiting factor for the performance of Mediterranean species, its exacerbation would be critical, especially for those species that have there their southernmost distribution limit (Castro et al., 2004; Hampe and Petit, 2005; Benavides et al., 2013)

Emergence and survival during the earliest life stages are critical for population dynamics (Harper, 1977). In fact, juveniles of woody species are considered to be more susceptible to climate and particularly to extreme events (Castro et al., 2005), responding quicker than adults to environmental changes (Lloret et al., 2009). Thus, viability and persistence of these populations rely heavily on the success of the current recruitment under the ongoing changing conditions. In Mediterranean areas, the coincidence of drought with high temperatures makes the summer season a critical bottleneck for life. Hence, recruitment in Mediterranean climate-type forests is episodic and depends on the appearance of favourable windows, *i. e.* rare wet summers entail the opportunity for establishment (Matías et al., 2012); whereas episodic events of severe drought occasionally cause massive seedlings' mortality (Herrero, 2012). In this line, recent studies carried out at large spatial scale using the data from the Spanish National Forest Inventory, revealed a relatively widespread regeneration failure in many forest stands, mainly in those dominated by pines like *Pinus sylvestris*, *P. uncinata*, *P. nigra*, species that naturally occur at the Iberian mountains (Vayreda et al., 2013; Carnicer et al., 2014; Tíscar and Linares, 2014). Additionally, other studies have shown a lack of regeneration of these and other species at their rear edge of their distributions (Peñuelas and Boada, 2003; Peñuelas et al., 2007;

73   Benavides et al., 2013), sometimes accompanied by a gradual replacement with more heat-,

74   drought- and shade-tolerant species, like *Q. ilex*, that becomes a great competitor under the

75   current climate and management changes (Galiano et al., 2010; Coll et al,. 2013; Carnicer et al.,

76   2014).

77   In parallel, encouraging studies have reported demographic responses that provide stabilizing

78   processes (either by compensation or mitigation) and advocate resilience and stability in

79   populations against the global warming (Doak and Morris, 2010; Lloret et al., 2012, 2013). For

80   instance, Benavides et al. (2015) found higher growth rates at low elevations of different tree

81   species along altitudinal gradients, despite a lower survival rate of recruits there. They

82   suggested that these higher individual growths during seedling life stage bestow more chances

83   to survive because they may overcome quicker this critical life stage, in terms of climate

84   sensitivity and damage from browsers (Zamora et al., 2001), counterbalancing at population

85   level the negative effect of global warming at the trailing edges. Moreover, they found a

86   diminishing sensitivity to climatic conditions of the successive cohorts of juveniles (*i. e.*

87   seedlings more sensitive than saplings), becoming relevant other fine scale factors that

88   attenuate the effects of climate on saplings performance. Within this context, other studies in

89   Mediterranean areas highlighted the decisive role exerted by these local environmental

90   conditions (biotic and abiotic factors) over the juveniles' survival and growth, leading to

91   aggregated patterns in safe sites (Quero et al., 2011; Ameztegui and Coll, 2015). In particular,

92   the nurse role of shrubs, ameliorating harsh conditions imposed by summer drought or

93   herbivore damages, is quite acknowledged in these areas (*e.g*. Gómez-Aparicio et al., 2004;

94   Quero et al., 2011).

95   Understanding how climate interacts with local factors over juveniles' performance in order to

96   mitigate global warming and propose management strategies to face it, is a research priority

97   that, so far, got little attention and effort. Moreover, it is especially interesting to compare the

98   performance of species at their rear edge (more vulnerable facing climatic changes) with others

99   at the center of their ranges to identify global responses to current warming, to predict future

100   species distributions and community compositions in Mediterranean areas, and to design

101   strategies to mitigate the impact of climate change over standing forests. In the present study,

102   we contribute to this goal analyzing the main factors that influence the regeneration of four of

103   the main dominant tree species in the Iberian Peninsula forests. Two of them have alpine and

104   temperate distributions with populations at their rear edge in the Spanish mountain ranges:

105   Mountain pine (*Pinus uncinata* Ram.) and European beech (*Fagus sylvatica* L.); and the other

106   two species have a typical Mediterranean distribution: Holm oak (*Quercus ilex* L.), with an

107   ample presence in the Iberian Peninsula, and European black pine (*Pinus nigra* Arn. ssp.

108   s*alzmannii* (Dunal) Franco), a Mediterranean mountainous pine. In particular, we studied the

109   effect of climate, local factors and the interactions among them to identify the main drivers

110   leading the regeneration process, assessed in terms of presence (occurrence), abundance and

111   mean annual growth of juveniles. We surveyed their entire elevational range in mountainous

112   areas as surrogates of the climatic range that each species experiences along its latitudinal

113   distribution. Using elevation as a surrogate for climate range is a useful tool to study responses

114   under different climatic scenarios, minimizing differences due to genetic variability and other

115   potential confounding variables determined by the specific characteristics of a region (Körner,

116   2007).

117

118   **2. Material and Methods**

119   *2.1. Study sites*

120   Data gathering was conducted in seven mountainous areas across Spain in late spring and

121   summer in 2010 and 2011 (Fig. 1). The entire sampling required two years, but each site was

122   sampled only once. For every species we sampled two pure natural forest sites located in

123   different mountain ranges, along five elevational transects. The stands had neither visible signs

124   of plantations, nor any evidence of management that could affect the current recruitment. The

125   upper and the lower transects were placed in the ecotones of each target species with the

126   adjacent communities. In the majority of the cases, the upper transects were located at the

127   treeline of these mountain ranges (*i. e.* transition from the uppermost closed forests to the

128   treeless mountainous vegetation). The three intermediate levels were located within the

129   altitudinal range of each species, with at least 100 m difference in altitude among them. Those

130   at the ends were located near the boundary with the ecotones, and the intermediate one in the

131   middle of the range. For *Quercus ilex*'s sampling, we only considered the three superior levels

132   (transects) as this species has no low elevation limit in the Iberian mountains. Table 1 shows

133   the main characteristics of the study sites.

134

135   *2.2. Recruitment sampling and measurements of environmental variables*

136   We established six plots within each elevational transect, separated at least 100 m. Three plots

137   were randomly located under closed canopy, and the other three in more open areas to include

138   contrasting light conditions within each forest and elevation, avoiding ravines, boulders or

139   other geomorphologic elements which could bias our measurements ameliorating the effect of

140   climate by local physiography (Dobrowski, 2011). In the centre of every plot we recorded the

141   number of juveniles in a 4 x 4 m plot (16 m^2-sized), recording the number per square meter, *i.*

142   *e.* each plot encompassed 16 observations of juveniles density from its 16 subplots of 1 m^2 size.

143   We counted the seedlings with at least one year, *i. e.* survivors after the first summer drought,

144   considered the main bottleneck for recruitment in Mediterranean areas (Jordano and Herrera,

145   1995; Castro et al., 2004; Linares and Tíscar, 2010), up to juveniles 1.50 m tall. Juveniles of

146 resprouting species (*Q. ilex* and *F. sylvatica*) were correctly identified from vegetative

147 offsprings (not considered in this study), following Espelta et al. (1995). We estimated their age

148 by counting the terminal bud scars (internodes) along the main stem and we sorted them into

149 two different age classes (Espelta et al., 1995), assuming a different sensitivity to the

150 environment (Collins and Carson, 2004; Benavides et al., 2015): S1: seedlings -from one to

151 five years-; S2: saplings -over five years-; (hereafter *juvenile* is only used when age is not

152 relevant and both age classes are considered). We identified the current shoot (not considered

153 for the study as the growing season was not over) and we measured the primary shoot growth

154 of the main stem not damaged by herbivores in previous years (growths occurred in 2007, 2008

155 and 2009), and averaged them. Shoot growth is a good indicator of environmental favorability

156 (Willms et al., 1998), as well as the impact of drought conditions on plant growth (Mutke et al.,

157 2003). Hence, we used mean annual growth as a proxy of their individual performance.

158 To evaluate the effects of climate, we rendered elevation and latitude data of each plot into

159 climatic variables using the Digital Climatic Atlas of the Iberian Peninsula (Ninyerola et al.,

160 2005), specifically we obtained the annual mean temperature (ºC) and mean annual

161 precipitation (mm).

