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1 **Stand-level drivers of tree-species diversification in Mediterranean pine forests after**
2 **abandonment of traditional practices**

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9 **Abstract**

10 The progressive abandonment of traditional forest management over the last few decades has led to
11 significant densification processes in most Mediterranean pine stands. In parallel, some of these
12 stands have also shown tree-species diversification processes, the occurrence of which is considered
13 essential for future adaptability and resilience to change. Here we aim to gain further understanding
14 of the main factors driving these diversification processes via a case-study approach using the long-
15 term-managed black pine (*Pinus nigra* Arn. ssp. *salzmannii*) forests of the Catalan Pre-Pyrenees (NE
16 Spain). For this purpose, we sampled 155 plots distributed in 8 different stands and analyzed the role
17 played by a number of microsite factors and stand attributes (including canopy openness and
18 heterogeneity) on the abundance of seedlings ($h < 1.3\text{m}$) and saplings ($h > 1.3\text{m}$; $dbh < 7.5\text{cm}$) of the
19 main tree-species in the area (i.e. black pine, evergreen oak and marcescent oaks). Results revealed
20 ongoing black pine recruitment limitation processes mainly associated to the high canopy cover of
21 the overstory and the increasing abundance of shrubs, which may compete with pines for light
22 resources. In contrast, we found that current environmental and stand-level conditions favor the
23 progressive advance of the recruitment of evergreen and marcescent oaks, which are able to establish
24 successfully under the dominant pine canopy. However, in the absence of canopy openings, light
25 levels may not allow the established oaks (in particular the evergreen *Quercus ilex*) to grow and
26 progress to higher developmental stages. Our findings bring deeper insight into the role of stand-
27 level factors regulating species diversification, and can be used by forest managers to adjust their
28 practices (e.g. by modifying the spatial and temporal patterns of silvicultural treatments such as
29 thinnings or selection cuttings) in order to favor this natural process and increase stand resilience.

30 **Keywords:** *Pinus nigra*, regeneration, oak recruitment, mixed forests, canopy attributes

31

32 **1. Introduction**

33 The distribution, structure and composition of Mediterranean forests have been shaped over
34 millennia by human practices (Debussche *et al.*, 1999; Vallejo, 2005; Nocentini and Coll, 2013).
35 Over time, this long history of human use has resulted in a significant reduction of the extent and
36 inherent structural and compositional diversity of Mediterranean forests (Ciancio and Nocentini,
37 2000; Blondel, 2006). In the context of the Iberian Peninsula, this long history of intense human-use
38 reached its peak at the end of the 19th century (Garcia-Ruiz *et al.*, 1996; Pausas *et al.*, 2004; Linares
39 *et al.*, 2010). However, the 20th century brought major socioeconomic changes leading to
40 generalized land abandonment processes in marginal areas –generally mountainous systems– and to
41 land-use intensification in broad valleys and coastal regions (Garcia-Ruiz *et al.*, 1996; Vicente-
42 Serrano *et al.*, 2004; Lasanta-Martinez *et al.*, 2005; Chauchard *et al.*, 2007). This, together with
43 extensive reforestation programs initiated with the aim of restoring the most heavily-degraded areas
44 –most of which with pine species–, have triggered extended encroachment and densification
45 processes in forest stands (Améztegui *et al.*, 2010; Navarro and Pereira, 2012).

46 Black pine-dominated forests (*Pinus nigra* Arn. ssp. *salzmannii*) in the Pre-Pyrenean range
47 (NE Spain) are clear examples of forests undergoing such processes. These forests were intensively
48 managed for timber harvesting and pasture grazing until the mid-20th century (Ruiz de la Torre,
49 2006), but from that point onwards the intensity of human practices decreased significantly (Vicente-
50 Serrano *et al.*, 2004). During the past few decades, just a few individual-tree selection cuttings
51 affecting only the most vigorous and well-shaped trees have been conducted on these forests
52 (Trasobares and Pukkala, 2004; Aunós *et al.*, 2009). Such lessening of human pressure (particularly
53 the strong decrease of silvicultural interventions and livestock grazing) has allowed the establishment
54 of new cohorts of the dominant pine species, causing a generalized densification of the stands
55 (DGCN, 2005) and a progressive process of colonization by late-successional tree species, mainly
56 *Quercus* species (e. g., Urbietta *et al.*, 2011; Carnicer *et al.*, 2013).

57 The promotion of diversified forests is gaining currency as an appropriate management
58 strategy to improve stand adaptability to environmental variations, including changes in disturbance
59 regimes (e.g. Campbell *et al.*, 2009; Thompson, 2009; Puettmann, 2011). Advancing knowledge of
60 the ecological factors driving tree-species diversification in Mediterranean forest stands is of major
61 interest, due to the particular vulnerability of this bioclimatic region to the effects of global change
62 (Lindner *et al.*, 2010). In the particular case of black pine-dominated forests, for example, the
63 occurrence of natural diversification processes allowing resprouting species such as oaks to establish
64 in the pine understory is reportedly essential for rapid vegetation recovery after the occurrence of
65 large wildfires (Puerta-Piñero *et al.*, 2011).

66 The progressive diversification of a given stand by tree species others than the ones
67 occupying the dominant canopy is a complex process, the success of which depends on a number of
68 factors acting at different spatio-temporal levels (seed dispersion into the stands, establishment of the
69 plants and growth to reproductive maturity) (Zavala *et al.*, 2011; Sheffer *et al.*, 2013). Seed arrival,
70 for example, is influenced by the abundance and spatial distribution of seed sources in the
71 surrounding landscape (Zamora *et al.*, 2010; González-Moreno *et al.*, 2011), but also depends on
72 other factors such as the abundance and behavior of seed dispersers or predators (Pérez-Ramos and
73 Marañón, 2008; Gonzalez-Rodriguez and Villar, 2012). Once the seeds are dispersed into the stands,
74 and in the absence of significant human disturbances and/or intensive browsing events, plant
75 establishment and future growth will be triggered by a combination of factors acting at micro-site
76 level: the environmental conditions of the site (climate, soil, etc.), the characteristics of the stand
77 (over- and understory structure and composition) and the attributes of the canopy layer (gap shape,
78 size) (e.g. Lookingbill and Zavala, 2000; Smit *et al.*, 2008; Garcia-Barreda and Reyna, 2013).

79 The occurrence of natural or anthropogenic small-scale disturbances leading to moderate
80 openings of the stands is a key element of the above mentioned process of tree-species
81 diversification. These openings generate heterogeneity in the understory and lead to micro-site-level

82 changes in environmental conditions (humidity, temperature) and resource availabilities (e.g. light,
83 soil water) allowing the seedlings of the dominant species and those coming from adjacent stands to
84 prosper (Runkle, 1981; Runkle and Yetter, 1987; Yamamoto, 2000; Ligot *et al.*, 2014).

85 This study aims to shed light on these processes which, contrary to other bioclimatic regions,
86 have so far been little explored in the Mediterranean. More specifically, we aimed to answer the
87 following questions: (i) have the sub-Mediterranean black pine forests undergone active regeneration
88 and tree-species diversification processes during the last decades?; (ii) which are the main stand-
89 level factors driving such processes?; and (iii) do the canopy openness and the gap attributes play a
90 key role on them?. For this purpose, we used the long-term-managed Sub-Mediterranean black pine
91 forest of the Catalan Pre-Pyrenees (NE Spain) as case study. We selected a number of stands
92 showing a large gradient of canopy openness and structural heterogeneity and analyzed the role
93 played by different stand-level factors in the abundance of the different species at different life-
94 history stages: seedlings and saplings. We expected stand structure and, particularly, canopy
95 attributes to play a key role in driving stand-level species diversification allowing species other than
96 pine to survive and prosper under the dominant pine canopy.

