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RESEARCH

Natural regeneration dynamics and diversity in *Pinus sylvestris* stands: recommendations for mediterranean forest management

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Abstract

In Serra da Nogueira (northern Portugal), a Natura 2000 site characterized by extensive *Quercus pyrenaica* forests, even-aged stands of *Pinus sylvestris* (62–68 years old), originally established for timber, currently lacks silvicultural strategies aligned with biodiversity, regeneration and resilience goals. This study analyzed natural regeneration, and species diversity at the plot scale in two even-aged *P. sylvestris* stands with contrasting regeneration status and structural conditions, under closed canopy and gap environments. We quantified seedling and sapling abundance by species and analyzed their response to stand structural and environmental variables, including basal area, canopy and shrub cover, LAI, phytovolume, and distance to seed sources. Diversity indices from the Hill series, principal component and redundancy analyses, and species response modeling using generalized additive and linear models were applied to identify key relationships. *P. sylvestris* seedling recruitment showed considerable variability and limited explanatory power in relation to stand basal area, preventing firm conclusions about optimal conditions. In contrast, *Q. pyrenaica* regeneration was abundant under basal areas $\approx$ 30–35 m^2ha^{-1}, based on a well-supported model. No clear relationship with basal area was found for *Castanea sativa*, but seedling abundance decreased with increasing distance to seed sources. Small canopy openings supported *P. sylvestris* regeneration and native broadleaf enrichment. These findings reflect species-specific responses to stand structure and dispersal constraints. Managing shrub cover and adjusting basal area emerge as key strategies to promote structurally complex, biodiverse stands through incorporation of native broadleaf species. This provides practical guidance to support biodiverse-oriented management in Mediterranean *P. sylvestris* stands.

Keywords Scots pine · Sustainable forest management · Species-specific responses · Generalized additive models · Forest biodiversity · Serra da nogueira

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Introduction

Silviculture has evolved to make forests more sustainable by integrating ecological, economic, and social factors into forest management. At the same time, increasing attention is being paid to ecosystem services such as carbon storage, climate regulation, and biodiversity conservation, which underpins many forest functions. Understanding and mimicking regeneration processes are essential for sustainable forestry and conservation, as they influence forest structure, ecophysiological traits, and ecosystem services (Pommerening et al. 2023). Recent research (Ezquerro et al. 2019; Mason et al. 2022) stresses structural heterogeneity and natural regeneration as strategies to enhance forest resilience, multifunctionality, and biodiversity conservation.

In this framework, multifunctional management is particularly suited for extensive forestry in areas with low timber potential, as outlined in the Portuguese National Forest Strategy (ENF 2015). This approach is also especially relevant in forests under special protection status, where ecosystem services hold significant value and forest management objectives extend beyond timber production, such as the Serra da Nogueira study area (Fig. 1).

The mountain, Serra da Nogueira, is part of the Montesinho/Nogueira Site of Community Importance (SIC), as defined by the European Commission's Habitats Directive (92/43/EEC), and the Montesinho/Nogueira Special Protection Zone (code PTCON0002) within the Natura 2000 network. As a result, many of its habitats are considered priority areas for conservation, both at national and European levels. A detailed description of the natural habitats of the Serra da Nogueira can be found in ALFA (2004). The landscape of the region is characterized by a mosaic of habitats, shaped by mountain agriculture, and is home to the largest and most well-preserved *Quercus pyrenaica* Willd. forests in Portugal (PSRN 2000). The mountain is predominantly covered by this species, with some scattered stands of other broadleaf and conifer species, particularly in upland areas.

Natural regeneration is increasingly viewed as a key component of ecological sustainability, as it promotes structural diversity and enhances forest resilience to climate-related disturbances (Schütz et al. 2012; Brang et al. 2014; Huth et al. 2025). Forest structure, shaped by parameters such as canopy cover, species composition, and regeneration methods, influences microclimate buffering and water availability, key factors for seedling establishment under partial canopy cover (Zellweger et al. 2020; De Frenne et al. 2021; Kemppinen et al. 2024).

In regular stands, promoting natural regeneration can initiate structural change, increasing vertical stratification and ecological complexity toward more continuous forest cover, in line with adaptive management goals (O'Hara and Ramage 2013; Brang et al. 2014; Puettmann et al. 2015). Consequently, transforming single-layered pure stands into more structurally and species-diverse forests is recommended to reduce vulnerability to extreme climate events (De Boeck et al. 2018; Messier et al. 2019; Pardos et al. 2021).

Managing for complexity is thus recognized as a cornerstone of sustainable forestry and climate change adaptation (Puettmann et al. 2009, 2015; Boncina 2011; O'Hara and Ramage 2013), supporting a shift toward nature-based silviculture that balances timber production with essential ecological processes (Mason et al. 2022). These approaches require more innovative strategies for forest management (Spiecker 2006). Moreover, the density and composition of regeneration play a crucial role in shaping the future character of forests.

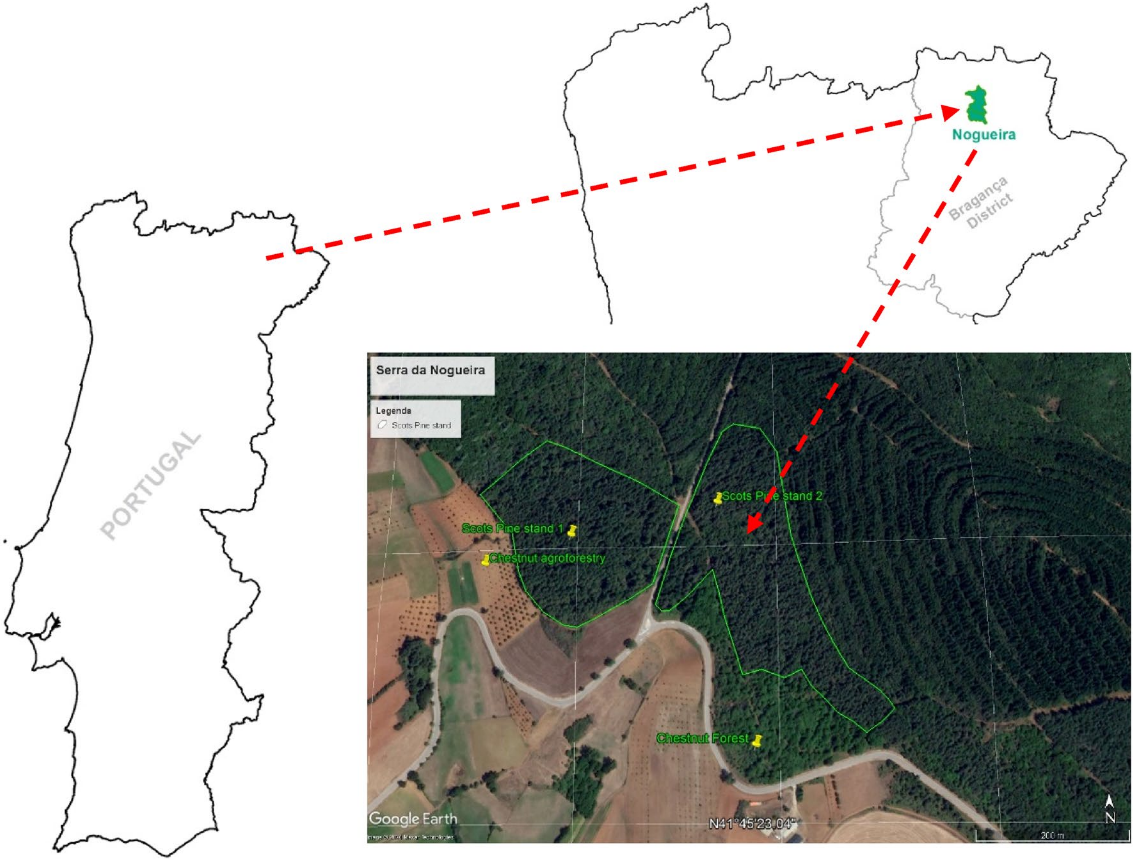

Fig. 1 Location of study site in Serra da Nogueira, Bragança District, northern Portugal. Layout of the study area within the Serra da Nogueira showing the main contour lines and the road dividing it into two distinct stands of *P. sylvestris*

In line with this, natural regeneration is increasingly viewed as a strategic component of sustainable forest development (Chazdon 2008).