162 The local environmental variables were selected assuming their influence on the recruitment,

163 either by modifying the physical environment or by competing for resources (in the case of co-

164 occurring vegetation). At plot level, we measured the slope that may hamper the establishment,

165 and the light availability, crucial for plant development. Light was assessed as the global site

166 factor (GSF), defined as the proportion of global solar radiation at a given location relative to

167 that in the open. To assess it, we took one hemispherical photograph in the centre of each plot

168 at 50 cm above the ground and we analyzed the images using the software HemiView 2.1

169 (Delta-T Devices, UK). In terms of biotic conditions at plot level, all adult trees (diameter at

170 breast height, dbh, over 7.5 cm) within a 10 m radius around the regeneration frame were

171 mapped and we measured their dbh, and then calculated the basal area (expressed as m²/ha) per

172 plot as an index of competition with adult trees. This radius size was consistent with that used

173 in other tree competition studies (He and Duncan, 2000; Gómez-Aparicio et al., 2011).

174 Finally, at microhabitat scale, we visually estimated in every 1-m² subplot the cover in

175 percentage of rocks that may physically impede juveniles thriving, and the cover of shrubs and

176 herbs, that may facilitate or compete with them. Moreover, a potential fecundity index was

177 assessed for each subplot, considering the conspecific adult trees previously mapped within the

178 10 m radius, together with those bigger than 20 cm of dbh located between 10-20 m from the

179 centre of the plot. This unitless index has two components (see Ribbens et al., 2004): one

180 related to the amount of seeds that an adult tree can produce (seed rain), proportional to the tree

181 size (dbh); and another that accounts for the seed dispersal capacity and assumes an

182 exponentially decline as the distance between a particular tree and the centre of each subplot

183 increases (Ribbens et al., 2004; Gómez-Aparicio et al., 2011).

184 $FI_i = \sum_{j=1}^{n} dbh_j^2 . e^{-dist_{ij}}$

185 Where, FI_i is the fecundity index for subplot i within a plot with n trees ($j = 1, 2, …n$), and $dist_{ij}$

186 is the distance of tree j to the centre of subplot i.

187

188 *2.3. Statistical analyses*

189 The density of individuals of both age classes (seedlings and saplings) along the elevation for

190 every species was compared using the Mann-Whitney U test. Similarly, the mean annual

191 growth of each species were compared along the five different transects (elevational levels)

192 using one-way ANOVA after a log-transformation.

193 Next, we evaluated the effects of climate (mean annual temperature and precipitation) and local

194 factors on the density and mean annual growth of juveniles of each species. Previous to the

195 modelling process, we carried out an analysis of correlation among the local variables to detect

196 multicollinearity among them (Zuur et al., 2010), (see Supplementary Information Table A.1).

197 When two variables were highly correlated ($\rho > 0.4$) for at least two species, we removed from

198 the pool the variable with less direct implications on recruitment. In particular, we discarded

199 basal area and slope because they were highly correlated to GSF, and to rock cover and

200 climatic variables, respectively. Basal area was considered an index for competition with adult

201 trees, and since competition among adults and juveniles is expected to be mainly related to light

202 availability, we kept GSF. Both rocks and slope impair physically the establishment of recruits,

203 however rockiness data were taken at subplot level and slope for the whole plot being less

204 accurate and precise than the former. In summary, we kept as explanatory variables, together

205 with temperature and precipitation, the cover of herbs, shrubs, rocks, GSF and FI (the latter

206 only considered for density data models, as it is not relevant for growth). In the case of *F.*

207 *sylvatica*, we had scarce observations and we decided to simplify more the models. Hence, we

208 discarded also the cover of herbs and shrubs because of their overall lack in most of the plots

209 and their high correlation with light availability (GSF). The interactions of annual temperature

210 with GSF, annual precipitation, and the cover of understorey vegetation were included in the

211 model, as well as the quadratic term of temperature to consider non-monotonic responses along

212 the gradient. Non-linear responses to other variables were not considered to avoid a great

213 complexity of the models.

214 Different statistical methods have been previously used to model regeneration and figure out

215 the environmental factors that mainly drive this process (a review in Moreno-Fernández et al.,

216 2015). In the present study, the density data of juveniles per m^2 (data at subplot level) of each

217 species followed a Zero-Inflated Poisson distribution (ZIP), as no recruit was found in a large

218 amount of the subplots surveyed, specifically in 72.2%, 80.4%, 93.9% and 76.1% of the

219   subplots for *P. uncinata*, *P. nigra*, *F. sylvatica* and *Q. ilex* respectively. Models fitting ZIP

220   distributions (ZIP models) account for this excess of zeros avoiding the underestimation of the

221   number of zeros and the overestimation of large count occurrence (Hall, 2000; Affleck, 2006;

222   Fortin and De Blois, 2007; Benavides et al., 2013). They consist of a two-step analysis, a

223   binomial distribution model analyzing the occurrence (observing or not recruits), and a Poisson

224   distribution model, conditional on the first, analyzing the abundance (number of recruits), both

225   processes evaluated all at once. Here, we decided to neglect the age class and pool seedlings

226   and saplings to increase the sample size due to the low number of observations in some plots

227   and the number of parameters to estimate (the environmental variables affecting both the

228   occurrence and abundance independently). On the other hand, the data of mean annual growth

229   of juveniles followed a normal distribution after a log-transformation, and due to the larger

230   sample size of this response variable (data at individual level) we run the analyses for each age

231   class separately.

232   We added random components into the intercepts of the linear predictors of the models (Hall,

233   2000) due to the hierarchical structure of our data, with likely different level of correlation

234   among observations within the same subplot (for growth data), plot, transect or site. We

235   considered 'site' as a fixed effect, as this variable only had two levels, therefore not enough to

236   estimate among-site variance (Bolker et al., 2009). The rest of the nested design (subplots

237   within a plot, plots within a transect) was considered in the random component for analysis of

238   mean annual growth. However, the statistical procedure used for ZIP modelling recommends

239   the use of just one random effect due to the complexity of the likelihood function (that includes

240   both processes: the binomial and Poisson models) and problems detected with the convergence

241   of the model. Thus, we preliminary fit the saturated models including both effects separately,

242   transect and plot, and we chose the model which harbored more variability (*i. e.* plot) using the

243   Akaike´s Information Criterion (AIC). Concerning the explanatory variables (fixed effects), we

244   selected the best model following the principle of parsimony to find the simplest model that

245   was not significantly worse than any more complicated in terms of AIC. We assumed that a

246   model was better than the previous one when the improvement of AIC was higher than two

247   units, *i. e.* at least two units smaller (Burnham and Anderson, 2002). We started by running the

248   saturated model, and then we removed one non-significant variable each time (Zuur et al.,

249   2009).

250   The Zero-Inflated Poisson Mixed Models (ZIP models) for density data and the Generalized

251   Linear Mixed Models (GLMM) for growth data were both fit for each species separately using

252   the SAS procedure NLMIXED (Pinheiro and Bates, 1995; SAS Institute Inc. 2008. SAS/STAT

253   9.2) that allows the optimization of the customized likelihood function of the ZIP models.

254

255   **3. Results**

256   *3.1. Abundance and growth data across the altitudinal levels*

257   The total amount of juveniles recorded and used in the occurrence and abundance analyses

258   were 1541 juveniles, sorted into 259 of *Q. ilex*, 564 of *P. nigra*, 608 of *P. uncinata* and 110 of

259   *F. sylvatica*. The altitudinal distribution of juveniles (Fig. 2a) showed that seedlings (S1) of

260   both Mediterranean species, *Q. ilex* and *P. nigra*, appeared mainly at higher altitudes compared

261   to the saplings (S2), whose distributions were more regularly spread along the entire altitudinal

262   range. For the other two species, there was no significant difference between age classes, with a

263   distribution slightly skewed towards higher altitudes in the case of *P. uncinata*, while

264   individuals of *F. sylvatica* appeared mainly in the lower areas of its range.