97

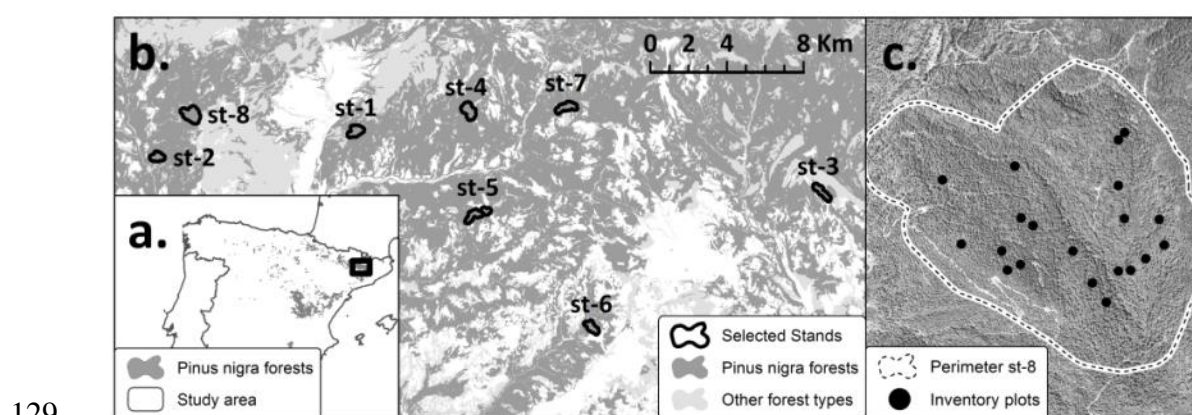
98 2. Materials and Methods

99 2.1. Study area and stands selection

100 The study was conducted in the Catalan Pre-Pyrenees, Northeastern Iberian Peninsula, in a
101 mountainous range limited at East and West by the basins of the rivers Segre and Cardener (between
102 1° 11' 6" and 1° 36' 57" E, and 41° 56' 57" and 42° 3' 43" N, DATUM WSG84) (Figure 1). These
103 mountains are formed by folded structures of sedimentary carbonate rocks (mainly lutite, marlstone,
104 limestone and conglomerate), characterized by vertical elevation ranging from 400-1000 m.a.s.l.
105 Climate in the area is sub-humid from Mediterranean-continental to Mediterranean-montane,
106 characterized by mean annual precipitation of around 700 mm and mean annual temperature around
107 12°C (Ninyerola *et al.*, 2005). Rainfall is usually concentrated in autumn and spring, and winter is
108 the season with least precipitation. In summer, short convective storms also provide significant
109 precipitation input (around 100-130 mm in average during the hottest months, July and August).
110 However, due to the high inter-annual variability in the occurrence of this type of rainfall events, the
111 occurrence of summer dry periods is not unusual. Within this general geographic context, the study
112 focused on the forests dominated by black pine (*Pinus nigra* Arn. ssp. *salzmannii*) which are the
113 most abundant in the study area.

114 A set of eight stands were selected along the study area (Figure 1) based on the following
115 three criteria: (i) patches larger than 2 hectares and clearly dominated by black pine at the canopy
116 level (i.e. with black pine occupancy > 90% of total basal area), (ii) not coming from recently
117 abandoned open-areas (i.e. agricultural land, grassland, shrubland), and (iii) with absence of signs of
118 any recent silvicultural interventions or grazing activity. The first criterion was checked with the help
119 of the third Spanish National Forest Inventory plots (which provided information on current structure
120 and composition) (DGCN, 2005), the Spanish National Forest Map 1:50.000 (DGCN, 2001), and the
121 third version of the Land Cover Map of Catalonia (CREAF, 2007). The second criterion was tested

122 by visually comparing the most recent aerial photographs of the area (taken in 2012) and the most
123 ancient ones (taken in 1956) and aimed at discarding from the study those young stands established
124 in open-areas recently abandoned which due to their young age were much less susceptible of
125 undergoing diversification processes by late-successional tree species (Puerta-Piñero *et al.*, 2012).
126 Twelve stands meeting the first two criteria were preselected and examined on-site in order to detect
127 signs of recent silvicultural interventions or grazing activity. Four of the twelve preselected stands
128 did not meet this criterion and were ultimately discarded from analysis.



129 **Fig. 1.** Location of the study area (a), the sampled stands (b), and the inventory plots within one of
130 the stands (c).
131

132 #2-column fitting image#

133 2.2. Remote sensing data acquisition and pre-processing

134 Two different sources of remote sensing data were used to characterize the forest canopy: aerial
135 Light Detection and Ranging (LiDAR) and multi-spectral aerial imagery (including red-green-blue
136 (RGB) and near-infrared (IR) bands). The LiDAR-derived data consisted in a two-meter resolution
137 DVM (Digital Vegetation Model) generated in the framework of the LiDARCAT project led by the
138 Cartographic and Geological Institute of Catalonia (ICGC). Flight dates ranged from April 2009 to
139 August 2009 and provided a minimum first-return density of 0.5 pulses·m⁻² and an overall quantity
140 of four height bins per first return. The RGB and near-IR data were obtained from multi-spectral
141 aerial photographs taken in the framework of the ICGC's annual coverage flights at 22 cm GSD

142 (ground sample distance). The imagery was taken in the same time period as the LiDAR data, with
143 DMC 26 and DMC 14 cameras.

144 The near-IR and the R bands from aerial images were used to calculate the NDVI
145 (Normalized Difference Vegetation Index) (Tucker, 1979). Then, both the DVM from LiDAR and
146 the calculated NDVI layers were clipped to the boundaries of the 8 selected stands, and used in an
147 object-oriented semi-automatic image analysis (carried out with eCognition Developer 8.9) to
148 classify the area within the stands into three classes: 'CLOSED CANOPY', i.e. area covered by the
149 main pine canopy showing a continuity larger than 10,000 m²; 'GAPS', i.e. area of less than 500 m²
150 not covered by (but surrounded by) the main pine canopy (Messier *et al.*, 2005; Schliemann and
151 Bockheim, 2011); 'OPEN AREA' for the rest of the area (which includes small canopy patches,
152 isolated trees and open areas larger than 500 m²). The accuracy of the semi-automatic classification
153 was visually assessed on 120 observation points distributed in the study area following a stratified
154 random sampling, one half (60) randomly located in the area automatically classified as 'GAPS', and
155 the other half in the area automatically classified as 'CLOSED CANOPY'. About 97% and 95% of
156 the points semi-automatically classified as 'GAPS' and 'CLOSED CANOPY', respectively, were
157 visually confirmed as belonging to each class. The accuracy of the method in classifying 'OPEN
158 AREA' was not tested because these areas were not the focus of this study.

