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

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

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1. Introduction

The distribution, structure and composition of Mediterranean forests have been shaped over millennia by human practices (Debussche et al., 1999; Vallejo, 2005; Nocentini and Coll, 2013). Over time, this long history of human use has resulted in a significant reduction of the extent and inherent structural and compositional diversity of Mediterranean forests (Ciancio and Nocentini, 2000; Blondel, 2006). In the context of the Iberian Peninsula, this long history of intense human-use reached its peak at the end of the 19th century (García-Ruiz et al., 1996; Pausas et al., 2004; Linares et al., 2010). However, the 20th century brought major socioeconomic changes leading to generalized land abandonment processes in marginal areas -generally mountainous systems- and to land-use intensification in broad valleys and coastal regions (García-Ruiz et al., 1996; Vicente-Serrano et al., 2004; Lasanta-Martinez et al., 2005; Chauchard et al., 2007). This, together with extensive reforestation programs initiated with the aim of restoring the most heavily-degraded areas -most of which with pine species-, have triggered extended encroachment and densification processes in forest stands (Ameztegui et al., 2010; Navarro and Pereira, 2012; Ruiz-Benito et al., 2012). Black pine-dominated forests (Pinus nigra Arn. ssp. salzmannii) in the Pre-Pyrenean range (NE Spain) are clear examples of forests undergoing such processes. These forests were intensively managed for timber harvesting and pasture grazing until the mid-20th century (Ruiz de la Torre, 2006), but from that point onwards the intensity of human practices decreased significantly (Vicente-Serrano et al., 2004). During the past few decades, just a few individual-tree selection cuttings affecting only the most vigorous and well-shaped trees have been conducted on these forests (Trasobares and Pukkala, 2004; Aunós et al., 2009). Such lessening of human pressure (particularly the strong decrease of silvicultural

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interventions and livestock grazing) has allowed the establishment of new cohorts of the dominant pine species, causing a generalized densification of the stands (DGCN, 2005) and a progressive process of colonization by late-successional tree species, mainly Quercus species (e.g., Urbiet et al., 2011; Carnicer et al., 2014; Vayreda et al., 2013).

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

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

The occurrence of natural or anthropogenic small-scale disturbances leading to moderate openings of the stands is a key element of the above mentioned process of tree-species diversification. These openings generate heterogeneity in the understory and lead to micro-site-level changes in environmental conditions (humidity, temperature) and resource availabilities (e.g. light, soil water) allowing the seedlings of the dominant species and those coming from adjacent stands to prosper (Runkle, 1981; Runkle and Yetter, 1987; Yamamoto, 2000; Ligot et al., 2014).

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

2. Materials and methods

2.1. Study area and stands selection

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

![Fig. 1](image-url) Location of the study area (a), the sampled stands (b), and the inventory plots within one of the stands (c).
A set of eight stands were selected along the study area (Fig. 1) based on the following three criteria: (i) patches larger than 2 hectares and clearly dominated by black pine at the canopy level (i.e., with black pine occupancy > 90% of total basal area), (ii) not coming from recently abandoned open-areas (i.e. agricultural land, grassland, shrubland), and (iii) with absence of signs of any recent silvicultural interventions or grazing activity. The first criterion was checked with the help of the third Spanish National Forest Inventory plots (which provided information on current structure and composition) (DGCCN, 2005), the Spanish National Forest Map 1:50.000 (DGCCN, 2001), and the third version of the Land Cover Map of Catalonia (CREAF, 2007). The second criterion was tested by visually comparing the most recent aerial photographs of the area (taken in 2012) and the most ancient ones (taken in 1956) and aimed at discarding from the study those young stands established in open-areas recently abandoned which due to their young age were much less susceptible of undergoing diversification processes by late-successional tree species (Puerta-Piñero et al., 2012). Twelve stands meeting the first two criteria were preselected and examined on-site in order to detect signs of recent silvicultural interventions or grazing activity. Four of the twelve preselected stands did not meet this criterion and were ultimately discarded from analysis.