265   For growth analyses, and after excluding the individuals damaged, we counted 1394 juveniles,

266   sorted into 233, 487, 584 and 90 juveniles of *Q. ilex*, *P. nigra*, *P. uncinata* and *F. sylvatica*,

267   respectively. The annual mean growth averaged per species and transect showed a different

268   pattern between the age classes (Fig. 2b). Seedlings showed a generalized lower growth at

269 higher elevations (but for *Q. ilex*), while the opposite trend was found in saplings, except for *F.*

270 *sylvatica*, although with non-significant variation along elevation.

271

272   *3.2. Factors affecting occurrence, abundance and growth patterns of regeneration*

273 The variables considered in this study, both climatic and local, barely explained the occurrence

274 of recruits, but for *P. uncinata*; while abundance and growth of juveniles were affected by the

275 variables considered, to a greater or lesser extent (Tables 2 and 3).

276 The ZIP models showed that the abundance of juveniles of every species was significantly

277 influenced by the climatic variables (temperature and/or precipitation). The selected models for

278 the two species with a northerner distribution, *F. sylvatica* and *P. uncinata*, showed a clear

279 quadratic effect of mean annual temperature (hollow-shaped curve for *F. sylvatica* and hump-

280 shaped for the *P. uncinata*); while the model for *Q. ilex* showed a positive linear effect of

281 temperature on juveniles' abundance. Precipitation favored the density of juveniles of *F.*

282 *sylvatica* and *P. nigra*, but affected negatively the abundance of *Q. ilex* and the occurrence of

283 *P. uncinata* recruits (Table 2).

284 The models also showed the direct influence of some local factors related to the co-occurring

285 vegetation on the recruitment pattern (Table 2). We found a negative effect of the cover of

286 herbaceous plants on the abundance of *Q. ilex* and *P. uncinata*. In addition, we detected indirect

287 effects of these biotic variables, interacting with temperature, like the effect of the shrub layer

288 on density of *P. uncinata* and occurrence of *P. nigra* juveniles, and the effect of herbs on the

289 abundance of the latter (Fig. 3). These interactions showed that moderate cover of shrubs

290 (<50%) facilitated the presence of juveniles of both pine species under not very stressful

291 temperatures; and that the cover of herbs impaired the abundance of *P. nigra* juveniles,

292 especially at high temperatures (more heat stress).

293 The GLMMs showed that GSF was the variable that affected the mean annual growth of

294 juveniles in most of the cases, together with climatic variables (Table 3). However, the

295 relationships were age- and species-specific. Juveniles of *P. uncinata* were affected by the

296 interaction of temperature and GSF, with a better performance in gaps with higher temperature,

297 or in cooler places under canopy (Fig. 4). S2 were also favored by annual precipitation and the

298 lack of rocks (Table 3). Growth of *P. nigra* seedlings (S1) were positively affected by

299 temperature and GSF. Light favored also the annual mean growth of *Q. ilex* saplings (S2);

300 while S1 were affected by temperature interacting with annual precipitation (Fig. 4). This

301 interaction showed that the growth increased at higher temperatures when the precipitation was

302 also high, and with low both precipitation and temperature. Finally, the models obtained for *F.*

303 *sylvatica* did not capture any variable affecting growth, but the rockiness hampering the growth

304 of S1, although the sample size of this species was much lower compared to the other species.

305

306 **4. Discussion**

307 The results of the present study showed the key role exerted by both climate and fine scale

308 factors on the distribution and performance of four tree species recruitment along altitudinal

309 ranges, being the direction and relevance of these effects species-specific according to the

310 idiosyncrasy of each species. They also highlighted that the use of complete altitudinal

311 gradients gives valuable information about how a species thrives along complete climate

312 gradients, and why it can be considered a very efficient alternative to experimental settings as

313 surrogates of performance of tree species along the global distribution range (Körner, 2007).

314 Besides, they pointed at the use of coexisting genuine Mediterranean species together with

315 species at their rear edge to infer hints on recruitment strategies and future composition of

316 forest communities.

317

318   *4.1. Relationship between climate and juvenile patterns along altitudinal gradients*

319   The two Mediterranean species, *Quercus ilex* and *Pinus nigra* presented an asymmetrical

320   distribution, with the young cohort (seedlings) being more abundant at higher elevations than

321   the old one (saplings). This suggests better conditions to survive the first years at higher

322   elevations, likely in terms of precipitation. Recent studies carried out in the Iberian Peninsula

323   showed an upward shift of *Q. ilex* recruits towards cooler areas (Urbieta et al., 2011; Vayreda

324   et al., 2013; Carnicer et al., 2014), as seedlings appeared negatively affected by low soil

325   moisture and increased temperature (Caldeira et al., 2014). Accordingly, its growth model in

326   this study showed that seedlings grew less in places more prone to droughts (warmer and drier).

327   The models for *P. nigra* showed that temperature boosted seedling growth, but it was annual

328   precipitation the climatic variable that significantly favored the abundance of juveniles. This

329   last result concurs with other studies pointing out that water supply, especially in early summer,

330   is the main limiting factor for the regeneration of this species (Urbieta et al., 2011; Vayreda et

331   al., 2013; Tíscar and Linares, 2011).

332   Nevertheless, the ZIP model for *Q. ilex* showed a positive effect exerted by temperature and

333   negative by precipitation over the abundance of juveniles, which runs in the opposite direction.

334   The divergences with the former studies may be related to the impossibility for analyzing both

335   cohorts separately, and most likely, due to the elevational range surveyed in this study that did

336   not cover the whole climatic gradient of this species in the Iberian Peninsula. Here, we just

337   considered the three upper transects (over 700 m a.s.l.) because there was no low limit for this

338   species.

339   The response of the other species to climate, the non-genuine Mediterranean, did not exhibit a

340   common pattern. Juveniles of *P. uncinata,* in agreement with some previous studies, were

341   negatively affected by the annual temperature, growing more at higher elevations (Grau et al.,

342   2013; but see Ameztegui and Coll, 2013), and presented a hump-shaped relationship with the

343   abundance of juveniles (Coll et al., 2013). This non-linear relationship implies the existence of

344   an optimum where juveniles peaked, that occurred at slightly higher altitudes than the mean

345   altitudinal range of the stands, and decreased very rapidly as altitude approached the treeline.

346   Similar asymmetric presence of elevational optima of juveniles upwards, compared to the

347   adults' mean distribution, have already been detected not only for this species (Batllori and

348   Gutiérrez, 2008), but also for others (Gworek et al., 2007; Lenoir et al., 2009; Benavides et al.,

349   2013; but see Rabasa et al., 2013). These studies suggest the existence of an ongoing upward

350   shift driven by warming, that may act either directly on the recruitment of the study species or

351   indirectly by limiting its competitive ability compared to other species more heat- and drought-

352   tolerant (Lenoir et al., 2010; Ameztegui and Coll, 2013). Moreover, annual precipitation

353   appeared as an important factor, although it exerted a differential effect over the occurrence of

354   juveniles (negative) and their performance (positive over the growth). This contradictory result

355   might be related to indirect effects of local factors that impair the recruitment, but once

356   seedlings are recruited, they performed better with high precipitation. However, we

357   acknowledge that this claim should be taken with caution because extrapolations of climatic

358   variables, like precipitation, harbour great uncertainty at these high elevations due to the scarce

359   meteorological stations up there (Benavides et al., 2007).

360   The outcomes for *F. sylvatica* showed the overall lack of recruitment with a small amount of

361   juveniles. Likewise, Vayreda et al. (2013) who analyzed the data from the Spanish National

362   Forest Inventory, found low abundance or no saplings in around 70% of the total plots where

363   this species dominates in the canopy. These results reflected the difficulties that this species

364   might be experiencing in these southern marginal areas of its distribution, where summer

365   drought greatly constraints *Fagus* recruitment (Kunstler et al., 2007, Silva et al., 2012). In this

366   direction, we found that precipitation favored the abundance of juveniles, as earlier studies

367   carried out in other European countries did (Kunstler et al., 2007; Klopcic et al., 2012, Silva et

al., 2012). Nevertheless, we found a hollow-shaped relationship of juvenile abundance with the annual temperature, caused by a surprisingly high density of them at low elevations. This unexpected result in the trailing area of the species distribution disagreed with previous studies conducted in north-eastern Spain, which evidenced an upslope shift of this species during the last century (Jump et al., 2007; Peñuelas et al., 2007). We infer that other factors, different from climate, underlie this trend and conceal the species primary response to climate in our study sites. Indeed, the lower transects of these sites had different stand structure, probably due to a different former management, with lower densities of multi-stemmed individuals than at mid-upper elevations (See Supplementary Information Fig. A2).