Understanding how forest regeneration develops is essential for anticipating future stand composition and ultimately, for sustaining forest ecosystems and their values (McWilliams et al. 2015). However, several studies have highlighted that natural regeneration is influenced by interacting ecological factors, often exhibiting non-linear dynamics (e.g.Moreno-Fernández et al. 2018a; Shen and Nelson 2018), and is shaped by local site conditions that challenge the generalization of regeneration drivers across regions (Liu 2025). It is important to note that natural regeneration is a dynamic process, requiring continuous monitoring and localized assessments that go beyond the resolution of large-scale inventories. In this regard, plot-scale studies remain essential to guide forest management in adapting to local structural conditions and microsite variability.

Thus, this study addresses a key knowledge gap by providing the first meaningful ecological assessment of natural regeneration in even-aged *Pinus sylvestris* L. stands in northern Portugal. Structural and microsite variables have been identified as key drivers of *P. sylvestris* regeneration under Mediterranean conditions (e.g., Barbeito et al. 2009, 2011; Calama et al. 2017; Kara and Topaçoğlu 2018; Moreno-Fernández et al. 2018a). However, the relationship between these variables and regeneration is often non-linear and may exhibit different responses depending on the site conditions, as highlighted earlier. Given this complexity, it is essential to assess how these variables interact with regeneration dynamics in specific environments, like the study area, where local factors can significantly influence regeneration outcomes. Such studies are essential for guiding forest management, particularly in areas where natural regeneration is key to maintaining stand continuity. Moreover, by modeling species-specific responses to stand and microsite conditions, this study aims to fill a recognized gap in applied knowledge, identifying easily measurable variables that can inform regeneration-oriented management and help develop context-sensitive silvicultural strategies.

In line with this framework, the study specifically aims to: (i) analyze the composition and structure of natural regeneration, in terms of seedlings and saplings, focusing on species diversity and abundance at the plot scale across two *P. sylvestris* stands with contrasting regeneration status; (ii) assess the influence of structural and microsite-level variables, such as basal area, shrub cover, and canopy cover, on regeneration of dominant species, and model the response of regeneration abundance to these variables using Generalized Linear Models (GLM) and Generalized Additive Models (GAM), to explore species-specific responses to stand structure and site conditions. The findings aim to provide insights to inform biodiversity-oriented forest management and the development of adaptive silvicultural strategies in Mediterranean ecosystems.

Materials and methods

Study site

The study was conducted in two adjacent, pure even-aged stands of *P. sylvestris* for timber production, located in the Serra da Nogueira (41°45’34"N, 6°54’53"W), northern Portugal, at an altitude of 980 m.a.s.l. (Fig. 1). The even-aged stands of *P. sylvestris* were, on average, 68 (S1) and 62 (S2) years old and covered an area of 5.5 ha (S1) and 6.5 ha (S2), respectively, spanning a total area of 12 ha. These stands are representative of other stands of this species in the Serra da Nogueira. These two adjacent stands present contrasting regeneration status, which justifies their comparison in this study. The terrain is mostly flat, with a slight slope of less than 5% in some parts.

Overall, the study area (Fig. 1) is bordered to the south by agricultural land, predominantly *Castanea sativa* Mill. orchards, and to the north and northeast by a stand of *Pseudotsuga menziesii* (Mirb.) franco. To the northeast and northwest, the area is bordered by natural forest patches dominated by *Q. pyrenaica*, which are mixed with other species, including *Prunus avium* L., *C. sativa*, *P. menziesii*, *Cupressus lusitanica* Mill., and various species of *Pinus*.

The study area has a Mediterranean climate, with dry, warm to mild summers, an average annual temperature of 12 °C, and an annual precipitation of around 1000 mm. The soils are classified as Dystric Leptosols, derived from schist, with some stoniness and few rock outcrops (Agroconsultores and Coba 1991).

The dominant shrub vegetation is composed primarily of *Rubus* spp., *Crataegus monogyna* Jacq., *Erica arborea* L., *Cytisus scoparius* L., *Genista falcata* Brot., and *Pteridium aquilinum* L.

Advanced regeneration of seedlings and saplings occurred in discrete patches or small clusters throughout the stands, with canopy openings irregularly distributed due to tree felling, wind, snow damage, or fallen trees (Fig. 2). Similar seedling distribution patterns have been reported for the species in Spain (González-Martínez and Bravo 2001; Pardos et al. 2005; Moreno-Fernández et al. 2018a).

The stands are communal property managed by Portuguese Forest Services. The stand basal area of *P. sylvestris* was 40.5 m^2 ha^{-1} (S1) and 34.7 m^2 ha^{-1} (S2), with tree densities averaging 434 trees ha^{-1} and 480 trees ha^{-1}, respectively. The dominant height averaged 24 m in S1 and 18 m in S2. Shrub cover averaged 14% in S1 and 6% in S2, while canopy cover reached 70% in S1 and 66% in S2.

Sampling design

Two study sites were selected as representatives of *P. sylvestris* in the Serra da Nogueira. To assess natural regeneration in the stands, we considered two levels: under the regular canopy of adult trees and in the gaps within the stands. The stands exhibited a homogeneous, even-aged structure, and the current gaps in the canopy did not follow any regular pattern. Therefore, a systematic sampling grid of 60 × 60 m was employed for the monitoring plots. The plots were randomly selected, numbered, and georeferenced.

A total of 14 concentric circular plots, with a maximum area of 500 m^2, were established in each *P. sylvestris* stand to monitor natural regeneration. Plots that coincided with gaps were excluded.

A system of concentric fixed-radius plots was used: 500 m^2 for trees ($r = 12.62$ m), 200 m^2 for saplings ($r = 7.98$ m), and 100 m^2 for seedlings ($r = 5.64$ m). In these plots, individuals were classified as trees if they had a diameter at breast height (dbh) greater than 10 cm; saplings if they had a dbh < 10 cm and a height > 2 m; and seedlings if they had a height < 2 m.

Fig. 2 Visual representation of stand structure and natural regeneration. Top row: the photos show discrete patches or small clusters of advanced regeneration of seedlings and saplings throughout the stands (*Q. pyrenaica* and *C. sativa* regeneration on the left and *P. sylvestris* regeneration on the right). Canopy openings are irregularly distributed due to tree felling, wind, snow damage, or fallen trees. Bottom row: a gap with a snag on the left and a gap resulting from tree felling on the right

A Trimble Geo XM 2008 Series hand-held Global Positioning System (GPS) was used to locate the plots in the field based on pre-entered coordinates. The leaf area index (LAI) was measured at the center of each plot using an ACCUPAR LP-80 Ceptometer.