159 2.3. *Sampling design and field inventory*

160 In order to cover a wide gradient of canopy openness and heterogeneity in the study area, we
161 established the field inventory plots using a stratified random design. First, a 20×20 m mesh was
162 created within each selected stand and the percentage of area covered by the 'GAPS' class in the area
163 surrounding each point in the mesh was computed. For this purpose we used a 18-m diameter of the
164 area of influence, equivalent to the mean dominant height for black pine in the selected stands. Then,
165 four classes of gap abundance were created (0: gap percentage ranging from 0 to 5%; 1: gap

166 percentage ranging from 5 to 15%; 2: gap percentage ranging from 15 to 30%; 3: gap percentage
167 above 30%). Those plots located at less than 10 m from patches classified as ‘OPEN AREA’ (e.g.
168 roads, agricultural field, harvested areas, etc.) were rejected. Second, 5 points in each class of gap
169 abundance were randomly selected in each stand and used to locate the inventory plots (160 in total,
170 20 per stand). Inventory plots were circular, with a 6-m radius centered at the randomly selected
171 points. In each plot, a set of site attributes including UTM central coordinates, slope and aspect were
172 collected. The tree canopy layer was characterized by identifying the species and measuring the
173 diameter at breast height (*dbh*) of all trees with *dbh* > 7.5 cm. Percentage of soil covered by woody
174 shrubs was also estimated. The most frequent shrubby species in the understory was common box
175 (*Buxus sempervirens* L.), followed by the two main juniper species in the area (*Juniperus communis*
176 L. and *Juniperus oxycedrus* L.), and the kermes oak (*Quercus coccifera* L.). Other species of the
177 genus *Crataegus*, *Rhamnus*, *Viburnum*, *Rubus*, *Lonicera*, etc. were also very frequently inventoried.
178 Finally, the abundance of stones, herbs and moss were visually estimated and classified into three
179 categories (*low*: less than 1/3 of the plot area; *medium*: between 1/3 and 2/3 of the plot area; and
180 *high*: more than 2/3 of the plot area)

181 Finally, tree-species regeneration was assessed by counting the number of seedlings (plants
182 shorter than 1.3 m) and saplings (plants taller than 1.3 m but with a *dbh* < 7.5 cm) of each species.
183 We also took a digital hemispherical photograph from the center of each plot under overcast sky
184 conditions using a Nikon CoolPix 4500 camera with an FC-E8 fish-eye lens. Five out of the 160
185 selected plots were rejected for subsequent analyses due to recent wild boar damage recorded when
186 visited.

187 2.4. Data processing

188 Both field and remote sensing-derived data were processed and grouped for subsequent analysis into
189 a number of response and explanatory variables. As response variables, we used the abundance of

190 regeneration found in the understory, grouped by development stage (seedlings and saplings), and
 191 functional types: (1) pines, only represented by the pine species dominating the tree canopy (*Pinus*
 192 *nigra* Arn. ssp. *salzmannii*); (2) evergreen oaks, represented by the only one species appearing in the
 193 area (*Quercus ilex* L.); and (3) semi-deciduous (marcescent) oaks, represented by two species
 194 (*Quercus faginea* Lam. and *Quercus cerrroides* Willk & Costa). Although the field inventories also
 195 recorded the presence of other broadleaved species (e.g. *Sorbus*, *Acer*), we discarded them from the
 196 analysis due to the shortage of individuals.

197 The quantitative explanatory variables derived from the field surveys and remote-sensing data
 198 included environmental descriptors of the sites and different variables related to stand structure and
 199 composition, including the gap attributes (see Table 1).

200 **Table 1**

201 Descriptive statistics of the quantitative explanatory variables presenting significant effects in the
 202 models (n = 155).

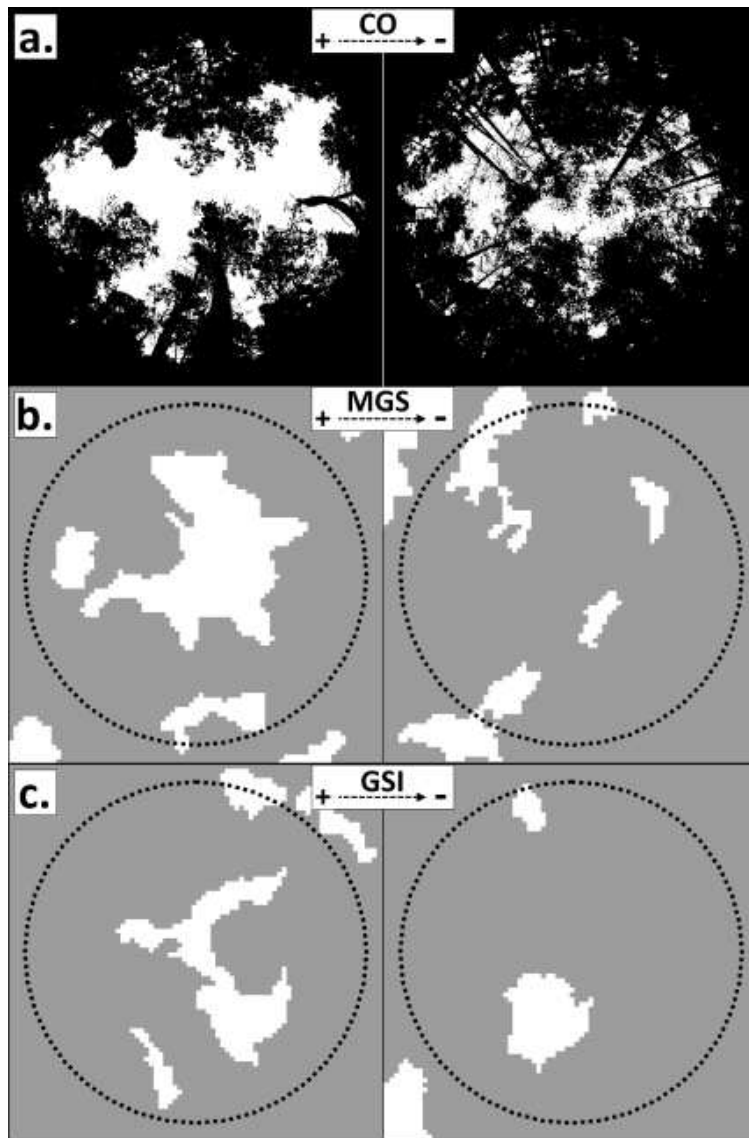
Variable, unit	Min.	Max.	Mean	Std. Dev.
<i>Site factors</i>				
CURVATURE Index	-1.77	2.17	0.10	0.65
NORTHNESS Index	-0.38	0.60	0.22	0.18
MARTONNE Index	28.47	35.47	32.69	1.27
<i>Stand structure & composition</i>				
MATURITY Index	0.00	0.99	0.22	0.26
G (Basal Area), m ² /ha	5.81	75.76	37.36	14.10
SHRUBS (woody shrubs cover), %	1.00	95.00	48.67	24.81
Grel_BL (relative G of broadleaves), ppu	0.00	0.22	0.03	0.05
Grel_Qm (relative G of marcescent <i>Q. spp.</i>), ppu	0.00	0.22	0.02	0.04
Grel_Qi (relative G of evergreen <i>Q. ilex</i>), ppu	0.00	0.16	0.00	0.02
CO (Canopy Openness), %	12.72	38.54	21.16	4.82
GSI (Gap Shape Index)	0.00	4.05	1.98	0.34
MGS (Mean Gap Size), meters	0.00	141.60	14.97	18.35

203

204 In relation to the first group of variables, we computed three different indexes
 205 (NORTHNESS, CURVATURE and MARTONNE) with the aim of broadly characterizing the
 206 climatic and topographic conditions at each plot. The NORTHNESS Index was calculated as the
 207 product of the slope (%) and the cosine of the aspect (degrees) measured in the field inventory

208 (Holden *et al.*, 2009). This index was used as a proxy for solar radiation budget at the plot surface,
209 and took higher positive values as aspect gets closer to North and slope increases, and lower negative
210 values as aspect gets closer to South and slope also increases. As aspect gets closer to East or West
211 and/or slope decreases, the NORTHNESS Index draws closer to 0. The CURVATURE Index was
212 calculated as a proxy of local topography, which is considered to be highly related to soil water
213 content distribution along a given slope (Gómez-Plaza *et al.*, 2001). For this purpose, we used the
214 equation proposed by Moore *et al.* (1991) on a 5-m-resolution digital elevation model. Higher
215 positive values indicate convex terrain and lower negative values indicate concave terrain. Finally,
216 the MARTONNE Index was calculated from the equation proposed by De Martonne (1926), as $M =$
217 $P \times (T + 10)^{-1}$, where M is the value of the index, P (mm) is annual precipitation, and T (°C) is
218 annual mean temperature. P and T were obtained from the Climatic Atlas of the Iberian Peninsula
219 (Ninyerola *et al.* 2005). The value of the MARTONNE index decreases with increasing aridity.