4.2. Downscaling: the importance of local factors and its interaction with climate

Recruitment is strongly conditioned by the spatial local heterogeneity as well. The structure and composition of the stand (adult trees) determines the quantity of seed rain, and together with the understorey vegetation and micro-topographic conditions, they determine the regeneration niche (Grubb 1977), *i. e.* the fine-scaled environment that allows juveniles to thrive.

In our study, considering the variables related to the stand structure, *i. e.* GSF (light availability) and the fecundity index (proxy for the potential seed rain), we found that the light availability favored the presence of *P. uncinata* juveniles, in accordance with its shade-intolerance nature (Batllori et al., 2009). However, its main effect was exerted over the growth of juveniles, as earlier studies reported in Mediterranean mountains (Gómez-Aparicio et al., 2008; Matías et al., 2011; Ameztegui and Coll, 2011, 2013; Barbeito et al., 2012; Benavides et al., 2013; Grau et al., 2013; Caldeira et al., 2014). In particular, the growth of *P. nigra* seedlings and *Q. ilex* saplings were both boosted by light; and its positive effect over the juveniles of *P. uncinata* was exacerbated by temperature, appearing higher growths in the gaps (high light availability) of warmer places (lower elevations). On the other hand, we found no

393   effect of the fecundity index on the density of juveniles of any study species. This suggests that,

394   since our forest stands were monospecific, the seed rain and dispersal were efficient enough to

395   reach every point and not to limit the recruitment.

396   The interaction of the understorey vegetation with the presence of juveniles was evidenced for

397   the study species, but for *F. sylvatica* sites where the understorey vegetation was rather

398   suppressed. Many works have previously investigated plant-plant interactions along gradients

399   of environmental severity (Callaway and Walker, 1997), with compelling evidence about the

400   nurse effect exerted by shrubs on recruits in Mediterranean and at high elevation areas (Castro

401   et al., 2004; Batllori and Gutierrez, 2008, 2009; Benavides et al., 2013; Grau et al., 2013;

402   Caldeira et al., 2014; Tíscar and Linares, 2014). Accordingly, we detected this positive effect

403   over the occurrence and abundance of juveniles of both pine species under moderate covers of

404   shrubs (under 50% of cover), which concurs with the results from Batllori et al. (2009), who

405   reported a shift from facilitation to competition as shrub cover increased. Moreover, we found

406   that this positive effect faded out at extreme temperatures (high temperatures for *P. nigra* and

407   low and high temperatures for *P. uncinata*), suggesting that facilitation disappears when the

408   external conditions become more stressful (Maestre et al., 2005; Tíscar and Linares, 2014). On

409   the other hand, we did not consider in this study the species identity effect of the shrubs, factor

410   that may be crucial in fading or neglecting this nursing effect due to, for instance, allelopathic

411   effects, architecture or herbivory appeal (Gómez-Aparicio et al., 2004; Baraza et al., 2006).

412   Herbs compete with seedlings for resources (Davis et al. 1999), and in Mediterranean

413   ecosystems this competition is mainly for soil water (Rey Benayas et al., 2005; Cuesta et al.,

414   2010, Caldeira et al., 2014). This is in accordance with the negative effect that herb cover had

415   on the abundance of our two Mediterranean species, *Q. ilex* and *P. nigra*, being especially

416   relevant for the latter at high temperatures, where the heat-stress and drought conditions were

417   greater. These indirect effects over recruitment have already being highlighted in previous

418   studies with *Q. ilex* and other Mediterranean species, showing the complexity of plant-plant

419   interactions, that not only fluctuate among years with the annual variation in climatic

420   conditions (Holmgren et al., 2012), but also may interact with other biotic conditions not

421   considered in our study, such as the canopy, the size or the age of the recruits (Cuesta et al.,

422   2010; Benavides et al., 2013; Caldeira et al., 2014).

423

424   **5. Conclusions**

425   In this study we have surveyed the natural recruitment patterns of four tree species along entire

426   elevational ranges to disentangle the different factors that, acting hierarchically, determine the

427   regeneration patterns, in terms of occurrence, abundance and growth of recruits. The

428   regeneration is a rather stochastic process, difficult to model due to the high variability in space

429   (from regional to microhabitat scales), time (among years and within a year) and nature (abiotic

430   and biotic including anthropogenic) of the factors involved. In this line, the performance of our

431   models was modest, especially for *F. sylvatica*, whose sample size was limited, but agreed with

432   the already reported difficulty for modelling this process in nature (Klopcic et al., 2012).

433   We acknowledge that an important driver for mid- and long-term patterns has been left out in

434   this study, changes in the land use and management (*e. g.* coppicing abandonment, free-range

435   livestock disappearance, specific species-oriented management, etc.). Notwithstanding, we

436   elicited some important results that can shed some light on the complex net of nested factors

437   that influence the natural regeneration of the study species. The four species have shown high

438   responsiveness to climatic variables (regional scale), especially in terms of abundance and

439   growth, with species influenced either by precipitation (*P. nigra* and *F. sylvatica*) or both

440   precipitation and temperature (*Q. ilex* and *P. uncinata*). Moreover, we detected within species

441   an ontogenetic differential sensitivity to climate (seedlings being more sensitive that saplings),

442   and with different environmental factors influencing the growth at different age classes. Light

443 availability, as a direct consequence of the stand structure (local scale), exerted an overall

444 positive effect on juvenile growth regardless of the age. Finally, variables at micro-habitat scale

445 played also a relevant role for the distribution models, supporting the competitive ability of

446 herbs and the facilitative role (with restriction) of shrubs reported in previous studies; and at the

447 same time, they modulated the effect of climate, exacerbating its negative effect on recruitment

448 in heat-stressful places through competition or mitigating it through the nurse effect. These

449 results and together with the disturbing climatic projections (Giorgi and Lionello, 2008;

450 Nogués-Bravo et al., 2008), seem a powerful argument to encourage forthcoming management

451 to pay more attention to these local variables in Mediterranean areas considering the

452 idiosyncrasy of each species, population and site. In particular, our results stand for boosting

453 regeneration by promoting some cover of shrubs that facilitates recruitment success (especially

454 for pines), removing the herb layer in more arid places or creating gaps to favor the juveniles'

455 growth (*e. g.* adjusting the frequency and intensity of intermediate cuttings). Nevertheless,

456 further studies are required to better understand how the local heterogeneity can contribute to

457 mitigate the effects of the ongoing global warming along environmental gradients, and to avoid

458 the natural regeneration failure.

459

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470

471   **7. References**

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683 **Figure captions**

684 **Figure 1.** Sampling design: a) site locations, b) diagram of transects layout within a site, c)

685 display of plots layout (grey squares) within a transect, and d) plot design. Two sites for every

686 species were sampled. Within each location, five transects were established at five elevations

687 (three in sites with *Quercus ilex*) coded as: upper (U), mid-up (MU), middle (M), mid-low

688 (ML) and lower (L) transects. Within each transect, six plots were established, three of them

689 under closed canopy and the other three in gaps. Each plot encompasses a 4 x 4 m central

690 squared regeneration plot -with 16 subplots of 1 m^2 size-, and round plots where adult trees

691 were mapped and measured: a 10-m radius area for every adult tree (>7.5 cm dbh), and 20-m

692 radius circle for bigger trees (> 20 cm dbh).