2.2. Remote sensing data acquisition and pre-processing

Two different sources of remote sensing data were used to characterize the forest canopy: aerial Light Detection and Ranging (LiDAR) and multi-spectral aerial imagery (including red–green–blue (RGB) and near-infrared (IR) bands). The LiDAR-derived data consisted in a two-meter resolution DVM (Digital Vegetation Model) generated in the framework of the LiDARCAT project led by the Cartographic and Geological Institute of Catalonia (ICGC). Flight dates ranged from April 2009 to August 2009 and provided a minimum first-return density of 0.5 pulses m⁻² and an overall quantity of four height bins per first return. The RGB and near-IR data were obtained from multi-spectral aerial photographs taken in the framework of the ICGC’s annual coverage flights at 22 cm GSD (ground sample distance). The imagery was taken in the same time period as the LiDAR data, with DMC 26 and DMC 14 cameras.

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

2.3. Sampling design and field inventory

In order to cover a wide gradient of canopy openness and heterogeneity in the study area, we established the field inventory plots using a stratified random design. First, a 20 × 20 m mesh was created within each selected stand and the percentage of area covered by the ‘GAPS’ class in the area surrounding each point in the mesh was computed. For this purpose we used a 18-m diameter of the area of influence, equivalent to the mean dominant height for black pine in the selected stands. Then, four classes of gap abundance were created: (0: gap percentage ranging from 0% to 5%; 1: gap percentage ranging from 5% to 15%; 2: gap percentage ranging from 15% to 30%; 3: gap percentage above 30%). Those plots located at less than 10 m from patches classified as ‘OPEN AREA’ (e.g. roads, agricultural field, harvested areas, etc.) were rejected. Second, 5 points in each class of gap abundance were randomly selected in each plot and used to locate the inventory plots (160 in total, 20 per stand). Inventory plots were circular, with a 6-m radius centered at the randomly selected points. In each plot, a set of site attributes including UTM central coordinates, slope and aspect were collected. The tree canopy layer was characterized by identifying the species and measuring the diameter at breast height (dbh) of all trees with dbh > 7.5 cm. Percentage of soil covered by woody shrubs was also estimated. The most frequent shrubby species in the understory was common box (Buxus sempervirens L.), followed by the two main juniper species in the area (Juniperus communis L. and Juniperus oxycedrus L.), and the kermes oak (Quercus cocifera L.). Other species of the genus Crataegus, Rhamnus, Viburnum, Rubus, Lonicera, etc. were also very frequently inventoried. Finally, the abundance of stones, herbs and moss were visually estimated and classified into three categories (low: less than 1/3 of the plot area; medium: between 1/3 and 2/3 of the plot area; and high: more than 2/3 of the plot area).

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

2.4. Data processing

Both field and remote sensing-derived data were processed and grouped for subsequent analysis into a number of response and explanatory variables. As response variables, we used the abundance of regeneration found in the understory, grouped by development stage (seedlings and saplings), and functional types: (1) pines, only represented by the pine species dominating the tree canopy (P. nigra Arn. ssp. salzmannii); (2) evergreen oaks, represented by the only one species appearing in the area (Quercus ilex L.); and (3) semi-deciduous (marcescent) oaks, represented by two species (Quercus faginea Lam. and Quercus cerrifolia Willk & Costa). Although the field inventories also recorded the presence of other broadleaved species (e.g. Sorbus, Acer), we discarded them from the analysis due to the shortage of individuals.

The quantitative explanatory variables derived from the field surveys and remote-sensing data included environmental descriptors of the sites and different variables related to stand structure and composition, including the gap attributes (see Table 1). In relation to the first group of variables, we computed three different indexes (NORTHENESS, CURVATURE and MARTONNE) with the aim of broadly characterizing the climatic and topographic conditions at each plot. The NORTHENESS Index was calculated as the product of the slope (%) and the cosine of the aspect (degrees) measured in the field inventory (Holden et al., 2009). This index was used as a proxy for solar radiation budget at the plot surface, and took higher positive values as aspect gets closer to North and slope increases, and lower negative values as aspect
Table 1