220 The structure and composition of the tree layer were characterized by total basal area of the
221 plot (G), contribution of non-dominant (i.e. non-black pine) species to total G, and a MATURITY
222 Index, calculated as the ratio of thick wood (with $dbh > 27.5$ cm) to total basal area. Finally, the
223 characteristics of the gaps were assessed by the Canopy Openness value (CO), calculated as the
224 overall percentage of gap area in the digital hemispherical photographs (obtained with GLA
225 software, Frazer *et al.*, (1999), and two variables reflecting size and shape of the gaps: MGS (Mean
226 Gap Size, in m²) and GSI (Gap Shape Index; see Figure 2). These two variables were calculated
227 using the Patch Analysis extension for ArcGIS (Rempel, 2012) in a 9-m-radius circle set around the
228 plot center (i.e. diameter of the area of influence = 18 m, equivalent to the mean dominant height for
229 black pine in the selected stands). They complement the information given by the CO (e.g. a plot
230 with a given CO could present many small gaps of a just a few large ones), yielding information on
231 the mean size of the gaps (MGS) and their irregularity (GSI) within the area of influence around the
232 plot, ranging from 1 when all gaps are circular to higher values when they are more irregular.



233

234 **Fig. 2.** Examples of plots showing (a) high and low values of CO (Canopy Openness, calculated
 235 from hemispherical photographs); (b) high and low values of MGS (Mean Gap Size, calculated from the
 236 analysis of remote-sensing data); and (c) high and low values of GSI (Gap Shape Index,
 237 calculated from the analysis of remote sensing data).

238 **#1-column fitting image#**

239 2.5. Data analyses

240 We first executed an exploratory analysis to check for potential colinearity problems between the
 241 candidate predictors. We only found significant correlation ($P < 0.001$) between MGS and CO
 242 (Pearson's correlation coefficient = 0.313, $n = 155$) but it was considered not high enough to cause
 243 colinearity problems. Later, the regeneration abundance of the different species and development
 244 stages in each ground inventory plot were regressed against the different micro-site explanatory

245 variables and stand structural and compositional characteristics through Generalized Linear Mixed-
246 effects Models (GLMM). Since the regeneration frequency data presented numerous 'zero' counts
247 and a few very high counts, GLMMs were constructed assuming a Poisson distribution of errors with
248 a log-link function. We used penalized quaslikelihood (PQL) with restricted maximum-likelihood
249 (REML) method to estimate GLMMs parameters (Breslow and Clayton, 1993). Because our data
250 were unbalanced, we used Satterthwaite's method to determine the approximate denominator
251 degrees-of-freedom for tests. Nesting of sample plots within the 8 surveyed stands was considered
252 using STAND as a random effect in the mixed model. Selection of variables for inclusion in the final
253 models was based on likelihood ratio tests comparing the full model (i.e. that including all the
254 potential predictors) against reduced models in terms of the Bayesian information criterion (BIC).
255 Information- theoretic methods such as BIC estimate statistics that quantify the magnitude of
256 difference between models, with lower BIC values indicating stronger empirical support for a model
257 (Hoeting *et al.*, 1999). Quadratic terms for basal area, woody shrubs cover, canopy openness and
258 mean gap size (e.g. $MGS^{0.5}$ and MGS) were tested in our models to account for nonlinear responses
259 of species to these structural attributes as well as some interactions selected on a rational basis. The
260 interaction between woody shrub cover and MGS (i.e. SHRUBS*MGS) was included to test whether
261 potential facilitative or competitive effects of shrubs on the regeneration were maintained or not in
262 gaps of different sizes. We also considered the interaction between GSI and MGS (i.e. GSI*MGS) to
263 analyze the potential role of the shape of the gaps (GSI) in attenuating or amplifying the effect of the
264 gap size on the different species regeneration.

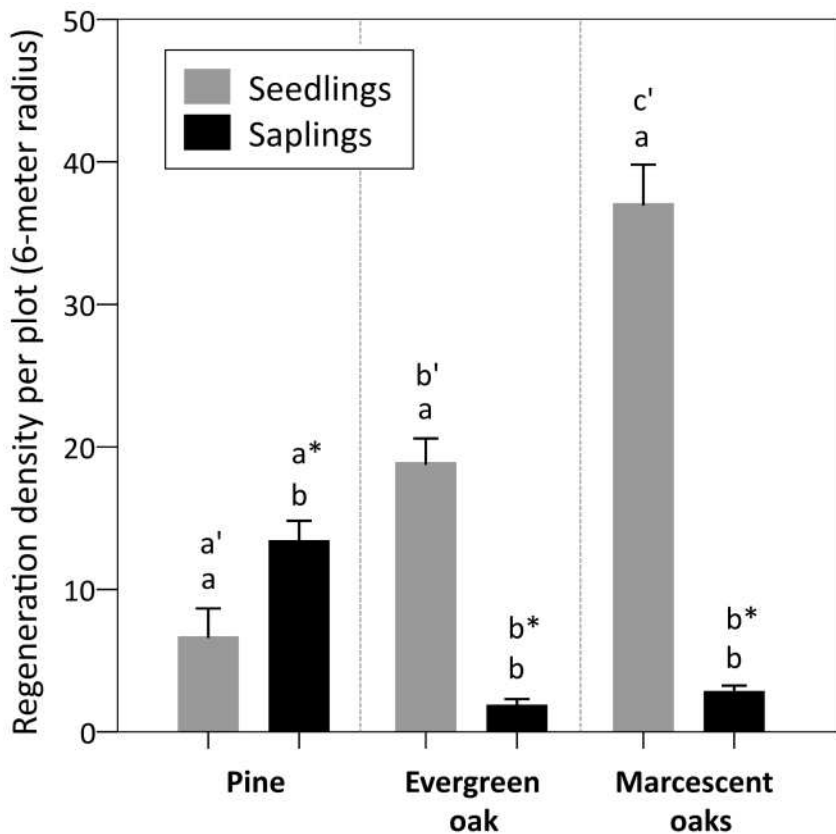
265 Once the final models had been generated for the different species and development stages
266 (i.e. seedlings and saplings), we performed linear regressions (with a zero intercept) between
267 observed regeneration density and predicted regeneration density, and used their slope and their R^2 to
268 measure the biases of the models (with an unbiased model having a slope of 1) and to estimate their
269 goodness-of-fit. In order to estimate the relative importance of each group of factors (site *vs.* stand

270 structure and composition), the final models were compared on the basis of BIC against models that
271 ignored the effect of one of the two groups, with higher variations in BIC indicating stronger effect
272 of the ignored group of factors. We also used the likelihood ratio test for model comparison, once the
273 models re-estimated by the maximum-likelihood method. GLMMs were obtained using the
274 GENLINMIXED command in IBM SPSS Statistics 22 software (IBM Corporation, 2013), while
275 model comparisons were performed using R 3.1.1 software (R Core Team, 2014) and the ‘lme4’ v.
276 1.1-7 (Bates, 2010) package.