693 **Figure 2**. a) Distribution of juveniles along the elevation for both age classes (S1: seedling -

694 from 1 to 5 years-, S2: saplings -over 5 years-) of every species (according to Mann-Whitney U

695 test * $p < 0.05$; *** $p < 0.001$). b) Mean growth averaged per elevational level and species for

696 both age classes S1 and S2. (L: lower transect; ML: mid-low transect; M: middle transect; MU:

697 mid-up transect; U: upper transect). Different letters show significant difference among the

698 elevational levels according to Kruskal-Wallis test and One-Way ANOVA

699 **Figure 3.** Effect of the significant interactions among mean annual temperature (T, ºC) and

700 different biotic variables on the density of juveniles estimated using Zero-Inflated Poisson

701 (ZIP) Mixed Models. The predicted values of density is the result of multiplying the predictions

702 for both ZIP submodels, the occurrence submodel (binomial model) that gives the probability

703 of finding a recruit (1-P), and the abundance submodel (Poisson model) that returns the number

704 of predicted juveniles when they are presence (λ).

705 **Figure 4.** Effect of the significant interactions among mean annual temperature and other

706 variables on the annual mean growth (MG, cm) of juveniles estimated using Generalized Linear

707   Mixed Models. (T: mean annual temperature -°C-; GSF: global site factor; P: mean annual

708   precipitation –mm-; S1: seedling from 1 to 5 years; S2: saplings over 5 years).

Table 1. Description of the study sites, with ranges or mean values (with the standard deviation in brackets) of main environmental characteristics (T: mean annual temperature, P: annual mean precipitation, BA: the basal area in 10 m-radius plots, Density assessed considering the conspecific adult individuals). Climatic variables were obtained at plot level using the Digital Climatic Atlas of the Iberian Peninsula, (Ninyerola et al., 2005)

Site	Target species	Coordinates	Altitudinal range (m)	T range (ºC)	T mean (°C)	P range (mm)	P mean (mm	Slope (%)	Density (trees ha^{-1})	BA (m^2 ha^{-1})	Dominant tree species downslope	Dominant tree species upslope
Montseny	*Q. ilex*	41º45' N 2º29'E	716-1092	9.8-12.3	11.2 (0.8)	811.2-1147.2	955 (112)	58 (7)	522.0 (383.2)	40.7 (14.1)	-	*F. sylvatica*
Guadarrama	*Q. ilex*	40º52' N 4º02' W	1138-1360	9.9-10.9	10.4 (0.4)	762.7-810	787 (16)	12 (11)	359.0 (203.3)	19.2 (13.5)	-	*P. sylvestris*
Solsona	*P. nigra*	42º10' N 1º42' E	567-1317	8.7-12.2	10.4 (1.2)	730.3-985.7	812 (65)	56 (13)	756.5 (314.2)	27.3 (13.3)	*Q. faginea, Q. ilex*	Treeline
Segura	*P. nigra*	38º28' N 2º27' W	1122-1498	11.3-12.6	12.0 (0.5)	698.3-980.2	843 (83)	33 (11)	235.5 (145.4)	26.3 (12.6)	*P. pinaster*	Treeline
Aigüestortes	*P. uncinata*	42º36' N 1º04' E	1817-2405	2.9-6.2	4.6 (1.0)	701.8-988.6	839 (112)	55 (14)	403.2 (308.5)	29.0 (20.5)	*Abies alba*	Treeline
Cerdanya	*P. uncinata*	42º21' N 1º27' E	1730-2198	3.9-6.3	5.2 (0.8)	1006-1209.5	1069 (68)	48 (18)	484.9 (333.8)	31.7 (14.5)	*Abies alba*	Treeline
Montseny	*F. sylvatica*	41º46' N 2º28' E	913-1614	6.9-11.8	9.0 (1.7)	811.2-1274.5	1066 (141)	52 (11)	522.0 (383.2)	40.7 (14.1)	*Q. ilex*	Treeline
Cebollera	*F. sylvatica*	42º04' N 2º 36' W	1173-1798	6.1-9.3	7.8 (1.1)	692.5-898.1	774 (48)	35 (11)	569.8 (455.3)	30.6 (12.9)	*Q. pyrenaica, Ilex aquilinum*	Treeline

Table 2. Final Zero-Inflated Poisson Mixed Models for the occurrence (absence) and abundance of juveniles. (Dashes mean variables not included in the final model; T: annual mean temperature -ºC-; P: annual precipitation -mm-; GSF: global site factor; Herbs, Shrubs and Rocks expressed as % of cover; ΔAIC: difference in AIC referred to the saturated model; EF: efficiency of modelling[1]; n= sample size -number of subplots surveyed-; SE: standard error; NC: not considered in the saturated model; * p < 0.05; ** p < 0.01; *** p < 0.001). The parameters estimated in the binary part (occurrence) are referred to the probability *P* finding no recruit (absence), being 1-*P* the probability of presence.

		Pinus uncinata	*Pinus nigra*	*Fagus sylvatica*	*Quercus ilex*
		ΔAIC= 24.1 EF= 0.456; n=960	ΔAIC= 23.6 EF= 0.475; n= 960	ΔAIC= 26.6 EF= 0.416; n= 960	ΔAIC= 18.8 EF= 0.358; n= 480
		Estimate (SE)	Estimate (SE)	Estimate (SE)	Estimate (SE)
Occurrence	Intercept	-13.684 (4.254)**	0.302 (0.417)	-1.521 (1.176)	-3.229 (0.849)
	Site	-	-5.935 (1.090) ***	-	-
	P	0.0168 (0.004)***	-	-	-
	Shrubs	-0.107 (0.048)*	-	NC	-
	Rocks	0.046 (0.014)**	-	-	-
	GSF	-9.406 (2.999)**	-	-	-
	Shrubs x T	0.029 (0.011)*	0.005 (0.001) ***	NC	-
Abundance	Intercept	-7.567 (2.694)**	-14.119 (2.618) ***	23.613 (8.600) *	-6.286 (4.388)
	Site	-	-	-	1.152 (0.534) *
	T	3.658 (1.178)**	0.328 (0.207)	-10.3483 (2.081)***	1.3126 (0.313)***
	T²	-0.382 (0.125)**	-	0.687 (0.132) ***	-
	P	-	0.011 (0.002) ***	0.0166 (0.003) ***	-0.011 (0.003) ***
	Herbs	-0.010 (0.002)***	0.081 (0.020)***	NC	-0.011 (0.006)*
	Shrubs	-0.044 (0.015)**	-	NC	-
	Herbs x T	-	-0.008 (0.002)***	NC	-
	Shrubs x T	0.008 (0.004)*	-	NC	-

[1] The modelling efficiency (EF) is assessed through: $EF = 1 - \left[\dfrac{\Sigma_{ij}(y_{ij}-\hat{y}_{ij})^2}{\Sigma_{ij}(y_{ij}-\bar{y}_{ij})^2}\right]$ where y_{ij} and $\hat{y}_{ij}$ are the observed and predicted data, and $\bar{y}_{ij}$ is the mean value for the response variable.

Table 3. Final Generalized Linear Mixed Models for the mean annual growth of juveniles. (Dashes mean variables not included in the final model; T: annual mean temperature -ºC-; P: annual precipitation -mm-; GSF: global site factor; Shrubs and Rocks expressed as % of cover; ΔAIC: difference in AIC referred to the saturated model; EF: efficiency of modelling[1] ; n: sample size -number of juveniles recorded per species and age class-; SE: standard error; S1: seedlings from 1 to 5 years; S2: saplings over 5 years; NC: not considered in the saturated model; * p < 0.05; ** p < 0.01; *** p < 0.001)