For the gaps, we began by dividing each stand into four quadrants (NE, SE, SW, NW) from the central point of the grid, and then surveyed the gaps in each quadrant. We selected the eight largest gaps, two in each quadrant of stand S1 and four in stand S2, one in each quadrant, due to the observed homogeneity within the gaps. To estimate the gap area, we measured the major and minor axes of the openings. Most gaps had an elongated shape close to an ellipsoid. Thus, these measurements were applied to the ellipse formula to calculate the gap area (Runkle 1981, 1992; Clinton et al. 1993; Battles et al. 1996; Gagnon et al. 2004; Sapkota 2009; Drössler et al. 2017). The area of the gaps ranged from 620 to 748 m^2 in S1 and from 804 to 2,531 m^2 in S2. In the center of each gap, two concentric plots of 200 m^2 for saplings ($r = 7.98$ m) and 100 m^2 for seedlings ($r = 5.64$ m) were established.

Data collection

The total number of individuals by species was registered for seedlings and saplings. In the tree category, the total height (h) of the five thickest trees and the dbh of all trees within the plots were measured. The age of the trees was obtained boring the thickest tree in each plot near the ground using a Haglöf increment borer. Shrub cover percentage (SC%) and canopy cover percentage (CC%) were assessed using a densitometer and a determination key of canopy and shrub cover, as used in the Portuguese National Forest Inventory (Ferreira et al. 2005). The height of the shrubs was also recorded by species to calculate the plot phytovolume. The distance to seed sources was measured using ArcGIS® software version 10.3.1 (ESRI 2015). It was only considered for *Q. pyrenaica* and *C. sativa*, calculated as the linear distance to the nearest conspecific adult tree in neighboring stands. For *P. sylvestris*, the distance from the center of the gap to the nearest trees defining the gap boundary was measured using a Vertex hypsometer and used as a proxy for proximity to potential seed sources. These trees were assumed to be similar in development to those in the adjacent sample plots. Although more detailed neighborhood-based seed source indices have been proposed for pine species (e.g., Ruano et al. 2015), the continuous structure of the surrounding canopy in our study area justified the use of this simplified distance-based approach.

The presence of gaps and the number of gap-makers (felled or dead/blown trees) were recorded, as well as their age, categorized into classes (0–3 years; 3–5 years; 5–10 years; and > 10 years). The age class of each gap was estimated by visually comparing the decay stage of fallen trees, remaining logs, and stumps within the gap. A similar approach has been successfully used in other studies (Barik et al. 1992; Chandrashekara and Ramakrishnan 1994; Zang and Wang 2002; Sapkota and Odén 2009). When stumps corresponding to different phases of felling were observed in the gaps, the age of the oldest gap-makers was noted. In the gaps, the heights of the border trees were assumed to be the same as the heights measured in the nearest sample plot.

The environmental variables used in the analyses were: basal area (G), quadratic mean diameter (dg), dominant diameter (ddom), number of trees per hectare (N), canopy cover (CC), shrub cover (SC), leaf area index (LAI), shrub phytovolume, gap age (Tgap), number of gap-makers (Gapm), and distances to seed sources of *C. sativa* (Dcs), *Q. pyrenaica* (Dqpy), and other broadleaf and conifer species (Dofr). These were used as explanatory variables in the ordination and modeling analyses.

Data analysis

The dominant height of each stand (hdom) was computed as the average height of the 100 thickest trees per hectare (Assmann 1970). The quadratic mean diameter (dg) corresponds to the dbh of the tree with the mean basal area. The dominant diameter (ddom) is the average dbh of the 100 thickest trees per hectare. The basal area of each tree was calculated using the formula $g=\pi/4\ (dbh^2)$, and the total basal area per hectare (G) was also determined. Stocking density was expressed as the number of trees per hectare (N).

Diversity indices were calculated based on presence-absence data from the sampling plots. These data were converted into frequency by dividing the number of occurrences of each species by the total number of records, yielding the relative abundance (pi). Since species richness and abundance are both fundamental for determining density, the following indices were estimated: the modified Shannon index ($\exp(H')=N_1$) (Keylock 2005), the reciprocal Simpson diversity index ($1/D=N_2$), the reciprocal of the proportional abundance of the most dominant species ($1/p_{max}=N\infty$) or the reciprocal of the Berger-Parker index, and species richness ($S=N_0$). These indices were arranged sequentially (N_0 to $N\infty$) in the Hill series (Hill 1973). The Hill series is a method used to represent biodiversity using a series of indices arranged sequentially, from species richness to more complex measures of diversity. The series helps in assessing not only the number of species (richness) but also the evenness of their distribution across a community. Simpson´s evenness (E_evenness), as described for example by Magurran (2004), were calculated. Packages *BiodiversityR* (Kindt and Coe 2005) and *vegan* (Oksanen et al. 2019) from software R version 4.0.3 (R Core Team 2020) were used to compute the indices, with additional data analysis performed in EXCEL 2016. Pearson correlation values among the indices and stand variables were also obtained.

Ordination analysis was performed using Canoco 4.5 & CanoDraw 4.0 for Windows (Leps and Smilauer 2003), based on datasets of species abundance and environmental (stand) variables for both seedlings and saplings in stands S1 and S2, to achieve a fine-grained analysis of regeneration at the microscale level. Principal component analysis (PCA) and redundancy analysis (RDA) were performed. In the ordination process, PCA was executed with the post-projection of stand variables onto the ordination axes. Following PCA, a redundancy analysis (RDA) was performed using the automatic selection of significant variables for the constrained axes. Analyses were carried out with the default logarithmic transformation of abundance values and the “center by species” option in Canoco 4.5 software. Insights from these analyses guided further investigation of species abundance response curves using generalized additive models (GAM) and generalized linear models (GLM) for the comprehensive dataset obtained in both stands. All explanatory variables related to stand structure, including G, hdom, dom, N, CC, and SC, as well as distance to seed source, LAI, and phytovolume, were tested in the models in relation to the abundance (response variable) of the main species. Particular emphasis was given to those variables that showed the most relevance in the preliminary analyses (PCA and RDA). Due to observed overdispersion, negative binomial models were applied, and a forward selection approach was adopted for variable inclusion.

Although only two stands were included, the replication at the plot level enabled a robust analysis of local regeneration dynamics. Stand-level differences were also discussed to provide ecological context for the observed patterns.

Table 1 Summary statistics of seedling and sapling counts in stand 1 (S1) and stand 2 (S2)

Stand	No of plots	Group (ha)	Mean	Std	Maximum	Minimum	Median
S1	14	Seedlings	10,071	5,415	14,400	1,600	10,500
		Saplings	1,389	1,571	5,250	50	775
S2	14	Seedlings	16,621	7,039	30,200	6,400	16,600
		Saplings	514	359	1,100	50	325

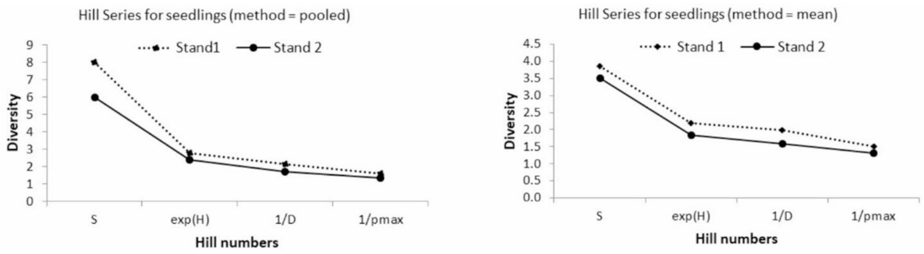

Fig. 3 Hill Series diversity curves for seedlings in *P. sylvestris* stands (Stand 1 and Stand 2), using pooled and average methods for diversity, as calculated with the *diversity()* function from the BiodiversityR package (Kindt and Coe 2005). S – species richness; exp(H′) – modified Shannon index; 1/D – Simpson index; 1/pmax – Berger–Parker index

Results

Diversity analysis

Seedlings

Natural regeneration of seedlings, which includes all tree species in the understory of *P. sylvestris* stands, was notably more abundant in S2 than in S1 (Table 1). However, the number of seedlings that matured into saplings, thus ensuring the continuity of the stands through natural regeneration, was higher in S1, with significant variation observed between plots. Notably, a substantial number of cones were observed on the forest floor in both *P. sylvestris* stands, which may support seed dispersal and regeneration potential.