277 **3. Results**

278 *3.1. Effect of site factors*

279 The exploratory analyses revealed more regeneration of *Quercus* species (in terms of number of
280 plants per inventoried surface) than pines in the study area (Figure 3). Oak regeneration was
281 basically present in the form of young seedlings, contrary to what was observed for pines where
282 more advanced stages (saplings) dominated. Regeneration of other deciduous tree species (grouping
283 species of the genus *Sorbus*, *Acer*, *Prunus*, etc.) was also found, but its abundance was very low both
284 for seedlings (\bar{x} : 2.6, σ : 12.0) and for saplings (\bar{x} : 1.6, σ : 3.7).



285

286 **Fig. 3.** Bar-plot showing mean and standard error of the regeneration density of the main tree species
 287 in the 155 inventory plots, separated into functional groups of species (Pine: *P. nigra*; Evergreen
 288 oak: *Q. ilex*, Marcescent oaks: *Q. faginea* & *Q. cerrroides*) and development stage (seedlings when h
 289 ≤ 1.3 m; saplings when $h > 1.3$ m and $dbh < 7.5$ cm). Plain letters indicate significant difference
 290 between seedlings and saplings of each species; letters with apostrophe (') indicate significant
 291 difference among seedlings of the different species; letters with asterisk (*) indicate significant
 292 difference among saplings of the different species.

293 **#1-column fitting image#**

294 The different variables used here to characterize the environmental characteristics of the sites
 295 were found to significantly affect the abundance of the regeneration of the studied species (Table 2).
 296 The presence of *Q. ilex* seedlings, for example, was more important in convex (i.e. ridges, spurs,
 297 upper slopes, etc.) than concave areas (i.e. valley bottoms, mid- and lower slopes, etc.), whereas
 298 pines and marcescent oak seedlings followed the opposite trend. The abundance of seedlings of
 299 evergreen oaks also showed a clear pattern in relation to site exposure, being higher with decreasing
 300 northness (i.e. conditions closer to south-facing slopes). Climatic aridity was also found to modulate
 301 the abundance of pine seedlings, which prefer drier sites. The abundance of saplings of the different
 302 species showed similar responses to site factors as seedlings, although some small differences

303 emerged (Table 3). In particular, the effect of northness shifted from non-significant in the case of
 304 pine seedlings to a positive effect on the abundance of pine saplings, and from non-significant (for
 305 seedlings) to negative (for saplings) in the case of marcescent oaks. Interestingly, climatic aridity
 306 emerged as one of the factors influencing the abundance of marcescent oaks saplings, which
 307 appeared to prefer drier sites.

308 **Table 2**

309 Coefficients for generalized linear mixed-effects models with log-link function of density of
 310 seedlings (per 6-meter radius plot) of pine, evergreen oak, and marcescent oaks in 8 sampled black
 311 pine-dominated stands. See Table 1 for abbreviations.

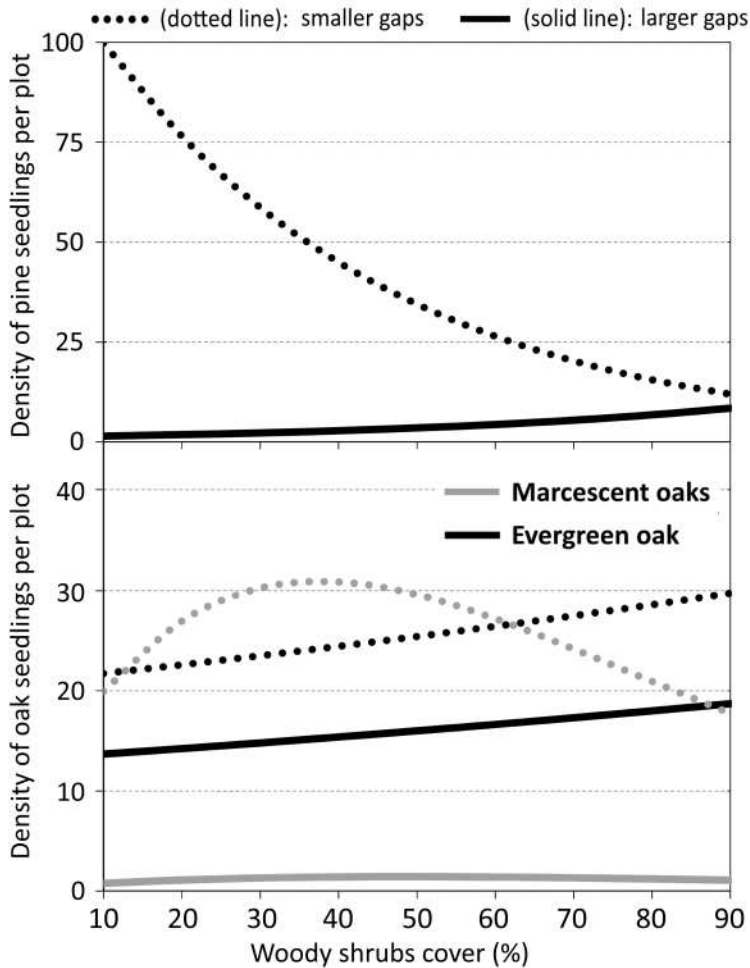
Target	Pine (<i>P. nigra</i>)				Evergreen oak (<i>Q. ilex</i>)				Marcescent oaks (<i>Q. faginea. Q. cerrioides</i>)				
	Est.	SE	t	Sig.	Est.	SE	t	Sig.	Est.	SE	t	Sig.	
Fixed effects													
Intercept	12.023	4.774	2.519	*	-12.720	1.880	-6.766	***	-4.787	1.412	-3.389	*	
<i>Site factors</i>													
CURVATURE	-0.559	0.082	-6.849	***	0.369	0.038	9.643	***	-0.266	0.024	-10.924	***	
NORTHNESS				NS	-1.673	0.154	-10.898	***				NS	
MARTONNE	-1.075	0.082	-13.093	***				NS				NS	
<i>Stand structure & composition</i>													
MATURITY	4.534	0.217	20.931	***				NS				NS	
G ^{0.5}	-0.354	0.043	-8.163	***	0.496	0.164	3.034	**	0.256	0.100	2.568	*	
G				NS	-0.040	0.013	-2.960	**	-0.026	0.008	-3.209	**	
SHRUBS ^{0.5}				NS				NS	0.607	0.066	9.129	***	
SHRUBS	-0.039	0.004	-10.756	***	0.004	0.001	3.011	**	-0.051	0.005	-10.193	***	
SHRUBS *MGS	0.0012	0.0002	6.550	***				NS	0.00014	0.00007	2.223	*	
CO ^{0.5}	10.276	1.740	5.905	***	5.855	0.769	7.611	***	3.202	0.567	5.646	***	
CO	-0.906	0.176	-5.157	***	-0.617	0.079	-7.784	***	-0.374	0.060	-6.279	***	
GSI	-3.124	0.396	-7.895	***	-0.189	0.140	-1.353	NS	-0.802	0.094	-8.497	***	
MGS ^{0.5}	2.109	0.211	10.003	***	0.383	0.093	4.098	***	0.534	0.076	7.050	***	
MGS	-0.528	0.052	-10.081	***	-0.077	0.017	-4.618	***	-0.135	0.019	-7.088	***	
GSI*MGS	0.103	0.011	9.734	***	0.014	0.003	4.721	***	0.00015	0.00007	2.223	***	
Random effects													
STAND Intercept	3.827	2.141	1.787	NS	0.315	0.176	1.795	NS	0.240	0.130	1.855	NS	

312 **Note:** Est. = Estimate; SE = Standard Error; Sig. = Significance level (*** = p < 0.001; ** = p < 0.01; * = p < 0.05;
 313 NS = p ≥ 0.05).