<table>
<thead>
<tr>
<th>Variable, unit</th>
<th>Min.</th>
<th>Max.</th>
<th>Mean</th>
<th>Std. Dev.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site factors</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CURVATURE Index</td>
<td>-1.77</td>
<td>2.17</td>
<td>0.10</td>
<td>0.65</td>
</tr>
<tr>
<td>NORTHESS Index</td>
<td>-0.38</td>
<td>0.60</td>
<td>0.22</td>
<td>0.18</td>
</tr>
<tr>
<td>MARTONNE Index</td>
<td>28.47</td>
<td>35.47</td>
<td>32.69</td>
<td>1.27</td>
</tr>
<tr>
<td>Stand structure &amp; composition</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MATUREITY Index</td>
<td>0.00</td>
<td>0.99</td>
<td>0.22</td>
<td>0.26</td>
</tr>
<tr>
<td>G (Basal Area), m²/ha</td>
<td>5.81</td>
<td>75.76</td>
<td>37.36</td>
<td>14.10</td>
</tr>
<tr>
<td>SHRUBS (woody shrubs cover), %</td>
<td>1.00</td>
<td>95.00</td>
<td>48.67</td>
<td>24.81</td>
</tr>
<tr>
<td>Grel_BL (rel. G of broadleaves), ppu</td>
<td>0.00</td>
<td>0.22</td>
<td>0.03</td>
<td>0.05</td>
</tr>
<tr>
<td>Grel_Qm (rel. G of marcescent Q. spp.), ppu</td>
<td>0.00</td>
<td>0.22</td>
<td>0.02</td>
<td>0.04</td>
</tr>
<tr>
<td>Grel_Qi (rel. G of evergreen Q. ilex), ppu</td>
<td>0.00</td>
<td>0.16</td>
<td>0.00</td>
<td>0.02</td>
</tr>
<tr>
<td>CO (Canopy Openness), %</td>
<td>12.72</td>
<td>38.54</td>
<td>21.16</td>
<td>4.82</td>
</tr>
<tr>
<td>GSI (Gap Shape Index)</td>
<td>0.00</td>
<td>4.05</td>
<td>1.98</td>
<td>0.34</td>
</tr>
<tr>
<td>MGS (Mean Gap Size), meters</td>
<td>0.00</td>
<td>141.60</td>
<td>14.97</td>
<td>18.35</td>
</tr>
</tbody>
</table>

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

The different variables used here to characterize the environmental characteristics of the sites were found to significantly affect the abundance of the regeneration of the studied species (Table 2).
The presence of *Q. ilex* seedlings, for example, was more important in convex (i.e. ridges, spurs, upper slopes, etc.) than concave areas (i.e. valley bottoms, mid- and lower slopes, etc.), whereas pines and marcescent oak seedlings followed the opposite trend. The abundance of seedlings of evergreen oaks also showed a clear pattern in relation to site exposure, being higher with decreasing northness (i.e. conditions closer to south-facing slopes). Climatic aridity was also found to modulate the abundance of pine seedlings, which prefer drier sites. The abundance of saplings of the different species showed similar responses to site factors as seedlings, although some small differences emerged (Table 3). In particular, the effect of northness shifted from non-significant in the case of pine seedlings to a positive effect on the abundance of pine saplings, and from non-significant (for seedlings) to negative (for saplings) in the case of marcescent oaks. Interestingly, climatic aridity emerged as one of the factors influencing the abundance of marcescent oaks saplings, which appeared to prefer drier sites.

### 3.2. Effects of stand structure and composition

Total basal area of the plot and woody shrub cover were found to significantly affect the recruitment of all three species. Basal area exhibited a negative effect on abundance of pine seedlings but a quadratic effect (i.e. first positive, later negative) on abundance of evergreen and marcescent oak seedlings. Similarly, shrub cover showed a negative effect on the abundance of pine seedlings but a positive effect on oak seedlings (although the effect was quadratic for marcescent oaks). Interestingly, the effect of shrub cover on the density of pine seedlings was almost null in stands with large gaps, in which pine regeneration was almost null (Table 2, Fig. 4). The regeneration models were not improved (in terms of BIC) by the inclusion of the visual
estimates of the plot stoniness, the herbaceous or the moss cover for any of the species. Finally, MATURITY index was positively correlated to the density of pine seedlings but did not affect oak seedlings. Surprisingly, no compositional factors (i.e. relative abundance of evergreen oak, marcescent oaks or broadleaves in general in the overstory) were found to have a significant effect on abundance of seedlings of any of the species studied. Only the abundance of broadleaves in the dominant canopy emerged as a factor negatively affecting abundance of pine saplings.