The distribution of seedlings across each stand reveals clear dominance patterns. In S2, *Q. pyrenaica* was the most abundant species, comprising 62% of the total. In S1, the seedling population was dominated by *Q. pyrenaica* and *P. sylvestris*, together representing 89% of the total seedlings. In S2, *Q. pyrenaica* and *C. sativa* accounted for 87% of the cumulative relative abundance.

Other species in the seedling floristic composition exhibited a relative abundance of less than or equal to 10%, including *P. menziesii*, *Quercus rotundifolia*, *C. lusitanica*, *Prunus spinosa*, and *P. avium*.

The Hill series (Fig. 3) and rank-abundance plots (Fig. 4) illustrate the diversity of the stands. The Hill series presents the range of the diversity of an ecosystem varying between S (corresponding to maximum diversity) and the value 1 (corresponding to the absence of diversity). The horizontal asymptote in S = 1 is interpreted either as the absence of diversity or as the presence of a unique species dominating the habitat and/or ecosystem.

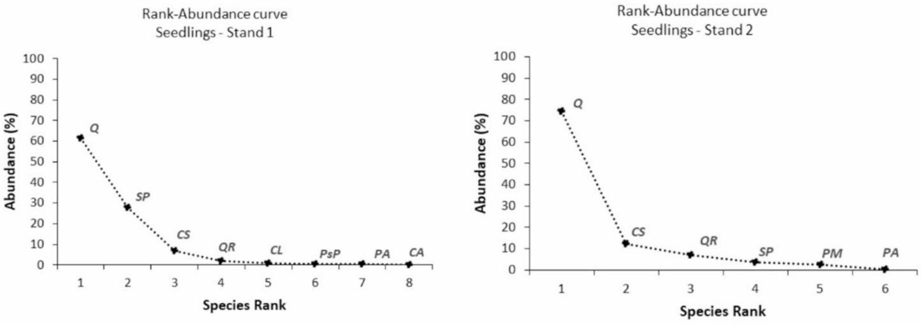

Fig. 4 Rank-abundance curves for seedlings in stands S1 and S2. Species are ordered by decreasing relative abundance (%)

As shown in Fig. 3, the Hill series curves for both stands were similar, with the curve for S1 slightly higher than that of S2, indicating a higher diversity in S1. Wilcoxon Rank Sum tests revealed significant differences in abundance between S1 and S2, however, no clear differences were detected for Hill numbers from N_0 to $N\infty$. Additionally, results for Simpson´s evenness (E_evenness) are provided: S ($p=0.718$), exp(H) ($p=0.050$), 1/D ($p=0.050$), Abundance ($p=0.012$), E_evenness ($p=0.352$), and 1/pmax ($p=0.050$).

The rank-abundance plots (Fig. 4), also known as Whittaker plots, clearly show the preponderance of *Q. pyrenaica* seedlings in both S1 and S2 stands.

Q - *Quercus pyrenaica*, SP - *Pinus sylvestris*, CS - *Castanea sativa*, QR - *Quercus rotundifolia*, CL - *Cupressus lusitanica*, PsP - *Prunus spinosa*, PA - *Prunus avium*, CA - *Cedrus atlantica*, PM - *Pseudotsuga menziesii*.

Ordination Analysis

Principal component analysis (PCA) and redundancy analysis (RDA) revealed the key factors influencing seedling distribution across the stands, providing a fine-grained understanding of regeneration dynamics (Fig. 5).

The first PCA axis, which explained nearly 70% of the total variation, captured the strongest contrast in species distribution, particularly between *P. sylvestris* and *C. sativa*. Only the three main species - *P. sylvestris*, *C. sativa*, and *Q. pyrenaica* - were included in the ordination analysis. In S1, *Q. pyrenaica* seedlings were more frequent in plots with lower basal area and were associated with gap-related variables such as gap age (Tgap), shrub cover (SC), and proximity to seed sources of the same species (Dqpy), suggesting that these factors may favor seedling establishment under more open structural conditions. The basal area of the stand (G) and the dominant diameter (ddom) were the stand variables most strongly associated with PCA axis 1. In the constrained ordination (RDA), these two variables were the only significant predictors, with the first and only canonical axis explaining 57% of the variability in species abundance (G alone accounting for 36.6%). Thus, the PCA and RDA analyses identified G and ddom as the primary structural factors influencing seedling distribution across the stands.

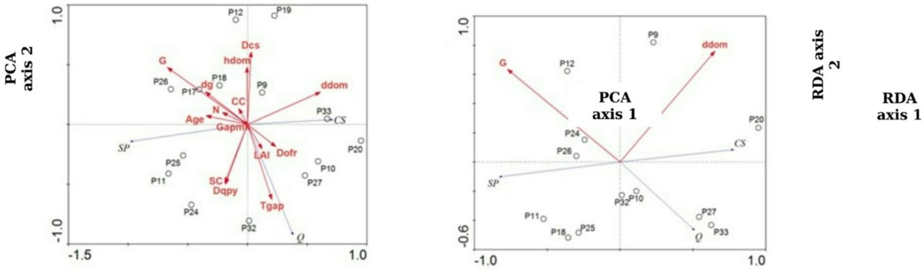

Fig. 5 PCA and RDA ordination plots for seedlings in stand S1. Arrows indicate the direction and relative contribution of each environmental variable to the ordination axes. Only the most influential variables were retained in the RDA. G: basal area (m^2ha^{-1}); dg: quadratic mean diameter; ddom: dominant diameter; N: number of trees per hectare; hdom: dominant height; CC: canopy cover; SC: shrub cover; LAI: leaf area index; Dofr: distance to seed source of other broadleaf species and conifers; Dcs: distance to seed source of *C. sativa*; Dqpy: distance to seed source of *Q. Pyrenaica*; Tgap: age of the gap; Gapm: number of gap-makers

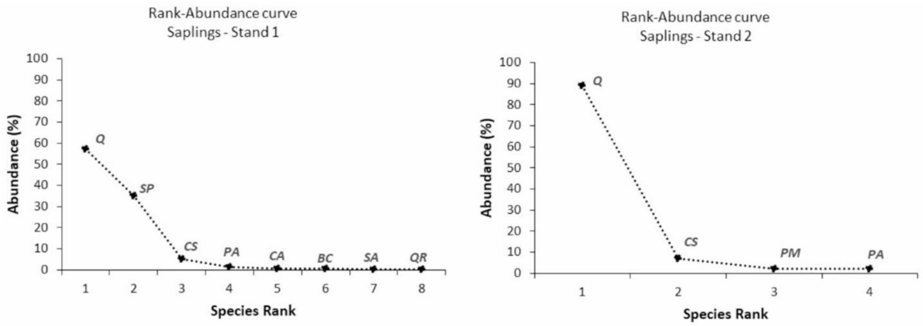

Fig. 6 Rank-abundance curves for saplings in stands S1 and S2. Species are ordered by decreasing relative abundance (%)

Saplings

The cohort of seedlings dominated by *Q. pyrenaica*, *P. sylvestris*, and *C. sativa* in S1 decreased in saplings but maintained the same trend (Fig. 6). However, *P. sylvestris* regeneration represented 35% of the saplings cohort in S1 and was practically a rarity in S2.