314 *3.2. Effects of stand structure and composition*

315 Total basal area of the plot and woody shrub cover were found to significantly affect the recruitment
 316 of all three species. Basal area exhibited a negative effect on abundance of pine seedlings but a

317 quadratic effect (i.e. first positive, later negative) on abundance of evergreen and marcescent oak
318 seedlings. Similarly, shrub cover showed a negative effect on the abundance of pine seedlings but a
319 positive effect on oak seedlings (although the effect was quadratic for marcescent oaks).
320 Interestingly, the effect of shrub cover on the density of pine seedlings was almost null in stands with
321 large gaps, in which pine regeneration was always very low. Similarly, the negative effect of the
322 shrub cover on the abundance of marcescent oaks seedlings was found to be attenuated in the case of
323 large gaps, as shown by the significant interaction between shrub cover and gap size (Table 2, Figure
324 4). The regeneration models were not improved (in terms of BIC) by the inclusion of the visual
325 estimates of the plot stoniness, the herbaceous or the moss cover for any of the species. Finally,
326 MATURITY index was positively correlated to the density of pine seedlings but did not affect oak
327 seedlings. Surprisingly, no compositional factors (i. e. relative abundance of evergreen oak,
328 marcescent oaks or broadleaves in general in the overstory) were found to have a significant effect
329 on abundance of seedlings of any of the species studied. Only the abundance of broadleaves in the
330 dominant canopy emerged as a factor negatively affecting abundance of pine saplings.



331

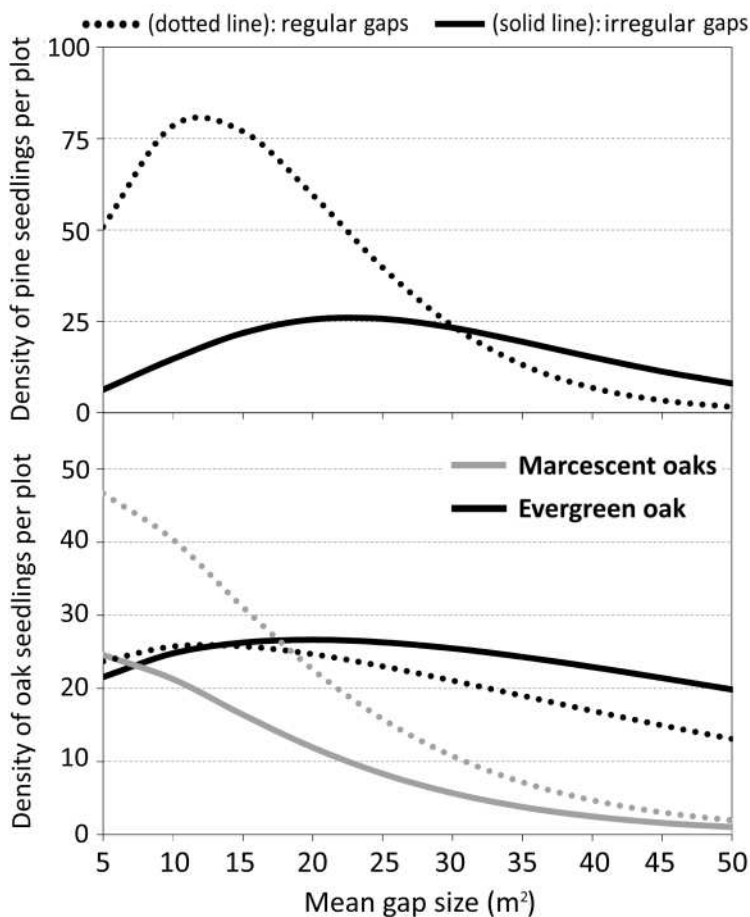
332 **Fig. 4.** Expected density of seedlings as a function of woody shrub cover and mean gap size (MGS
 333 when smaller gaps = 10 m²; MGS when larger gaps = 50 m²), according to the models presented in
 334 Table 2. For variables other than SHRUBS and MGS, mean values are used (Table 1). Plots were 6-
 335 meter radius.

336 **#1-column fitting image#**

337

338 All the gap attributes considered in the analysis showed significant effects on recruitment of
 339 all three species. Overall CO always showed a quadratic effect, revealing the existence of different
 340 optimal levels of CO depending on species. Gap attributes had wider effects on the abundance of
 341 young seedlings compared to saplings. In fact, only CO was found to modulate the abundance of the
 342 saplings of all three functional groups of species (Table 3). In the particular case of pines, CO values
 343 maximizing the abundance were significantly lower for saplings than for pine seedlings (Figure 6).
 344 Conversely, the effect of CO on abundance of evergreen oak saplings was positive and thus
 345 markedly different to its effect on the abundance of oak seedlings (Figure 6). Finally, the abundance

346 of both young seedlings and saplings of marcescent oak showed a fairly similar quadratic response to
 347 CO. For a given CO, the density of seedlings of all the species was found to be higher under small
 348 canopy gaps, or large ones if irregularly shaped. Interestingly, the interaction between the mean
 349 shape and mean size of the gaps was found to be significant in all cases, with the most irregular gaps
 350 attenuating the general negative effect of large gaps on seedling recruitment (Figure 5). Overall, we
 351 found the marcescent oaks to be much more sensitive to large openings than the evergreen ones
 352 (Figure 5).



353
 354 **Fig. 5.** Expected seedling density as a function of mean gap size and mean gap shape (GSI when
 355 circular gaps = 1.6; GSI when irregular gaps = 2.4) according to the final models presented in Table
 356 2. For variables other than MGS and GSI, mean values are used (Table 1). Plots were 6-meter radius.

357 **#1-column fitting image#**

358

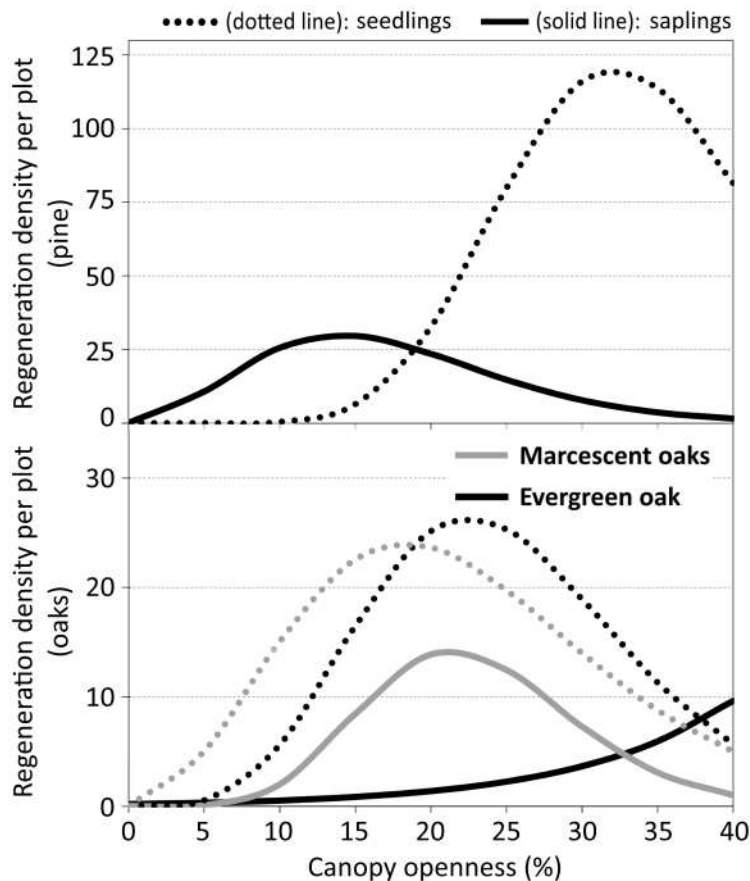
359 **Table 3**

360 Coefficients for generalized linear mixed-effects models with a log-link function for sapling density
 361 (per 6-meter radius plot) of pine, evergreen oak, and marcescent oaks in the 8 sampled black pine-
 362 dominated stands. See Table 1 for abbreviations.

