



Patterns of sessile oak regeneration and its main drivers in an old-growth sessile oak–European beech forest

Any Mary Petritan¹ · Florin Lucian Toiu¹ · Nicu Constantin Tudose¹ · Ion Catalin Petritan²

Received: 6 May 2025 / Revised: 27 June 2025 / Accepted: 24 July 2025 / Published online: 12 August 2025
© The Author(s) 2025

Abstract

Understanding the regeneration dynamics of sessile oak (*Quercus petraea*) under unmanaged forest conditions is crucial for sustaining oak-dominated ecosystems, particularly in the context of close-to-nature silviculture and climate change. In this study, we assessed the natural regeneration of sessile oak in a well-preserved old-growth forest reserve in Western Romania. Detailed inventories of seedlings and saplings across 27 canopy gaps of varying sizes revealed that while oak regeneration is currently abundant—accounting for 48% of total regeneration density—seedlings are predominantly confined to first regeneration development stage, with fewer individuals reaching sapling size. Principal component analysis and multiple regression modelling based on Boruta feature selection, identified light availability, browsing pressure, competition from European beech (*Fagus sylvatica*), and ground vegetation cover as critical factors influencing regeneration success, with their importance varying by development stage. Light was the principal driver for advanced regeneration stages ($R^2=0.14$), whereas seedling density was primarily shaped by browsing intensity and overstory oak composition ($R^2=0.28$). Despite the successful establishment of seedlings, the transition to larger size classes remains constrained by suboptimal light conditions and biotic competition, suggesting a bottleneck in sessile oak recruitment under the current disturbance regime. These findings highlight the need for targeted management interventions—such as promoting canopy openness, managing competing vegetation, and mitigating browsing pressure to support oak regeneration and ensure long-term stand sustainability.

Keywords Light availability · Browsing pressure · Ground vegetation competition · Natural regeneration · Natural forest

Introduction

Besides European beech (*Fagus sylvatica* L.), oak species—particularly sessile oak (*Quercus petraea* [Matt.] Liebl.) and pedunculate oak (*Quercus robur* L.)—are among the most widespread and ecologically important broadleaved tree species in European temperate forests,

harbouring rich biodiversity and holding considerable economic value (Leuschner and Ellenberg 2017; Mölder et al. 2019). Due to their higher drought tolerance, oak species are likely to become increasingly important components of mixed-species forest stands under future climatic conditions (Leuschner 2020; Kasper et al. 2021). To better cope with predicted drier and warmer climates, not only mixed stands of species with contrasting ecological traits and varying drought resistance are preferred, but also the use of natural regeneration as part of nature-oriented management approaches, such as close-to-nature forestry (Brang et al. 2014; Schütz et al. 2012). Ensuring the natural regeneration of the dominant tree species is a fundamental requirement for the successful implementation of such management strategies (Tinya et al. 2020). However, close-to-nature management, which typically avoids the creation of large canopy gaps, can disadvantage light-demanding species like

Communicated by Gediminas Brazaitis.

✉ Ion Catalin Petritan
petritan@unitbv.ro

¹ National Institute for Research and Development in Forestry “Marin Dracea”, 13 Closca Str., 500040 Brasov, Romania

² Department of Forest Engineering, Forest Management Planning and Terrestrial Measurements, Faculty of Silviculture and Forest Engineering, Transylvania University, 1 Ludwig Van Beethoven Str., 500123 Brasov, Romania

oaks and favor the regeneration of more shade-tolerant species (Bauhus et al. 2013; Petrovska et al. 2023).

These regeneration challenges are not only of ecological importance but also carry broader implications for forest policy and sustainable management. The importance of sustaining natural regeneration processes in native forest ecosystems has been increasingly recognized at the European level. Strategies such as the New EU Forest Strategy for 2030 and the EU Biodiversity Strategy for 2030 emphasize the critical role of resilient, biodiversity-rich forests in climate adaptation, carbon sequestration, and the preservation of ecosystem services. Moreover, achieving the Sustainable Development Goals (SDG 15—Life on Land; SDG 13—Climate Action) requires the maintenance and restoration of natural forest dynamics, including regeneration under natural disturbance regimes. In this context, understanding the factors that enable or constrain the regeneration of key native species, such as sessile oak, is essential for informing both conservation strategies and sustainable forest management practices across Europe.