Q - *Quercus pyrenaica*, SP - *Pinus sylvestris*, CS - *Castanea sativa*, QR - *Quercus rotundifolia*, BC - *Betula celtiberica*, PA - *Prunus avium*, CA - *Cedrus atlantica*, SA - *Salix* spp. PM - *Pseudotsuga menziesii*.

In Fig. 7, curves of the Hill series for saplings in S1 and S2 stands are presented. No differences were detected for all the indices, including abundance, with the Wilcoxon Rank Sum test (S ($p = 0.231$); exp(H) ($p = 0.077$); 1/D ($p = 0.140$); Abundance ($p = 0.369$); E_eveness ($p = 0.077$); 1/pmax ($p = 0.191$)).

In the ordination procedure which was similar to that described before for seedlings, basal area and shrub cover were the most relevant stand variables both in S1 and S2. The variables G and SC explained 52.4% of the variability in abundance of species *Q. pyrenaica*, *P. sylvestris*, and *C. sativa* in the redundancy analysis (RDA) for S1 (33% for G alone), and

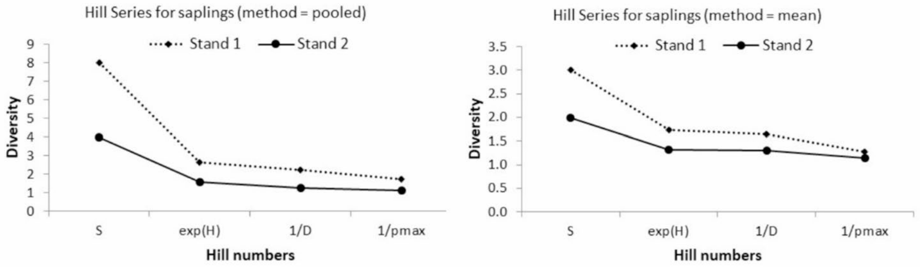

Fig. 7 Hill Series diversity curves for saplings in *P. sylvestris* stand S1 and S2, using pooled and average methods for diversity, as calculated with the *diversity()* function from the BiodiversityR package (Kindt and Coe 2005). S – species richness; exp(H) – modified Shannon index; 1/D – Simpson index; 1/pmax – Berger–Parker index

48.1% of variability in abundance of species *Q. pyrenaica*, and *C. sativa* in the RDA for S2 (32% for G alone) (see Supplementary Material, Fig. Sp1 and Sp2).

Gaps

In gaps of both S1 and S2 stands, seedlings of species *Q. pyrenaica* were the most abundant as also observed at the stand level. *P. sylvestris* and *C. sativa* (in this order) followed in the species rank. On average, more individuals of *Q. pyrenaica* were counted in the gaps (1.22 m^{-2}) than in the sample plots (0.62 m^{-2}) of S1. Maximum values of 3.38 m^{-2} and 1.73 m^{-2} were observed in gaps and sample plots, respectively, in S1. However, no significant difference was detected in the Wilcoxon Rank Sum tests ($p=0.628$).

In S2, the average number of seedlings of *P. sylvestris* was higher in the gaps (0.29 m^{-2}) than in the sample plots (0.10 m^{-2}) ($p=0.047$).

Concerning saplings, in S1 the highest counts were observed in plots in comparison to gaps, but without significant differences in average values or medians for the species *Q. pyrenaica*, *P. sylvestris*, and *C. sativa*. In S2 only, *Q. pyrenaica* saplings were simultaneously observed in gaps and plots, their number being similar.

A positive correlation between gap size and age of the gaps was confirmed ($r=0.56$).

Response of natural regeneration of key species in relation to stand variables

Among the analyzed variables, the results showed that the abundance of *Q. pyrenaica* seedlings was best explained by a negative binomial GAM model, with linear effects of hdom and nonlinear effects of G, which was significant, explained 59% of the deviance (Fig. 8). Table 2 summarizes the estimated parameters of the models fitted for each species, including both parametric and smooth terms, highlighting the significance of stand variables such as G, hdom, and distance to seed source (DCS).

The exploratory analysis of *P. sylvestris* abundance revealed that the best-fitting model was the negative binomial GAM with a nonlinear effect of basal area, although it explained only 14% of the deviance. For *C. sativa*, the best response was associated with distance to the seed source. In this case, the negative binomial GLM with a linear effect of distance to the seed source explained 29% of the deviance.

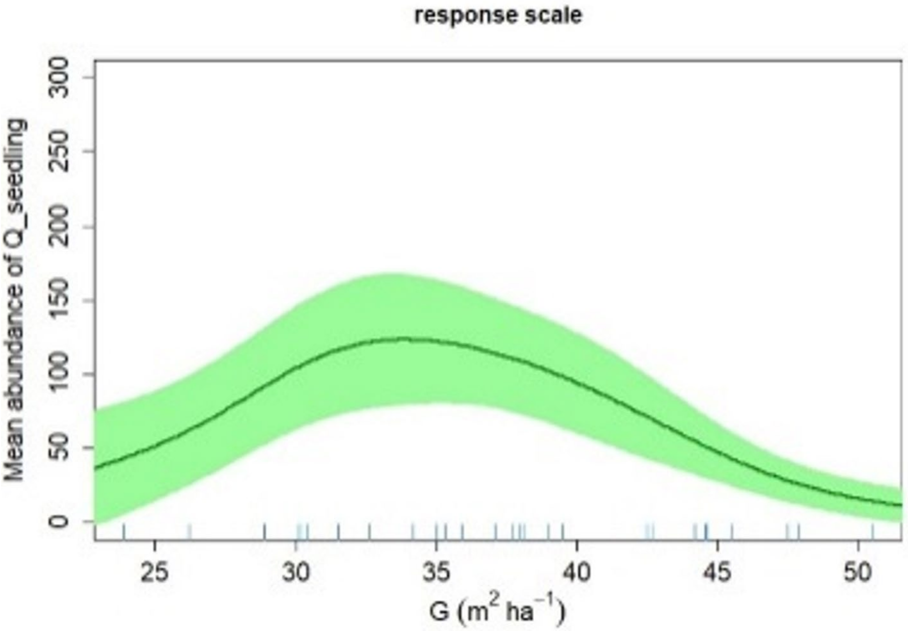

Fig. 8 Response curves showing the abundance of *Q. pyrenaica* (Q) seedlings as a function of stand basal area (G), with 95% confidence bands

Table 2 Summary of fitted GAM models for natural regeneration of the three main species

Species	Parameter	Estimate	Std. Error	Z value	*p*-value
Q. pyrenaica	Intercept	6.683	0.883	7.568	<0.001
	hdom	−0.111	0.041	−2.682	0.007
Smooth terms: s(G) (edf=3.01; Ref.df=3.75); $\chi^2 = 24.95$; $p<0.001$					
C. sativa	Intercept	3.437	0.330	10.413	<0.001
	DCS	−0.011	0.003	−3.184	0.001
P. sylvestris	Intercept	2.585	0.328	7.892	<0.001
Smooth terms: s(G) (edf=2.00; Ref.df=2.00); $\chi^2 = 5.90$; $p=0.052$					

Models fitted using the mgcv package in R. Parametric coefficients refer to linear terms; smooth terms capture non-linear effects. G - stand basal area (m^2 ha^{-1}); hdom - dominant height (m); DCS - distance to nearest *C. sativa* seed source (m); edf - estimated degrees of freedom; Ref.df - reference degrees of freedom; Chi.sq - chi-square statistic