All the gap attributes considered in the analysis showed significant effects on recruitment of all three species. Overall CO always showed a quadratic effect, revealing the existence of different optimal levels of CO depending on species. Gap attributes had wider effects on the abundance of young seedlings compared to saplings. In fact, only CO was found to modulate the abundance of the saplings of all three functional groups of species (Table 3). In the particular case of pines, CO values maximizing the abundance were significantly lower for saplings than for pine seedlings (Fig. 6). Conversely, the effect of CO on abundance of evergreen oak saplings was positive and thus markedly different to its effect on the abundance of oak seedlings (Fig. 6). Finally, the abundance of both young seedlings and saplings of marcescent oak showed a fairly similar quadratic response to CO. For a given CO, the density of seedlings of all the species was found to be higher under small canopy gaps, or large ones if irregularly shaped. Interestingly, the interaction between the mean shape and mean size of the gaps was found to be significant in all cases, with the most irregular gaps attenuating the general negative effect of large gaps on seedling recruitment (Fig. 5). Overall, we found the marcescent oaks to be much more sensitive to large openings than the evergreen ones (Fig. 5).

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

The final model for predicting the abundance of both seedlings and saplings of the studied functional groups included variables related to the environmental characteristics of the sites and to the structure and composition of the adult stands (Table 4). Most of the models produced unbiased estimates of regeneration density (i.e. slopes of predicted vs. observed density were all close to 1), with the exception of those related to pine seedlings and evergreen oak saplings which showed slope values of the predicted vs observed data of 0.92 and 1.22, respectively. The models predicting the abundance of oak regeneration (both seedlings and saplings) and pine saplings explained a percentage of variance in the data (i.e. adjusted-R²) that was higher than 60%. However, our models did not adequately predict the presence of pine seedlings.

Table 2

<table>
<thead>
<tr>
<th>Target</th>
<th>Fixed effects</th>
<th>Evergreen oak (Q. ilex)</th>
<th>Marcescent oaks (Q. faginea, Q. cerrioides)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Intercept</td>
<td>Est. 12.023  SE 4.774</td>
<td>Est. -12.720  SE 1.880  Sig. -6.766</td>
</tr>
<tr>
<td></td>
<td>CO&lt;sup&gt;0.5&lt;/sup&gt;</td>
<td>-0.559  0.082</td>
<td>0.369  0.038  9.643  ***</td>
</tr>
<tr>
<td></td>
<td>CO&lt;sup&gt;1&lt;/sup&gt;</td>
<td>-0.040  0.013</td>
<td>-1.673  0.154  -10.898  ***</td>
</tr>
<tr>
<td></td>
<td>SHRB&lt;sup&gt;0.5&lt;/sup&gt;</td>
<td>-1.075  0.082</td>
<td>-13.093                           ***</td>
</tr>
<tr>
<td></td>
<td>SHRB&lt;sup&gt;1&lt;/sup&gt;</td>
<td>0.0012  0.0002</td>
<td>6.550                           ***</td>
</tr>
<tr>
<td></td>
<td>SHRB&lt;sup&gt;1&lt;/sup&gt; + MGS</td>
<td>0.0012  0.0002</td>
<td>6.550                           ***</td>
</tr>
<tr>
<td></td>
<td>STAND Intercept</td>
<td>3.827  2.141</td>
<td>1.787                           NS</td>
</tr>
</tbody>
</table>

Note: Est. = Estimate; SE = Standard Error; Sig. = Significance level (** = p < 0.001; * = p < 0.01; ns = p > 0.05).