		P. uncinata	*P. nigra*	*F. sylvatica*	*Q. ilex*
S1		ΔAIC=63.4	ΔAIC=53.4	ΔAIC=10.9	ΔAIC= 9.8
		EF= 0.298; n=252	EF= 0.484; n=195	EF= 0.192; n=64	EF= 0.277, n=109
		Estimate (SE)	Estimate (SE)	Estimate (SE)	Estimate (SE)
	Intercept	9.027 (2.896)**	-2.586 (0.992) *	3.992 (0.295) ***	371.00 (111.36) **
	T	-2.819 (1.078) *	0.463 (0.077) ***	-	-32.109 (9.309) **
	T^2	0.257 (0.1) *	-	-	-
	P	-	-	-	-0.451 (0.141) **
	Rocks	-	-	-0.020 (0.009) *	-
	GSF	-5.858 (2.2230) *	3.617 (1.304) *	-	1.133(0.743)
	GSF x T	1.436 (0.477) **	-	-	-
	T x P	-	-	-	0.039 (0.012) **
S2		ΔAIC=28.7	ΔAIC=44.11	ΔAIC=15.2	ΔAIC= 31.7
		EF=0.294; n=332	EF=0.514; n=292	EF= 0.357; n=26	EF= 0.358, n=124
		Estimate (SE)	Estimate (SE)	Estimate (SE)	Estimate (SE)
	Intercept	0.073 (1.059)	1.845 (0.824) *	1.814 (0.258) ***	3.175(0.557)***
	Site	-	2.131 (0.613) **	-	-1.185(0.533)*
	T	-0.764 (0.170) ***	-	-	-
	P	0.007 (0.001) ***	-	-	-
	Shrubs	-	0.014 (0.006) *	NC	-
	Rocks	-0.028 (0.010) **	-	-	-
	GSF	-	2.729 (3.155)	-	2.917 (1.072)*
	GSF x T	0.765 (0.201) ***	-	-	-

[1] The modelling efficiency (EF) is assessed through: $EF = 1 - \left[\frac{\Sigma_{ij}(y_{ij}-\hat{y}_{ij})^2}{\Sigma_{ij}(y_{ij}-\bar{y}_{ij})^2}\right]$ where y_{ij} and $\hat{y}_{ij}$ are the observed and predicted data, and $\bar{y}_{ij}$ is the mean value for the response variable.
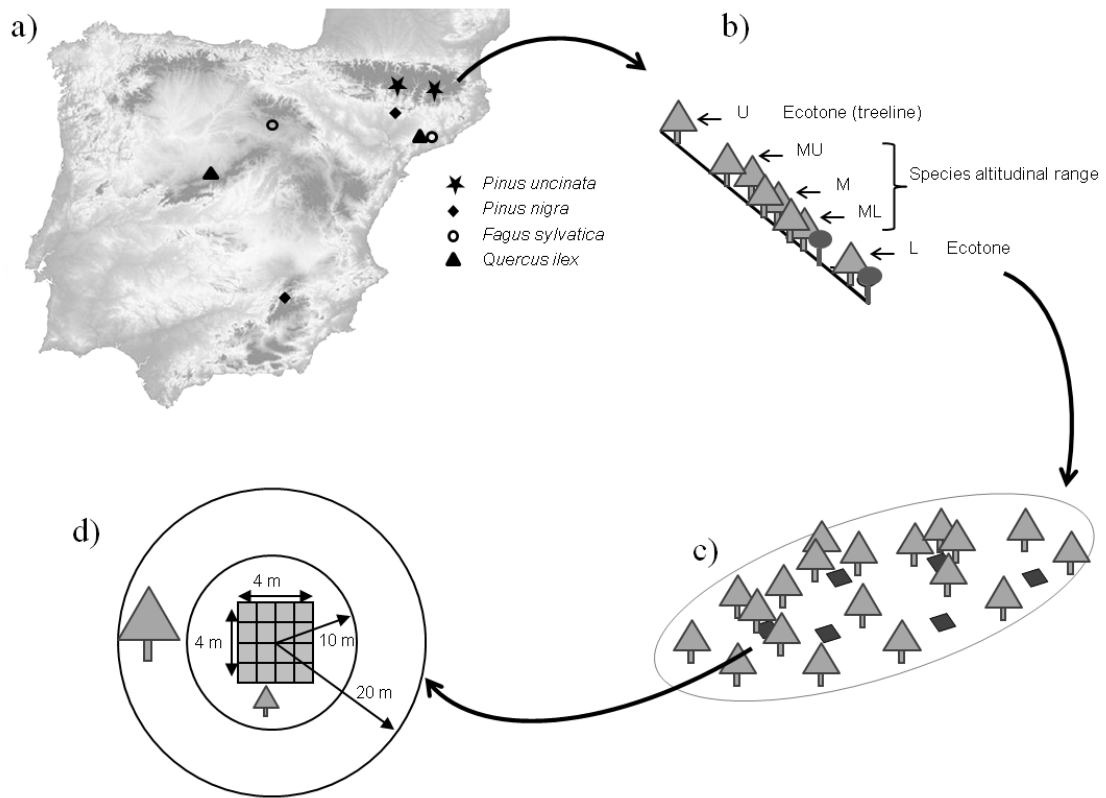
Fig. 1

Fig. 2

Pinus uncinata

T (°C) — Shrub cover (%)

Pinus nigra

T (°C) — Shrub cover (%)

Pinus nigra

T (°C) — Herb cover (%)

No. juveniles
1
2
3
4
5
6

Fig. 3

P. uncinata (S1)

T (°C) — GSF

MG (cm)
1.0
1.5
2.0
2.5
3.0

P. uncinata (S2)

T (°C) — GSF

MG (cm)
0.5
1.5
2.5
3.5
4.5
5.5
6.5

Q. ilex (S1)

T (°C) — P (mm)

MG (cm)
0.5
2.5
4.5
6.5
8.5
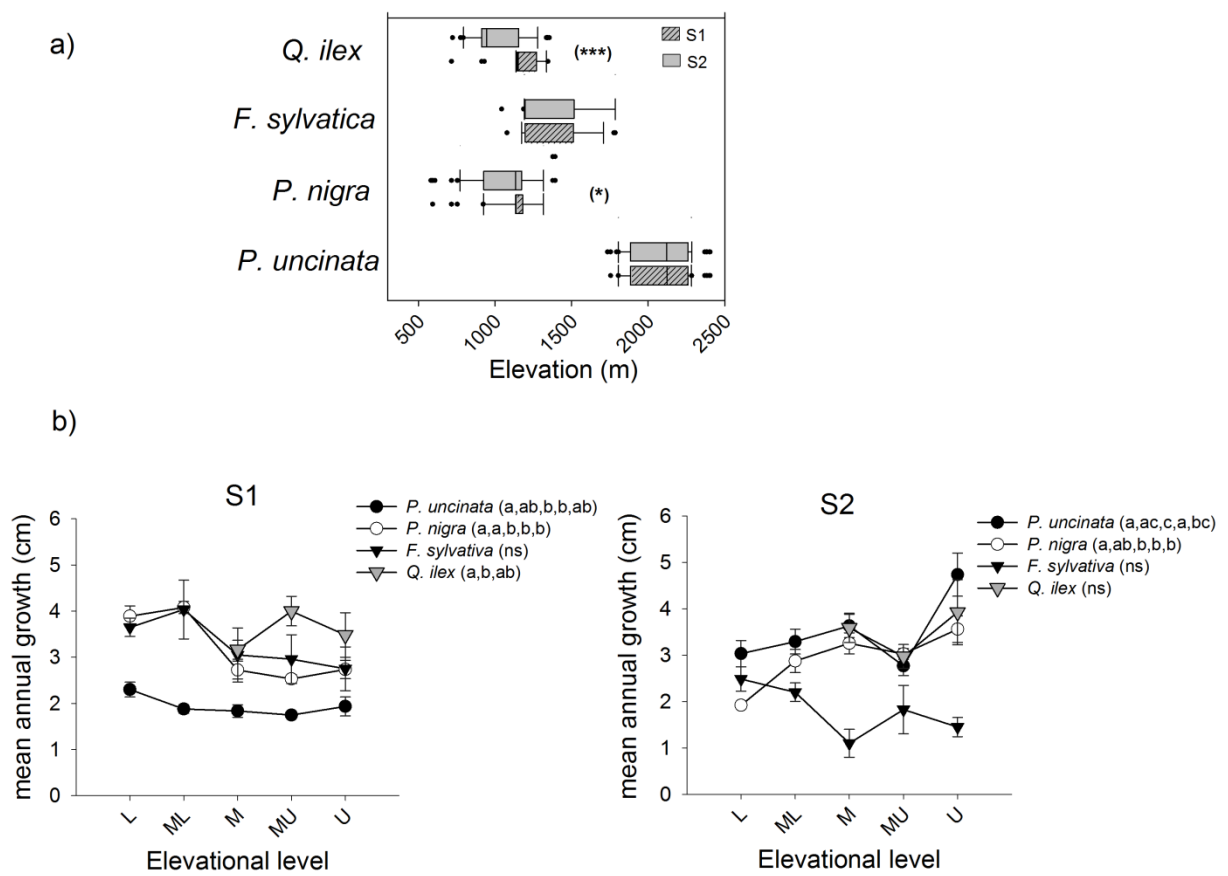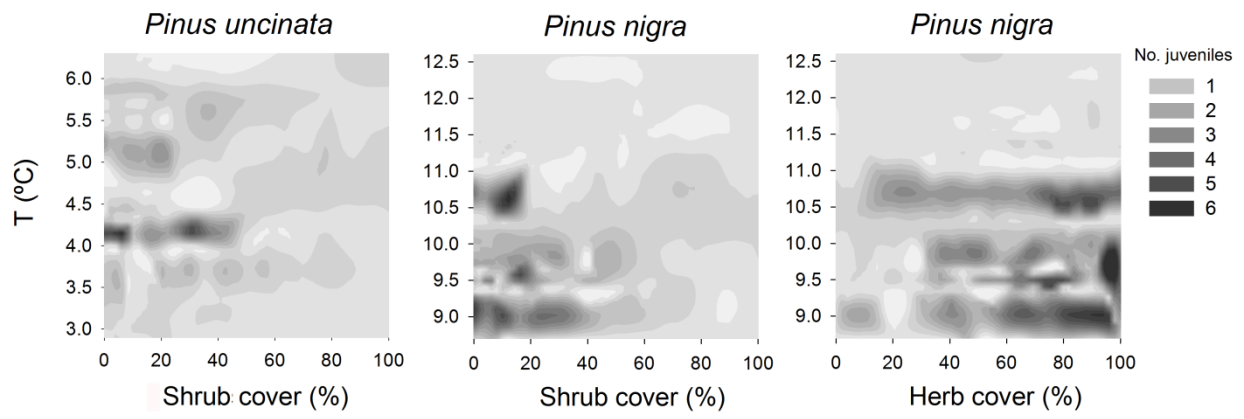
Fig. 4