Discussion

Diversity analysis

Seedlings

The results highlight the complex dynamics of seedling regeneration within *P. sylvestris* stands, where species composition and stand structure play a meaningful role. Among the regenerating species *Q. pyrenaica*, in particular, plays a central role in these dynamics; however, its regeneration strategy remains relatively understudied (Camisón et al. 2015). Environmental factors such as light availability and shrub cover are also likely to influence regeneration processes (Pardos et al. 2007; Barbeito et al. 2009; Tinya et al. 2019), but their effect on the seedling layer was not strongly supported by the present data. Shrub cover, however, showed relevance for sapling abundance, as discussed in the next section. Given the potential importance of light, the use of more sensitive indicators such as canopy transmittance may be required to better capture its role in early regeneration stages, as referred by Kara and Topaçoğlu (2018). The Hill series (Figs. 3 and 7) illustrates ecosystem diversity, where a gentler slope of the curve generated by the sequence of indices indicates greater evenness and, consequently, higher overall diversity (Godinho-Ferreira et al. 2010). Although the Hill series curves were similar between stands, a significant difference was detected in total seedling abundance, not in diversity indices themselves. The contrasting seedling abundances between the two stands suggest that local microclimatic conditions may influence the recruitment of *Q. pyrenaica* and *C. sativa*, which is consistent with the findings of Godinho-Ferreira and Azevedo (2005), who reported that the Mediterranean climate can support diverse regeneration species under specific conditions. In particular, the recruitment of *C. sativa* in S2 is likely related to its proximity to seed sources combined with favorable microsite conditions (Silla et al. 2018). The co-dominance of *Q. pyrenaica* and *P. sylvestris* in the seedling layer of stand S1 likely reflects species-specific responses to fine-scale variation in light availability, with each occupying distinct regeneration niches shaped by their contrasting shade tolerances (Sánchez-Gómez et al. 2006; Pardos et al. 2008; Sevilla 2008; Barbeito et al. 2009; Calama et al. 2015; Camisón et al. 2015; Kara and Topaçoğlu 2018). *For Q. pyrenaica*, seedling abundance increased as G decreased, possibly due to improved light availability, as CC was also lower in S2. Germination is influenced by both the quantity and quality of light (Copeland and McDonald 2001), and is also dependent on species-specific temperament (Pardos et al. 2005).

The dominance of *Q. pyrenaica* in both stands underlines its ecological relevance in Mediterranean forests, likely reflecting its adaptability to variable light conditions beneath the *P. sylvestris* canopy. Furthermore, the substantial recruitment of *C. sativa* near stands of the same species emphasizes the importance of seed dispersal mechanisms and the role of animal interactions in shaping forest dynamics (Pardos et al. 2005). In particular, Pérez-Camacho et al. (2023) observed that Eurasian jays (*Garrulus glandarius*) cache acorns following hierarchical spatial strategies influenced by vegetation structure and the proximity to seed sources, which has significant implications for oak regeneration patterns. The regeneration of *C. sativa* in our study was negatively correlated with the distance to seed sources, suggesting a strong limitation related to seed dispersal. However, other ecological factors may also influence its establishment. Bacilieri et al. (1993) reported that its prolonged germination period may increase exposure to seed predators (Sork 1984) and late frost damage. They also stressed the importance of soil moisture as a key factor for seedling establishment in Mediterranean environments.

Overall, these field observations suggest that early regeneration is shaped by a combination of structural attributes and seed availability (Castro et al. 2004a; Pons and Pausas 2007; Calama et al. 2017; Moreno-Fernández et al. 2018b; Tinya et al. 2019). These aspects are further explored in Sect. 4.2., where multivariate analysis provides a more detailed understanding of species-specific responses to stand variables.

Encouraging a variety of species within *P. sylvestris* stands can enhance the ecosystem resilience and support natural processes. This is in line with the broader goal of preserving biodiversity in Mediterranean woodland environments.

Saplings

The sapling cohort results indicate a consistent trend in species composition from the seedling stage in stand S1, dominated by *Q. pyrenaica*, *P. sylvestris*, and *C. sativa*. Notably, *P. sylvestris* increased slightly from approximately 29% in the seedling layer to about 35% among saplings, while *Q. pyrenaica* declined marginally (from about 62–59%) and *C. sativa* remained stable (around 5%). In contrast, in S2, *Q. pyrenaica* increased its dominance from approximately 75–90%, while *C. sativa* declined from about 10–5%, and *P. sylvestris*, already scarce among seedlings (around 3%), became virtually absent among saplings. This pattern suggests limited recruitment of *P. sylvestris* under the local conditions in S2. Despite S2 exhibiting lower basal area, reduced shrub cover (SC% = 6.0 vs. 12.2), and slightly lower canopy cover (CC% = 66.4 vs. 70.7), *P. sylvestris* was virtually absent among saplings. These structural conditions would typically be expected to favor, or at least sustain, the level of *P. sylvestris* regeneration observed in S1, especially since regeneration increased under comparatively denser conditions in that stand. Previous studies have identified lower G and moderate canopy closure as favorable for *P. sylvestris* regeneration (e.g., Barbeito et al. 2009; Kara and Topaçoğlu 2018), which makes the absence of saplings in S2, and the increase in S1, particularly unexpected. This suggests that other factors, such as biotic interactions or micro-site constraints, may have exerted a stronger influence than stand structure alone.

Regarding *Q. pyrenaica*, although it remained dominant among saplings in both stands, its slight decrease in S1 suggests early-stage mortality, possibly associated with the higher shrub cover and basal area observed there. This pattern may reflect complex interactions between abiotic stress and herbivory, as noted by Guignabert et al. (2020), who reported that shrub cover can exert contrasting effects on regeneration depending on the intensity of environmental stress and the type of herbivore present, with positive effects declining under extreme drought or when shrub structure favors rodent activity. This may be related to the ecological behavior of the species, as *Q. pyrenaica* is considered an intolerant to intermediate shade species (Sevilla 2008; Camisón et al. 2015), and therefore may present reduced survival under denser canopies. Nonetheless, *Q. pyrenaica* has also shown relatively high survival under limiting light in controlled experiments, displaying physiological and morphological traits typically associated with shade tolerance, such as increased specific leaf area and low shoot-to-root ratio (Sánchez-Gómez et al. 2006). Furthermore, it has been reported to be sensitive to excessive radiation, showing photoinhibition and reduced gas exchange under full sunlight conditions (Gómez-Aparicio et al. 2006). These apparently contrasting observations highlight the importance of contextual factors such as microsite conditions, developmental stage, and biotic stressors when interpreting shade responses in field conditions. Such dynamics are consistent with the gap-phase regeneration pattern described by Camisón et al. (2015), who reported that dense canopies may suppress sapling development despite abundant seedling banks, with recruitment increasing near canopy gaps or in previously disturbed stands. In contrast, the marked increase in S2 is consistent with the GAM model for seedlings, which explained 59% of the deviance and indicated higher recruitment under intermediate basal area levels, conditions that match the structure of S2. This suggests that initial establishment conditions likely favored continued development into the sapling stage. Herbivory and trampling may also contribute to early mortality in Mediterranean *Q. pyrenaica* forests (Gómez et al. 2003; Baraza et al. 2004; Silla and Escudero 2006).

The diversity indices and abundance measures showed no significant differences between the two stands. This suggests that the overall community structure remains stable despite the differences in species-specific regeneration patterns. The redundancy analysis emphasized the influence of basal area and shrub cover as key stand variables influencing sapling abundance, with G alone explaining the majority of the variability in both stands. These findings support the idea that stand structure attributes and understory conditions play a key role in shaping regeneration dynamics.