Despite these growing policy efforts, scientific knowledge regarding oak regeneration mechanisms in unmanaged old-growth forests remains fragmented. While studies of natural regeneration in old-growth forests have demonstrated the ability of shade-tolerant trees, such as beech and silver fir, to regenerate successfully under gap canopy conditions (Diaci et al. 2012; Feldmann et al. 2020; Orman et al. 2021; Petrovska et al. 2023), information about oak regeneration under similar conditions is still limited (Diaci et al. 2008; Bobiec et al. 2011; Petritan et al. 2013; Jaloviar et al. 2020), mainly due to the rarity of such forests in Europe. Similar to observations in North America, the failure of oak regeneration and the replacement by more shade-tolerant species have also been frequently observed in European unmanaged oak forests (Feist et al. 2004; Bobiec et al. 2011; Saniga et al. 2014). In mixed oak old-growth forests, European beech and European hornbeam often outcompete oak regeneration (Bobiec et al. 2011; Petritan et al. 2013; Brzezicki et al. 2016). In multi-species beech-oak forests, such as the Sitno Reserve in Slovakia, sessile oak has failed to regenerate despite an intermediate disturbance regime, with species such as *Acer* spp. and *Fraxinus excelsior* (L.) increasingly dominating the regeneration layer (Jaloviar et al. 2020). Similarly, difficulties for oaks to naturally regenerate have also been observed in managed oak stands (Van Couwenberghe et al. 2013; Tinya et al. 2020, 2025).

Natural regeneration success is the result of several successive processes—establishment, survival, and growth—which depend not only on light availability through canopy gaps but also on factors such as acorn production, acorn germination, seedling survival, water and nutrient availability, competition from herbaceous and woody vegetation,

pathogen pressures, and browsing (Ligot et al. 2013; Anni-ghöfer et al. 2015; Kohler et al. 2020; Modrow et al. 2020; Demeter et al. 2021; Axer et al. 2021). In a comprehensive review, Kohler et al. (2020) emphasized the limited explanatory power of existing studies and called for further research on oak regeneration processes. They also highlighted that management recommendations advocating small canopy openings—as promoted under close-to-nature approaches—should be critically evaluated, given the lack of a robust scientific foundation.

Gap dynamics in mixed oak old-growth forests remain relatively understudied in Europe (Diaci et al. 2008; Petritan et al. 2013; Jaloviar et al. 2020; Dobrowolska et al. 2022), resulting in a fragmented understanding of oak regeneration under natural disturbance regimes. In one of the best-preserved sessile oak-dominated old-growth forests in Europe (Petritan et al. 2012), a comprehensive survey found that canopy disturbance is predominantly small-scale, with 60% of canopy gaps smaller than 100 m² and only a few larger gaps (Petritan et al. 2013). Despite sessile oak being the dominant canopy species, it was poorly represented in the advanced regeneration layers, suggesting that current gap dynamics may not support successful oak recruitment under natural conditions.

In order to determine whether sessile oak is indeed regenerating in this old-growth forest, particularly during the early stages of regeneration, we conducted a detailed survey of all seedlings and saplings taller than 4 cm in 27 gaps of varying sizes, including the largest ones.

This study aims to investigate the regeneration dynamics of sessile oak within an unmanaged old-growth forest ecosystem. We hypothesize that sessile oak regeneration successfully initiates under canopy gap conditions but is constrained in its advancement by limited light availability, competition from shade-tolerant species, and herbivory pressure. By analyzing regeneration patterns across multiple developmental stages, we seek to disentangle the relative importance of biotic, abiotic, and structural drivers influencing oak recruitment success. Understanding these dynamics is crucial for informing adaptive management strategies in oak-dominated forest ecosystems under changing climatic and disturbance regimes. To test this hypothesis, we address the following research questions: (1) Is sessile oak effectively regenerating under old-growth forest conditions, and to what extent is its scarcity in later developmental stages indicative of recruitment bottlenecks? (2) How do light availability, biotic interactions (competition and browsing), and stand structure interact to shape sessile oak regeneration at different ontogenetic stages?

Materials and methods

Study site

The study was carried out in the best-preserved part (22.1276E 46.1722N) of the old-growth forest reserve Runcu-Grosi, in the Zarand Mountains, Western Romania, dominated by the sessile oak forests. The area investigated accounted 32.3 ha and had a south-westerly aspect, being situated between 442 and 680 m a.s.l., with an average terrain inclination of 16° (Petritan et al. 2013) (Fig. 1). The region is situated at the transition of the Central European to sub-Mediterranean temperate bioclimate (Heinrichs et al. 2016). Average annual precipitation is about 687 mm and the mean annual temperature about 9.8 °C (Monorostia, 150 m a.s.l., the closest hydrometric station). Luvisols and cambisols, with medium to high storage for water and nutrient, have developed on crystalline schists as bedrock. Beside the sessile oak, the other main tree species is European beech (*Fagus sylvatica*), but also other species as turkey oak (*Quercus cerris*), hornbeam (*Carpinus betulus*), Norway maple (*Acer platanoides*), sycamore (*Acer pseudo-platanus*) cherry (*Prunus avium*), silver lime (*Tilia tomentosa*) and wild service tree (*Sorbus torminalis*) may rarely occur (Petritan et al. 2012).