Fig. 3. Bar-plot showing mean and standard error of the regeneration density of the main tree species in the 155 inventory plots, separated into functional groups of species (Pine: P. nigra; Evergreen oak: Q. ilex, Marcescent oaks: Q. faginea & Q. cerrioides) and development stage (seedlings when h ≤ 1.3 m; saplings when h > 1.3 m and ddbh < 7.5 cm). Plain letters indicate significant difference between seedlings and saplings of each species; letters with apostrophe (’) indicate significant difference among seedlings of the different species; letters with asterisk (*) indicate significant difference among saplings of the different species.
The effect of stand structural variables was particularly important to explain pine and marcescent oaks regeneration (both seedlings and saplings), as indicated by the larger increase in BIC observed when the structural factors were dropped from the final models. In contrast, site factors explained the highest portion of the variance of evergreen oak abundance (Table 4).

Table 3
Coefficients for generalized linear mixed-effects models with a log-link function for sapling density (per 6-m radius plot) of pine, evergreen oak, and marcescent oaks in the 8 sampled black pine-dominated stands. See Table 1 for abbreviations.

<table>
<thead>
<tr>
<th>Target</th>
<th>Fixed effects</th>
<th>Evergreen oak (Q. ilex)</th>
<th>Marcescent oaks (Q. faginea, Q. cerrioides)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Est. SE t Sig.</td>
<td>Est. SE t Sig.</td>
<td>Est. SE t Sig.</td>
</tr>
<tr>
<td>Intercept</td>
<td>-1.777 2.651 -0.670 NS</td>
<td>-5.997 1.946 -3.081 ++</td>
<td>-1.654 5.046 -0.328 NS</td>
</tr>
<tr>
<td>Site factors</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>CURVATURE</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NORTHESS</td>
<td>0.974 0.176 5.535 +++</td>
<td>-3.609 0.436 -8.272 +++</td>
<td>-1.465 0.363 -4.030 +++</td>
</tr>
<tr>
<td>MARTONNE</td>
<td>-0.193 0.040 -4.799 +++</td>
<td></td>
<td>-0.651 0.078 -8.299 +++</td>
</tr>
<tr>
<td>Stand structure &amp; composition</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MATURE</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>G              0.5</td>
<td>1.329 0.201 6.620 +++</td>
<td>1.838 0.576 3.191 ++</td>
<td>0.034 0.004 -7.801 +++</td>
</tr>
<tr>
<td>G              0.75</td>
<td>-0.131 0.017 -7.734 +++</td>
<td>-0.161 0.049 -3.290 +++</td>
<td>-0.091 0.021 -4.389 +++</td>
</tr>
<tr>
<td>SHRUBS+MGS</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grel, BL</td>
<td>-2.065 0.644 -3.206 ++</td>
<td></td>
<td></td>
</tr>
<tr>
<td>CO                 0.5</td>
<td>3.360 0.993 3.385 +++</td>
<td></td>
<td></td>
</tr>
<tr>
<td>CO                 0.75</td>
<td>-0.449 0.105 -4.258 +++</td>
<td>0.097 0.015 6.327 +++</td>
<td>-0.916 0.171 -5.355 +++</td>
</tr>
<tr>
<td>GSI</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MGS              0.5</td>
<td>0.325 0.049 6.618 +++</td>
<td>-0.229 0.059 -3.869 +++</td>
<td>-0.161 0.004 -6.388 +++</td>
</tr>
<tr>
<td>MGS</td>
<td>-0.016 0.004 -3.688 +++</td>
<td></td>
<td></td>
</tr>
<tr>
<td>GSI+MGS</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Random effects</td>
<td>Est. SE Z Sig.</td>
<td>Est. SE Z Sig.</td>
<td>Est. SE Z Sig.</td>
</tr>
<tr>
<td>STAND Intercept</td>
<td>0.222 0.125 1.784 NS</td>
<td>0.769 0.441 1.745 NS</td>
<td>1.466 0.836 1.754 NS</td>
</tr>
</tbody>
</table>