The dominance of *Q. pyrenaica* and the maintenance of *C. sativa* among saplings indicate that these species are well-adapted to local conditions, ensuring their continued prevalence in the regeneration process. Conversely, the reduced presence of *P. sylvestris* in S2 may require targeted management interventions to enhance its recruitment, such as promoting favorable microsites for its establishment. In this context, recent findings by Cudjoe et al. (2025) revealed that neighborhood competition significantly reduced aboveground biomass accumulation in *P. sylvestris*, while having no significant effect on *Q. pyrenaica*, highlighting the species-specific nature of competitive dynamics in young mixed stands. Additionally, recent findings suggest that *P. sylvestris* is increasingly vulnerable to extreme drought events even in regions previously considered climatically favorable, raising concerns about its resilience under future climate scenarios (Bose et al. 2024).

Overall, the observed patterns underline the importance of understanding site-specific variables and their interactions in driving regeneration success. These insights are essential for developing adaptive silvicultural strategies tailored to Mediterranean montane forests, especially in protected area contexts where resilience and biodiversity are prioritized.

Gaps

In both stands, gaps hosted higher numbers of *Q. pyrenaica* seedlings than other species, supporting the idea that these gaps create favorable microsites for regeneration. *P. sylvestris* and *C. sativa* (in this order) followed in the species rank. However, no significant difference was detected ($p = 0.628$). For seedlings of *P. sylvestris* and *C. sativa*, only a very small advantage for gaps in comparison to sample plots was observed. The *P. sylvestris* seedling recruitment was observed *in loco* essentially at the limits of the gaps coinciding with the shading effect of the trunks, despite the fact that *P. sylvestris* germination is delayed under low light intensities (Castro et al. 2004a). According to Calama et al. (2015), the optimal radiation for germination suggested for *P. sylvestris* is 35% full sunlight. So, if *P. sylvestris* behaves as a demanding light species in the northernmost latitudes, it seems to prefer the moderate light conditions in southernmost latitudes (central Spain), at least during the early stages of growth (Pardos et al.

2008; Calama et al. 2015). Our observations indicate a species behavior similar to that reported in central Spain, where germination is favored under moderate to high shade conditions. In S2, *C. sativa* seedlings showed no clear gap-related pattern ($p=0.980$) despite the lower basal area compared to S1.

Shrub cover in gaps appeared to negatively affect broadleaf regeneration, highlighting the importance of careful shrub management. Opening the tree canopy could prove beneficial when aiming to create more diverse stands with an increased presence of broadleaf species, namely *Q. pyrenaica*. This pattern aligns with findings by Camisón et al. (2015), who observed that *Q. pyrenaica* regeneration is often episodic and strongly associated with canopy openings, particularly in secondary forests or after disturbance, while sapling development tends to be suppressed under closed-canopy conditions. Accordingly, shrub cover control should be integrated into regeneration strategies. The analysis of seedling recruitment in gaps permits an understanding of the role of small-scale disturbances in these ecosystems and the prediction of how regeneration may respond to partial felling, thus facilitating the implementation of optimal forestry management practices (Bengtsson et al. 2000; Coates 2000).

Understanding gap dynamic processes is fundamental for developing silvicultural systems that closely mimic natural disturbance patterns, which in turn promote successful seedling recruitment (Lertzman et al. 1996; Palik and Pederson 1996; Brockway and Outcalt 1998).

Concerning saplings, in S1 the highest counts were observed in plots in comparison to gaps, but without significant differences in average values or medians for the species *Q. pyrenaica*, *P. sylvestris*, and *C. sativa*. In S2, only *Q. pyrenaica* saplings were found in both gaps and plots, with similar counts in each. These patterns are consistent with previous findings on seedlings and saplings, suggesting that small gaps may provide suitable microsites for *Q. pyrenaica*, while the recruitment of *P. sylvestris* appears to depend on additional microsite conditions beyond the canopy opening. This supports the idea that, under the conditions observed, the canopy structure in S1 may have been more favorable to *P. sylvestris* regeneration than in S2.

Response of natural regeneration of key species in relation to stand variables

The regeneration of *Q pyrenaica* (Fig. 8) shows an increasing trend with basal area up to 33 m^2 ha^{-1}, maintaining seeding abundance levels up to 70 seedlings for G values between 30 and 40 m^2 ha^{-1}, demonstrating notable plasticity. Despite this, regeneration tends to be driven by more open canopies. In the PCA, *Q. pyrenaica* was positioned in the opposite direction to G, suggesting that its regeneration may be more frequent in structurally more open conditions than those associated with *P. sylvestris*, under the relatively uniform structure of even-aged stands. It was instead located closer to variables such as Tgap, SC, and Dqpy, all projecting along PCA axis 2. These variables were not retained in the RDA, which focused on the dominant structural gradients of axis 1. This pattern suggests that *Q. pyrenaica* regeneration may be influenced both by intermediate G levels and by microsite-level heterogeneity, including gap dynamics and localized seed availability, which are not fully captured by the main structural gradient in the RDA.

Regarding the *P. sylvestris*, a more unimodal response was observed, with regeneration being more abundant at intermediate G values (40–45 $m^2\ ha^{-1}$). However, the model explained only 14% of the deviance and confidence intervals were wide, so this pattern should be interpreted with caution. These G values are substantially higher than those recommended by Kara and Topaçoğlu (2018), who suggested thresholds below 15 $m^2\ ha^{-1}$ for seed germination and 12 $m^2\ ha^{-1}$ to support seedling development in shelterwood systems. This contrast highlights the variability in regeneration responses and suggests that G alone is insufficient to explain seedling recruitment. Indeed, G is a stand-level structural metric that does not directly account for fine-scale heterogeneity in light availability. Small canopy gaps, frequently observed in our study area, may occur even in stands with relatively high G and provide favorable microsites for *P. sylvestris* regeneration. This was evident in S1, where localized regeneration occurred within small gaps despite high average G. These findings are consistent with those of Castro et al. 2004b); Pardos et al. (2007); Barbeito et al. (2009), who showed that small openings promote recruitment under Mediterranean conditions. Likewise, Gaudio et al. (2011) and Kara and Topaçoğlu (2018) observed that *P. sylvestris* seedlings can be established under shade, but height growth is favored by moderate light. The weak overall relationship observed in our model may also reflect site-specific variability. In S2, which had lower G than S1, *P. sylvestris* regeneration was sparse (Fig. 4). This imbalance may have increased residual variability and masked broader trends. Unmeasured factors such as soil characteristics, herbivory, or disturbance history could help explain this discrepancy but were not assessed in this study. Even under favorable seedbed conditions, *P. sylvestris* regeneration remained strongly limited by browsing pressure in other temperate pine systems (Mason et al. 2024), emphasizing the need to account for biotic constraints when interpreting regeneration outcomes.

Variables such as canopy cover, shrub phytovolume, and LAI did not contribute significantly to the model. Although canopy cover did not emerge as a significant predictor in our models, its potential influence on regeneration through microclimatic buffering has been recognized in previous studies (Barbeito et al. 2009; Rodríguez-García et al. 2011; Guignabert et al. 2020). These authors emphasize that overstory canopy can mitigate temperature and moisture extremes, thereby facilitating seedling survival under Mediterranean conditions. In our case, the narrow variation in canopy cover between stands may have limited its explanatory power, and other structural variables such as basal area and shrub cover may better capture the environmental gradients relevant to regeneration. Nevertheless, light availability is widely recognized as a key driver of *P. sylvestris* regeneration (Carus 2004; Pardos et al. 2007; Barbeito et al. 2009; Kara and Topaçoğlu 2018). Several studies point to canopy openness, light transmittance, and the vertical structure of the stand (e.g., height to crown base) as stronger predictors than G alone (Nyman 1963; Gingrich 1967; Kara and Topaçoğlu 2018). These factors influence understory microclimate, especially light and soil moisture, which are critical to regeneration success. As highlighted by Niinemets and Valladares (2004), photosynthetic performance and leaf-level traits vary along natural light gradients, but their expression is strongly modulated by co-occurring stresses such as drought and heat, which interact non-additively. This multidimensional role of shade is further emphasized by Valladares et al. (2016), who describe shade not merely as a reduction in irradiance, but as a complex environmental condition that shapes plant responses to both abiotic and biotic stressors. In this view, regeneration success under shade is influenced not only by light availability but also by trade-offs in resource use, ontogenetic stage, and biotic interactions such as competition and herbivory. These mechanisms help explain the variability in regeneration outcomes observed even under structurally similar canopies. Such divergence reinforces the importance of microsite-specific constraints and physiological plasticity in shaping regeneration success. These findings align with studies highlighting the influence of local overstory structure on *P. sylvestris* regeneration. For instance, Moreno-Fernández et al. (2018a) found that sapling density was negatively associated with the diameter of adult trees within a 7–8 m radius, suggesting a local inhibition effect likely driven by reduced light availability and altered microclimate beneath larger trees. Although our study did not explicitly incorporate spatial predictors, the observed association between regeneration and canopy openings points in the same direction, reinforcing the role of fine-scale structural heterogeneity in promoting natural regeneration.