Target	Pine (<i>P. nigra</i>)				Evergreen oak (<i>Q. ilex</i>)				Marcescent oaks (<i>Q. faginea. Q. cerrroides</i>)			
	Est.	SE	t	Sig.	Est.	SE	t	Sig.	Est.	SE	t	Sig.
Fixed effects												
Intercept	-1.777	2.651	-0.670	NS	-5.997	1.946	-3.081	**	-1.654	5.046	-0.328	NS
<i>Site factors</i>												
CURVATURE				NS	0.659	0.112	5.886	***				NS
NORTHNESS	0.974	0.176	5.535	***	-3.609	0.436	-8.272	***	-1.465	0.363	-4.030	***
MARTONNE	-0.193	0.040	-4.799	***				NS	-0.651	0.078	-8.299	***
<i>Stand structure & composition</i>												
MATURITY				NS				NS				NS
G ^{0.5}	1.329	0.201	6.620	***	1.838	0.576	3.191	**				NS
G	-0.131	0.017	-7.734	***	-0.161	0.049	-3.290	***	-0.034	0.004	-7.801	***
SHRUBS ^{0.5}	0.421	0.076	5.521	***				NS	1.517	0.298	5.097	***
SHRUBS	-0.049	0.006	-7.995	***				NS	-0.091	0.021	-4.389	***
SHRUBS*MGS				NS				NS				NS
Grel_BL	-2.065	0.644	-3.206	**				NS				NS
CO ^{0.5}	3.360	0.993	3.385	***				NS	8.474	1.672	5.068	***
CO	-0.449	0.105	-4.258	***	0.097	0.015	6.327	***	-0.916	0.171	-5.355	***
GSI				NS				NS				NS
MGS ^{0.5}	0.325	0.049	6.618	***	-0.229	0.059	-3.869	***				NS
MGS	-0.016	0.004	-3.688	***				NS				NS
GSI*MGS				NS				NS				NS
Random effects												
STAND Intercept	0.222	0.125	1.784	NS	0.769	0.441	1.745	NS	1.466	0.836	1.754	NS

363 **Note:** Est. = Estimate; SE = Standard Error; Sig. = Significance level (*** = p < 0.001; ** = p < 0.01; * = p < 0.05;
 364 NS = p ≥ 0.05).

365



366

367 **Fig. 6.** Expected regeneration density as a function of canopy openness (CO) according to the final
 368 models presented in Table 2 and Table 3. For variables other than CO, mean values are used (see
 369 Table 1).

370 **#1-column fitting image#**

371 *3.3. Relative importance of site and stand structural attributes in driving tree-species*

372 *regeneration*

373 The final model for predicting the abundance of both seedlings and saplings of the studied functional
 374 groups included variables related to the environmental characteristics of the sites and to the structure
 375 and composition of the adult stands (Table 4). Most of the models produced unbiased estimates of
 376 regeneration density (i.e. slopes of predicted vs. observed density were all close to 1), with the
 377 exception of those related to pine seedlings and evergreen oak saplings which showed slope values
 378 of the predicted vs observed data of 0.92 and 1.22, respectively. The models predicting the
 379 abundance of oak regeneration (both seedlings and saplings) and pine saplings explained a
 380 percentage of variance in the data (i.e. adjusted-R²) that was higher than 60%. However, our models

381 did not adequately predict the presence of pine seedlings (adjusted-R² value of 0.25). The effect of
 382 stand structural variables was particularly important to explain pine and marcescent oaks
 383 regeneration (both seedlings and saplings), as indicated by the larger increase in BIC observed when
 384 the structural factors were dropped from the final models. In contrast, site factors explained the
 385 highest portion of the variance of evergreen oak abundance (Table 4).

386 **Table 4**

387 Comparison of the alternative models for the three target species using Bayesian Information
 388 Criterion (BIC). Final models are those presented in Tables 2 and 3; partial models are the same after
 389 extracting the variables of a given group; and null models only included the intercept in the fixed
 390 effects. Higher variation in BIC (Δ BIC) indicates stronger effect of the ignored group of factors.
 391 Final and partial models always fitted significantly better ($P < 0.001$) than the respective null models
 392 according to the likelihood ratio (LR) test.

Target		Final model		Null model		Partial models	
Group	Species	Slope (bias)	Adjusted R ²	BIC _{FM}	BIC _{NM}	Δ BIC ₁ (no site)	Δ BIC ₂ (no structure)
Seedlings	<i>Pine</i>	0.92	0.25	2,461.9	3,586.3	141.9.	1,117.3
	<i>Evergreen oak</i>	1.03	0.63	2,210.1	2,573.0	202.6	160.8
	<i>Marcescent oaks</i>	1.02	0.74	3,168.2	3,694.4	68.1	453.8
Saplings	<i>Pine</i>	1.04	0.67	2,132.1	2,694.3	34.8	546.3
	<i>Evergreen oak</i>	1.22	0.60	752.5	950.3	91.3	47.5
	<i>Marcescent oaks</i>	1.05	0.63	853.7	1,071.3	86.2	108.7

393 **4. Discussion**

394 *4.1. Factors behind pine retreat*

395 We found a scarcity of young *P. nigra* seedlings in the understory of the monitored stands,
 396 suggesting ongoing recruitment limitation processes in this species. The observed recessive trend in
 397 this species has already been reported for other areas of the Iberian Peninsula (e. g., Urbieta *et al.*,
 398 2011; Carnicer *et al.*, 2013; Tiscar and Linares, 2014) and has also been observed for other
 399 Mediterranean pines (Urbieta *et al.*, 2011; Carnicer *et al.*, 2013). One of the main factors likely
 400 triggering this regeneration decrease is the low light availability that characterizes the understory of
 401 most pine stands in the Mediterranean although other factors such as the presence of a competitive
 402 grass layer can also play an important role (Lucas-Borja *et al.*, 2011; Prévosto *et al.*, 2012). In the

403 particular case of black pine, which is considered one of the most shade-tolerant European pine
404 species (Niinemets and Valladares, 2006), our models put the optimum CO for pine seedlings at
405 around 30-35%, which is higher than the CO preferred by oak seedlings. Changes in land-use
406 practices over the past few decades have notably affected the structure of most pine stands (Montes
407 *et al.*, 2005; Martin-Alcon *et al.*, 2012) and may have worsened the conditions for their regeneration.
408 In our study area, for example, we found higher pine seedlings in stands with a high presence of big
409 trees (with *dbh* > 27.5 cm) but low basal area values. However, this type of mature moderately
410 opened stand is fairly uncommon nowadays (Aunós *et al.*, 2009) due to the generalized abandon of
411 forest management that has led to active densification of the stands (Poyatos *et al.*, 2003). These
412 processes are relatively slow and have only recently reached density levels high enough to hinder
413 pine recruitment, as indicated by the higher presence of pine saplings compared to young seedlings
414 in the understory of the stands. Other factors, such as the increasing abundance of shrubs associated
415 to a general decline in grazing by domestic livestock, may also act as an aggravating factor for black
416 pine regeneration (Tiscar and Linares, 2014). Competition for light is probably at the origin of the
417 observed negative effects of shrub cover on pine seedlings. Increasing abundance of the shrubby and
418 herbaceous layer also contributes by creating an organic soil layer that acts as a physical barrier
419 preventing fallen seeds from contacting the mineral soil, which is the most appropriate seedbed for
420 pine germination (del Cerro Barja *et al.*, 2009; Lucas-Borja *et al.*, 2011). In this work we did not find
421 a significant effect of the grass layer on pine and oaks regeneration, probably due the low variation
422 found on this variable among the sample stands. Finally, we found a shift in both pine seedlings and
423 saplings towards drier sites. This might be explained by the different temporal dynamics of the tree
424 and shrub densification processes which occur more slowly in drier locations (Poyatos *et al.*, 2003;
425 Coop and Givnish, 2007; Améztegui *et al.*, 2010).