Figure A1. Mean values of local abiotic variables along the altitudinal transects in every type of forest. Error bars represent the standard errors, and different letters show significant differences. (GSF: global site factor; T: annual mean temperature; P: mean annual precipitation; L: lower transect; ML: mid-low transect; M: middle transect; MU: mid-up transect; U: upper transect).
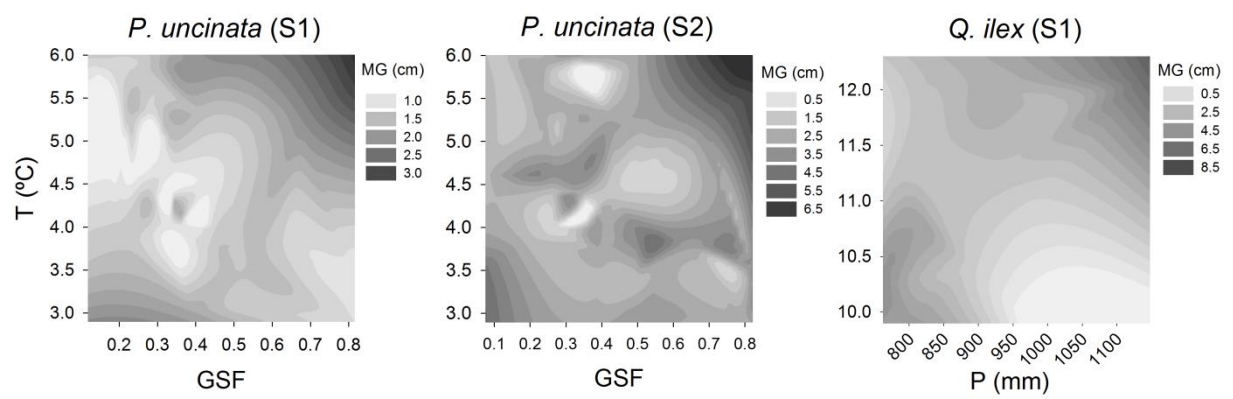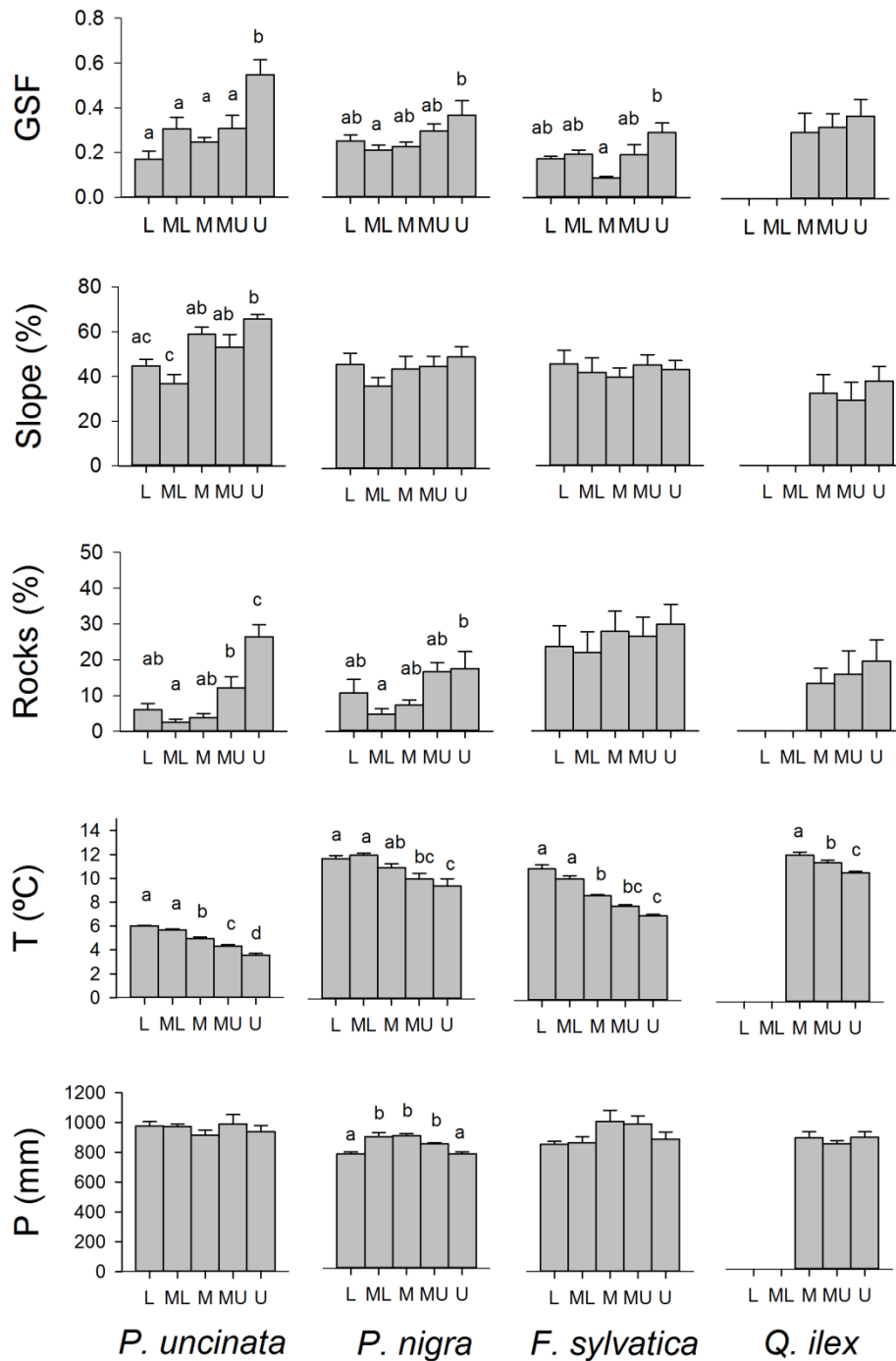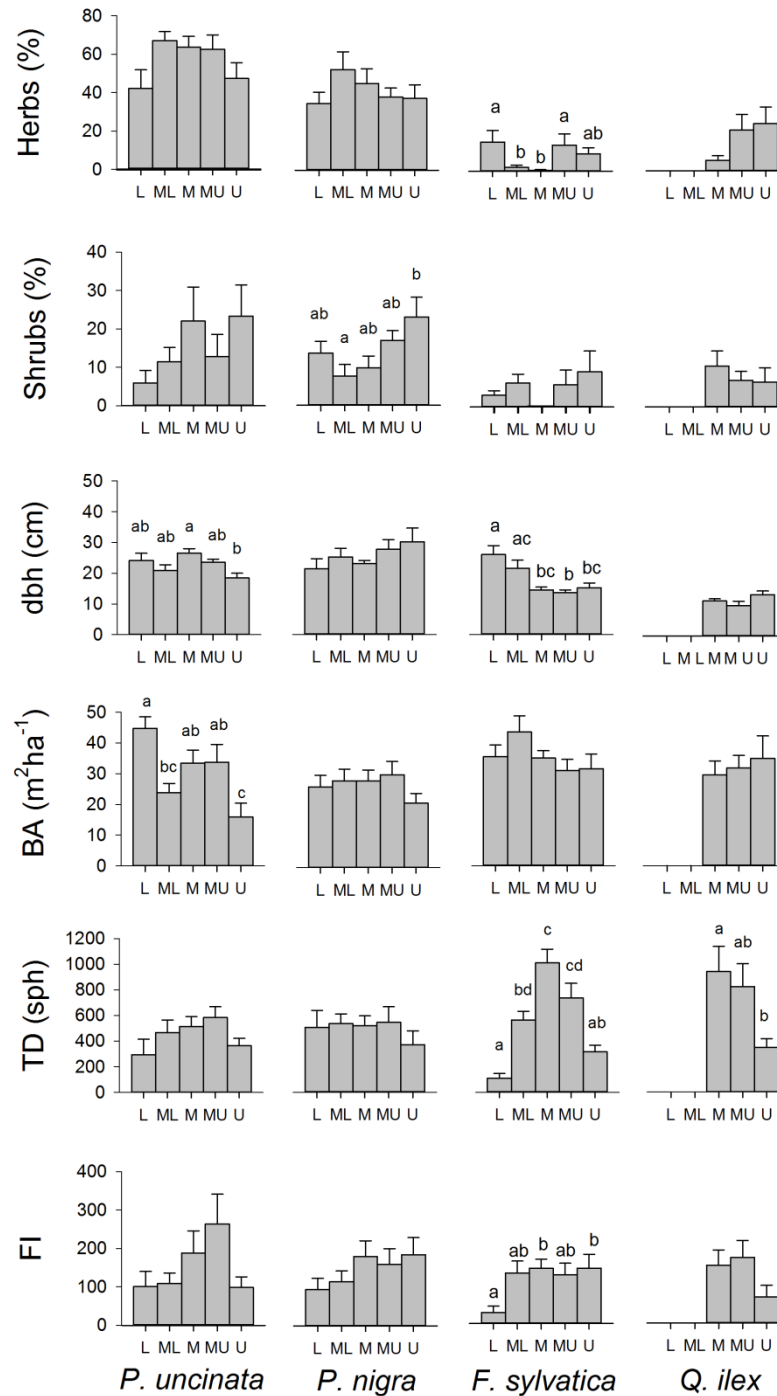
Figure A2. Mean values of local biotic variables along the altitudinal transects in every type of forest. Error bars represent the standard errors, and different letters show significant differences. (FI: fecundity index; BA: basal area considering all adult trees regardless of the species; TD: tree density of conspecific adult trees; L: lower transect; ML: mid-low transect; M: middle transect; MU: mid-up transect; U: upper transect).