It is important to note that our results are based on a single-time assessment of regeneration. As such, it was not possible to differentiate between germination cohorts, assess seedling survival, or measure temporal dynamics. Moreover, spatial metrics were not included, limiting our understanding of fine-scale regeneration structure. Still, this survey provides a solid baseline for future monitoring, which is essential given the scarcity of similar studies in Portuguese *P. sylvestris* stands. The observed tendency for regeneration to peak at intermediate G values suggests a potential management guideline, but more detailed and replicated studies are needed to confirm this pattern in order to support appropriate silvicultural practices aimed at promoting natural regeneration in stand management. In the PCA, *P. sylvestris* regeneration was strongly aligned with G on the first axis. G was also retained as the most important predictor in the RDA, reinforcing its role as a key structural driver for this species.

The distance to seed sources was particularly noteworthy in the ordination analysis for *C sativa*, whose seedling presence was negatively correlated with Dcs. This pattern reinforces the key role of limited dispersal in shaping regeneration, especially for species relying on barochory and animal-mediated seed movement (Pardos et al. 2005; Pérez-Camacho et al. 2023). This result aligns with expectations and was further supported by the GLM. In the PCA, *C. sativa* was aligned with ddom rather than G, and ddom was also retained in the RDA, reinforcing its explanatory strength. These findings suggest that regeneration of *C. sativa* is associated with the presence of large dominant trees and is strongly constrained by seed availability, whereas G does not appear to influence its establishment. This is consistent with findings by Silla et al. (2018), who reported increased regeneration of *C. sativa* with the G of nearby trees of the same species, underscoring the role of adult individuals in facilitating seedling recruitment and refuting the traditional view that this species cannot regenerate without cultural inputs.

Management implications based on study results

The study provides valuable insights into regeneration dynamics at the stand level, with important implications for forest management. The study suggests that small canopy openings may support *P. sylvestris* seedling recruitment under certain conditions, as observed in S1, although this response was not consistent across stands. The results also support the potential for broadleaf enrichment in pure stands. The findings from S1 suggest that silvicultural reproduction methods that create small canopy openings, mimicking small natural disturbances, while maintaining overstory shelter, may be particularly effective in promoting *P. sylvestris* regeneration and enhancing stand structural heterogeneity. However, due to the limited number of stands with advanced regeneration available for analysis in Serra da Nogueira, these results should be interpreted with caution and validated through further research. Additionally, experimentation with this approach would help optimize recruitment during the initial establishment stages. However, this aligns with findings by Barbeito et al. (2011), who reported that regeneration success in Mediterranean *P. sylvestris* shelterwood systems depended not only on canopy manipulation but also on microsite conditions, especially soil disturbance. Their multiscale analysis showed that stand-level variables alone could not fully explain regeneration patterns, reinforcing the importance of integrating structural and site-level interventions. To balance removal and regeneration over time, management should integrate both gap creation to initiate or release regeneration and closed canopy sections to ensure the continuity of mature harvestable trees (Drössler et al. 2017). The response of *Q. pyrenaica* to stand basal area suggests that regeneration is favored under intermediate canopy densities (around 33–35 $m^2\ ha^{-1}$). For *P. sylvestris*, the model showed considerable variability and limited predictive power, preventing firm conclusions about optimal stand conditions. These results highlight the need for further investigation, particularly under varying structural contexts. Fostering the enrichment of pure stands with broadleaf species is recommended for both ecological and economic reasons (Knoke et al. 2008), as it enhances forest resilience and biodiversity.

In general, the trends in *P. sylvestris* management align with a shift towards creating more heterogeneous structures (e.g., Calama et al. 2017; Drössler et al. 2017). For instance, in northern Europe, such as Germany, large-scale pure *P. sylvestris* stands are being converted into mixed and more structured forests (Spathelf and Ammer 2015). Similarly, in many developed Mediterranean countries, forest management trends are moving towards greater stand diversity, fostering the formation of mixed pine-oak stands (Sheffer 2012). It has been suggested that higher structural diversity in forest stands contributes to climate change mitigation and adaptation, by enhancing functional diversity and reducing disturbance risks (Ercanli 2018; Spathelf and Bolte 2025). Thus, enriching *P. sylvestris* stands with broadleaf species offers a promising silvicultural pathway for uneven-aged, biodiverse structures. While Calama et al. (2017), highlight that semi-regular or multi-aged *P. sylvestris* structures may increase vulnerability to fire, the specific context of our stands, combined with broadleaf enrichment, likely mitigates this risk.

Seedling density within the stands (Table 1) appears sufficient for successful regeneration overall. However, sparse regeneration in certain areas suggests the need for targeted interventions. Given that the light requirements of *P. sylvestris* saplings increase with size/age (Gaudio et al. 2011), as is also the case for *Q. pyrenaica* and *C. sativa*, two more light-demanding broadleaf species, canopy openings should be considered once a reasonable and viable number of seedlings has been established in the understory (5–10 years), in order to promote the recruitment of saplings.

Finally, the study findings suggest that managing stand density and shrub cover emerges as a key strategy for promoting natural regeneration. Management efforts should prioritize fostering the regeneration of broadleaf species, such as *Q. pyrenaica* and *C. sativa*, in favorable areas to enhance stand stratification, biodiversity, and resilience. Additionally, as the distance from *C. sativa* seed sources was negatively correlated with seedling density, this highlights the importance of maintaining nearby seed sources or creating ecological corridors to facilitate seed dispersal.

Conclusions

This study highlights that natural regeneration dynamics within *P. sylvestris* stands are shaped by canopy characteristics, species-specific traits, and microsite conditions. *Q. pyrenaica* emerged as the dominant species among seedlings and saplings, reflecting its adaptability to Mediterranean environments, while *P. sylvestris* showed limited regeneration in S2, despite its lower stand density, suggesting that stand structure alone does not explain its absence. The regeneration of *C. sativa* appeared locally constrained by seed source proximity, indicating dispersal limitation as a key factor.

The lower basal area generally favored the establishment of broadleaf species, especially *Q. pyrenaica*. *P. sylvestris* regeneration followed an unimodal trend and appeared more variable and context-dependent, highlighting the need to consider additional ecological factors beyond stand structure. Shrub cover also influenced regeneration patterns, reinforcing the importance of its management in silvicultural planning.

Adaptive management strategies should aim to create conditions that foster natural regeneration and promote structural and species diversity, thereby enhancing the resilience and both the ecological and economic value of Mediterranean forest ecosystems. While the observed patterns provide useful guidance, further research with broader replication and refined light measurements would strengthen the evidence base and support more targeted silvicultural interventions.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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