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

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

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

4.1. Factors behind pine retreat

We found a scarcity of young P. nigra seedlings in the understory of the monitored stands, suggesting ongoing recruitment limitation processes in this species. The observed recessive trend in this species has already been reported for other areas of Iberian Peninsula (e.g., Urbieita et al., 2011; Carnicer et al., 2014; Tiscar and Linares, 2014) and has also been observed for other Mediterranean pines (Urbieita et al., 2011; Carnicer et al., 2014). One of the main factors likely triggering this regeneration decrease is the low light availability that characterizes the understory of most pine stands in the Mediterranean although other factors such as the presence of a competitive grass layer can also play an important role (Lucas-Borja et al., 2011; Prévosto et al., 2012). In the particular case of black pine, which is considered one of the most shade-tolerant European pine species (Niinemets and Valladares, 2006), our models put the optimum CO for pine seedlings at around 30–35%, which is higher than the CO preferred by oak seedlings. Changes in land-use practices over the past few decades have notably affected the structure of most pine stands (Montes et al., 2005; Martin-Alcon et al., 2012) and may have worsened the conditions for their regeneration. In our study area, for example, we found higher pine seedlings in stands with a high presence of big trees (with dbh > 27.5 cm) but low basal area values. However, this type of mature moderately opened stand is fairly uncommon nowadays (Aunós et al., 2009) due to the generalized abandon of forest management that has led to active densification of the stands (Poyatos et al., 2003). These processes are relatively slow and have only recently reached density levels high enough to hinder pine recruitment, as indicated by the higher presence of pine saplings compared to young seedlings in the understory of the stands. Other factors, such as the increasing abundance of shrubs associated to a general decline in grazing by domestic livestock, may also act as an aggravating factor for black pine regeneration (Tiscar and Linares, 2014). Competition for light is probably at the origin of the observed negative effects of shrub cover on pine seedlings. Increasing abundance of the shrubby and herbaceous layer also contributes by creating an organic soil layer that acts as a physical barrier preventing fallen seeds from contacting the mineral soil, which is the most appropriate seedbed for pine germination (del Cerro Barja et al., 2009; Lucas-Borja et al., 2011). In this work we did not find a significant effect of the grass layer on pine and oaks regeneration, probably due the low variation found on this variable among the sample stands. Finally, we found a shift in both pine seedlings and saplings towards drier sites. This might be explained by the different temporal dynamics of the tree and shrub densification processes which occur more slowly in drier locations (Poyatos et al., 2003; Coop and Givnish, 2007; Ameztegui et al., 2010).

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

Our analysis showed a progressive advance of broadleaved species recruitment (especially evergreen and marcescent oak species) under the pine canopy, consistently with trends observed by other authors (e.g., Urbieita et al., 2011; Carnicer et al., 2014; Coll et al., 2013; Vayreda et al., 2013). This process is mostly mediated by acorn dispersers such as jays which preferentially cache the acorns from neighboring seed sources in these formations (Gómez, 2003). The very high abundance of young Quercus seedlings compared to saplings reveals the fairly recent origin of these processes and may be a response to two different drivers: (i) the relatively recent abandon of intensive grazing practices (Zamora et al., 2010; Navarro-González et al., 2013) and (ii) the ongoing densification of the forest stands and associated lack of light in the understory which prevents these shade-tolerant species (Niinemets and Valladares, 2006) from thriving to more advanced developmental stages. Our results provide evidence of the important role that site factors play in the observed niche regeneration partitioning between evergreen and marcescent oaks, with evergreens being more competitive in harsher site conditions (i.e., south-facing

Table 4

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

<table>
<thead>
<tr>
<th>Target</th>
<th>Group</th>
<th>Species</th>
<th>Final model</th>
<th>Null model</th>
<th>Partial models</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Slope (bias)</td>
<td>Adjusted $R^2$</td>
<td>BIC$_{TM}$</td>
</tr>
<tr>
<td>Seedlings</td>
<td>Pine</td>
<td>0.92</td>
<td>0.25</td>
<td>2461.9</td>
<td>3586.3</td>
</tr>
<tr>
<td></td>
<td>Evergreen oak</td>
<td>1.03</td>
<td>0.63</td>
<td>2210.1</td>
<td>2573.0</td>
</tr>
<tr>
<td></td>
<td>Marcescent oaks</td>
<td>1.02</td>
<td>0.74</td>
<td>3168.2</td>
<td>3694.4</td>
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<tr>
<td>Saplings</td>
<td>Pine</td>
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<td>0.67</td>
<td>2132.1</td>
<td>2694.3</td>
</tr>
<tr>
<td></td>
<td>Evergreen oak</td>
<td>1.22</td>
<td>0.60</td>
<td>752.5</td>
<td>950.3</td>
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<tr>
<td></td>
<td>Marcescent oaks</td>
<td>1.05</td>
<td>0.63</td>
<td>853.7</td>
<td>1071.3</td>
</tr>
</tbody>
</table>