Table A.1. Spearman correlation coefficients among environmental variables found in the study sites according to the dominant species (shrubs, herbs and rocks assessed as percentage cover; GSF: Global Site Factor; BA: basal area considering adult trees of every species found in the plot; FI: fecundity index, T: annual mean temperature; P: mean annual precipitation; (*) $p<0.05$; (**) $p<0.01$; (***) $p<0.001$).

		slope	shrubs	herbs	rocks	GSF	BA	FI	T	P
Pinus uncinata	slope	1	-0.006	-0.101(**)	0.509(***)	0.275(***)	-0.287(***)	0.019	-0.658(***)	-0.123(***)
	shrubs	-	1	-0.357(***)	-0.032(*)	0.223(***)	-0.195(***)	-0.06	-0.329(***)	-0.228(***)
	herbs	-	-	1	-0.331(***)	-0.313(***)	0.017	0.022	0.171(***)	0.380(***)
	rocks	-	-	-	1	0.389(***)	-0.287(***)	-0.082(***)	-0.361(***)	-0.107(**)
	GSF	-	-	-	-	1	-0.578(***)	-0.217(***)	-0.362(***)	-0.336(***)
	BA	-	-	-	-	-	1	0.413(***)	0.452(***)	0.065(*)
	FI	-	-	-	-	-	-	1	-0.025	0.02
	T	-	-	-	-	-	-	-	1	0.271(***)
	P	-	-	-	-	-	-	-	-	1
Pinus nigra	slope	1	0.326(***)	0.196(***)	0.405(**)	-0.164(***)	-0.013	0.324(***)	-0.624(***)	-0.231(***)
	shrubs	-	1	-0.265(***)	0.063(*)	0.099(***)	-0.141(***)	0.265(***)	-0.311(***)	-0.187(***)
	herbs	-	-	1	-0.044	0.025	-0.138(***)	-0.009	-0.272(***)	0.081(**)
	rocks	-	-	-	1	0.233(***)	-0.247(***)	0.009	-0.195(***)	-0.040
	GSF	-	-	-	-	1	-0.482(***)	-0.190(***)	-0.004	-0.084(**)
	BA	-	-	-	-	-	1	0.318(***)	0.036	0.120(***)
	FI	-	-	-	-	-	-	1	-0.370(***)	-0.020
	T	-	-	-	-	-	-	-	1	0.126(***)
	P	-	-	-	-	-	-	-	-	1
Fagus sylvatica	slope	1	-0.326(***)	0.015	0.320(***)	0.072(*)	0.209(***)	0.006	0.170(***)	0.487(***)
	shrubs	-	1	0.113(***)	-0.203(***)	0.418(***)	-0.201(***)	-0.304(***)	0.005	-0.449(***)
	herbs	-	-	1	0.200(***)	0.521(***)	-0.424(***)	-0.221(***)	-0.203(***)	-0.029
	rocks	-	-	-	1	0.095(**)	-0.038	0.016	-0.067(*)	0.09(**)
	GSF	-	-	-	-	1	-0.391(**)	-0.183(***)	-0.070(*)	0.024
	BA	-	-	-	-	-	1	0.336(***)	0.239(***)	0.150(***)
	FI	-	-	-	-	-	-	1	-0.300(***)	0.021
	T	-	-	-	-	-	-	-	1	0.163(***)
	P	-	-	-	-	-	-	-	-	1
Quercus ilex	slope	1	-0.562(***)	-0.638(***)	0.705(***)	-0.579(***)	0.434(***)	0.401(***)	0.340(***)	0.883(***)
	shrubs	-	1	0.309(***)	-0.390(***)	0.392(***)	-0.503(***)	-0.358(***)	-0.148(***)	-0.322(***)
	herbs	-	-	1	-0.466(***)	0.381(***)	-0.483(***)	-0.299(***)	-0.274(***)	-0.325(***)
	rocks	-	-	-	1	-0.412(***)	0.358(***)	0.134(***)	-0.167(***)	0.507(***)
	GSF	-	-	-	-	1	-0.738(***)	-0.291(***)	-0.399(***)	-0.272(***)
	BA	-	-	-	-	-	1	0.482(***)	0.393(***)	0.653(***)
	FI	-	-	-	-	-	-	1	0.253(***)	0.343(***)
	T	-	-	-	-	-	-	-	1	0.396 (***)
	P	-	-	-	-	-	-	-	-	1