426 4.2. Factors driving tree-species diversification in black pine forests

427 Our analysis showed a progressive advance of broadleaved species recruitment (especially evergreen
428 and marcescent oak species) under the pine canopy, consistently with trends observed by other
429 authors (e. g., Urbieta *et al.*, 2011; Carnicer *et al.*, 2013; Coll *et al.*, 2013). This process is mostly
430 mediated by acorn dispersers such as jays which preferentially cache the acorns from neighboring
431 seed sources in these formations (Gómez, 2003). The very high abundance of young *Quercus*
432 seedlings compared to saplings reveals the fairly recent origin of these processes and may be a
433 response to two different drivers: (i) the relatively recent abandon of intensive grazing practices
434 (Zamora *et al.*, 2010; Navarro-González *et al.*, 2013) and (ii) the ongoing densification of the forest
435 stands and associated lack of light in the understory which prevents these shade-tolerant species
436 (Niinemets and Valladares, 2006) from thriving to more advanced developmental stages. Our results
437 provide evidence of the important role that site factors play in the observed niche regeneration
438 partitioning between evergreen and marcescent oaks, with evergreens being more competitive in
439 harsher site conditions (i.e. south-facing slopes and shallower soils) while marcescents are more
440 competitive in sites with higher soil moisture availability. In contrast, other variables related to stand
441 structure and canopy attributes seem to very similarly affect regeneration rates of all oaks. Contrary
442 to pines, shrubs were found to be a positive driver of oaks recruitment under the pine canopy. Oak
443 recruitment largely depends on seed dispersers like jays and mice that cache acorns at suitable
444 places, such as shrubs (Gómez, 2003). Shrubs could also improve germination and emergence
445 conditions and facilitate seedling survival by improving nutrient and water availability, reducing soil
446 compaction, and offering protection against browsing by ungulates (Rousset and Lepart, 1999;
447 Gómez-Aparicio *et al.*, 2005; Kunstler *et al.*, 2007; Smit *et al.*, 2008). However, our results indicate
448 that in some situations the shrubby layer can increase its development in terms of cover and biomass
449 up to a point at which the positive effect on marcescent oak recruitment turns negative.

450 Despite their contrasting leaf habit, both evergreen and marcescent oak seedlings showed
451 fairly similar preferences in terms of overstory structure, with maximum recruitment occurring at

452 around 15-25% CO (which matches the average CO currently found in the monitored black pine-
453 dominated stands; see Table 1). Several studies have described the relatively high moisture levels
454 that *Q. ilex* requires to effectively germinate and establish (Broncano *et al.*, 1998). These
455 requirements are usually found under moderately-closed pine canopies, where the water status of the
456 plants is generally improved through the protection provided by the overstory from direct exposure
457 to light and high evaporative demands (Retana *et al.*, 1999; Lookingbill and Zavala, 2000; Caldeira
458 *et al.*, 2014). Interestingly, we found the evergreen and the marcescent oaks to have noticeable
459 different preferences in terms of spatial distribution and morphology of gaps in the forest canopy. In
460 the case of the marcescent oaks, seedling recruitment was found to be particularly important under
461 small or irregularly shaped canopy gaps, confirming their high sensitivity to high light exposure
462 found in stands with large and more regular (i. e. circular) openings (Marañón *et al.*, 2004; Gómez-
463 Aparicio *et al.*, 2008). On the other hand, the evergreen oak's seedling bank was rather similar along
464 the sampled gradient of gap sizes and shapes; which indicates its higher tolerance to direct light
465 exposure, in agreement with what was previously reported in other mountain areas (Gómez-Aparicio
466 *et al.* 2008).

467 Once the oak seedlings have established, the evergreen and marcescent oaks seem to have
468 different environmental requirements in order to grow and reach more advanced developmental
469 stages. Previous studies have shown higher height growth in young seedlings of evergreen oaks
470 compared to marcescent ones under shade conditions (Gómez-Aparicio *et al.*, 2006; Prévosto *et al.*,
471 2011). However, the marcescents presented in general better performance suggesting that the
472 stronger vertical growth of *Q. ilex* occurred at the expense of root growth and overall fitness. In our
473 study, we found considerably higher density of saplings of the marcescent oaks (*Q. faginea*, *Q.*
474 *cerrrioides*) than the evergreen *Q. ilex* under the closed-canopy conditions that characterize most of
475 the studied stands, which may suggest a higher capacity of the first for coping with low light levels
476 (i.e. canopy openness). Under shade conditions, the established *Q. ilex* are nevertheless able to

477 persist without significant net growth (Espelta *et al.*, 1995; Garcia-Barreda and Reyna, 2013),
478 forming dense seedling banks and perpetuating through repeated shoot dieback and re-sprout until
479 light conditions improve (Johnson, 2009).

480 4.3. Management implications.

481 Our study analyzes the factors driving the current tree-species diversification of long-term-managed
482 *P. nigra* stands in the Catalan Pre-Pyrenees (NE Spain). These diversification processes are
483 characterized by the gradual return of shade-tolerant broadleaved species, and are considered to
484 enhance the capacity of these systems to adapt and respond to rapid environmental changes. In those
485 areas where these processes do not occur naturally, forest managers could envisage practices
486 designed to help generate a diversity of traits of responses to change (e.g. drought tolerance, seed
487 mobility, resprouting ability) and promote functional redundancies (i.e. coexisting species with
488 similar response traits, which would provide resilience in terms of maintaining productivity and other
489 functions in the face of species loss). The results of our study bring insights into the role of a number
490 of stand-level drivers that modulate these processes. This information can be used by forest
491 managers to adjust their practices oriented to modify stand structure and canopy attributes in order to
492 favor this natural diversification process and increase stand resilience to the various components of
493 global change. In the particular case of Mediterranean *P. nigra* stands, we show current levels of
494 both canopy closure and shrub cover are adequate to allow the establishment of *Quercus* seedlings
495 but too high to permit pine regeneration. In addition, the low level of light reaching the understory
496 hampers the growth of established oaks (particularly *Q. ilex*) which may prove unable to reach
497 sapling and pole stages. If the densification of the pine canopy continues at the current rate, the light
498 arriving at the understory will probably soon become too low to allow oak recruitment, in which case
499 the currently active diversification process would likely slow until small-scale disturbances occur.
500 According to our results, the application of frequent low-intensity selection cuttings could revert this

501 process by helping to maintain an adequate amount of light for oaks seedlings to establish in the
502 understory. If this type of management is applied in a heterogeneous way, with low to medium
503 variation of intensity along the stand, and it is accompanied by understory treatments such as partial
504 shrub-layer removal, pine regeneration and growth and oak seedling development would be also
505 favored and the future persistence of the mixed stand promoted.

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518

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