Fig. 6. Expected regeneration density as a function of canopy openness (CO) according to the final models presented in Table 2 and Table 3. For variables other than CO, mean values are used (see Table 1).
slopes and shallower soils) while marcescent oak seedlings are more competitive in sites with higher soil moisture availability. In contrast, other variables related to stand structure and canopy attributes seem to very similarly affect regeneration rates of all oaks. Contrary to pines, shrubs were found to be a positive driver of oaks recruitment under the pine canopy. Oak recruitment largely depends on seed dispersers like jays and mice that cache acorns at suitable places, such as shrubs (Gómez, 2003). Shrubs could also improve germination and emergence conditions and facilitate seedling survival by improving nutrient and water availability, reducing soil compaction, and offering protection against browsing by ungulates (Rousset and Lepart, 1999; Gómez-Aparicio et al., 2005; Kunstler et al., 2007; Smit et al., 2008). However, our results indicate that in some situations the shrubby layer can increase its development in terms of cover and biomass up to a point at which the positive effect on marcescent oak recruitment turns negative.

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

Once the oak seedlings have established, the evergreen and marcescent oaks seem to have different environmental requirements in order to grow and reach more advanced developmental stages. Previous studies have shown higher height growth in young seedlings of evergreen oaks compared to marcescent ones under shade conditions (Gómez–Aparicio et al., 2006; Prévosto et al., 2011). However, the marcescents presented in general better performance suggesting that the stronger vertical growth of Q. ilex occurred at the expense of root growth and overall fitness. In our study, we found considerably higher density of saplings of the marcescent oaks (Q. faginea, Q. cerrisoides) than the evergreen Q. ilex under the closed-canopy conditions that characterize most of the studied stands, which may suggest a higher capacity of the first for coping with low light levels (i.e. canopy openness). Under shade conditions, the established Q. ilex are nevertheless able to persist without significant net growth (Espelta et al., 1995; García-Barreda and Reyna, 2013), forming dense seedling banks and perpetuating through repeated shoot dieback and re-sprouting until light conditions improve (Johnson et al., 2009).

4.3. Management implications

Our study analyzes the factors driving the current tree-species diversification of long-term-managed P. nigra stands in the Catalan Pre-Pyrenees (NE Spain). These diversification processes are characterized by the gradual return of shade-tolerant broad-leaved species, and are considered to enhance the capacity of these systems to adapt and respond to rapid environmental changes. In those areas where these processes do not occur naturally, forest managers could envisage practices designed to help generate a diversity of traits of responses to change (e.g. drought tolerance, seed mobility, resprouting ability) and promote functional redundancies (i.e. coexisting species with similar response traits, which would provide resilience in terms of maintaining productivity and other functions in the face of species loss). The results of our study bring insights into the role of a number of stand-level drivers that modulate these processes. This information can be used by forest managers to adjust their practices oriented to modify stand structure and canopy attributes in order to favor this natural diversification process and increase stand resilience to the various components of global change. In the particular case of Mediterranean P. nigra stands, we show current levels of both canopy closure and shrub cover are adequate to allow the establishment of Quercus seedlings but too high to permit pine regeneration. In addition, the low level of light reaching the understory hampers the growth of established oaks (particularly Q. ilex) which may prove unable to reach sapling and pole stages. If the densification of the pine canopy continues at the current rate, the light arriving at the understory will probably soon become too low to allow oak recruitment, in which case the currently active diversification process would likely slow until small-scale disturbances occur. According to our results, the application of frequent low-intensity selection cuttings could revert this process by helping to maintain an adequate amount of light for oaks seedlings to establish in the understory. If this type of management is applied in a heterogeneous way, with low to medium variation of intensity along the stand, and it is accompanied by understory treatments such as partial shrub-layer removal, pine regeneration and growth and oak seedling development would be also favored and the future persistence of the mixed stand promoted.

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