Field sampling

From the 321 canopy gaps identified and mapped in the study area (Petrițan et al. 2013), we selected 27 expanded gaps for a detailed regeneration survey (Fig. 1). The expanded gap was defined as the area delimited by the positions of the trunks of the surrounding trees that formed the canopy opening (Runkle 1992). In 2013, in each of these gaps, all seedlings and saplings taller than 4 cm (excluding current-year seedlings) and smaller than 7 cm in DBH were recorded. Previous studies have shown that sessile oak, a mid- to light-demanding species, can establish in small gaps, but requires better light conditions for optimal development (Dobrowolska 2006, 2022; Tinya et al. 2020). Therefore, we randomly selected the largest seven expanded gaps (> 800 m²) identified in the study area, as they were assumed to provide the most favorable light conditions for oak regeneration (Petrițan et al. 2013). To ensure a balanced experimental design, we additionally selected 9 medium-sized gaps (400–800 m²) and 11 small gaps (< 400 m²). These medium and small gaps were randomly selected, with a selection probability proportional to their relative frequency within each 100 m² size class.

Nine circular plots were established within each selected expanded gap: one in centre of the gap, four halfway from the centre to the gap edge and four at the edge of the gap along the cardinal directions. The area of the circular

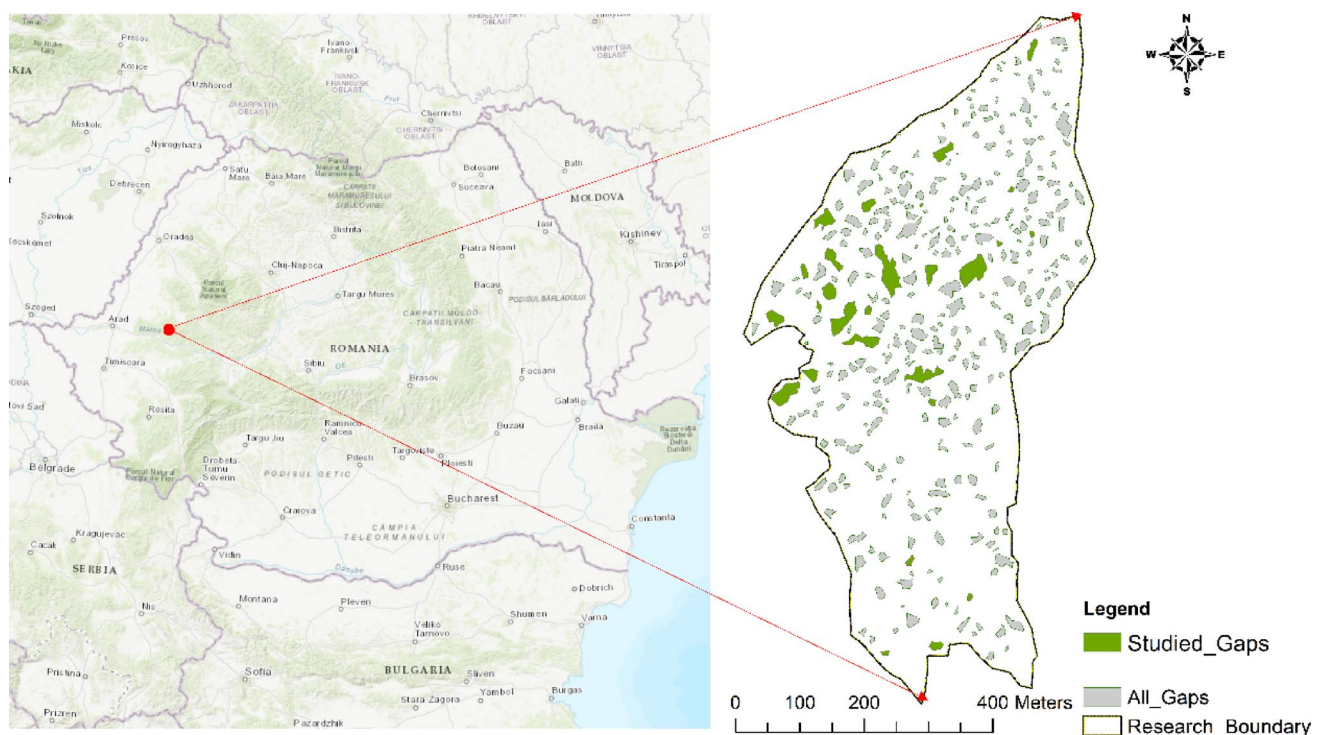


Fig. 1 Location of the study area in Romania with the expanded gaps within the study site Sources of left panel: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community. (Color figure online)

sampling plots varied according to the three expanded gaps size categories: 5 m² for the small, 10 m² for medium and 20 m² for the large gaps. In gaps, where the distance from centre to edge was too small and did not allow the plots to be independent on a cardinal direction, the plot located at the edge of the extended gap was not more considered. All tree seedlings/saplings in the sample plots were recorded as species and their height was measured. Each seedling/sapling are classified as browsed (browsed on main shoot, on side shoots, or both) or no-damaged.

The light conditions were quantified in the centre of each sample plot by taking a hemispherical photo at 1.3 m above the forest floor with a Canon EOS Rebel T3i professional camera, equipped with a CMOS sensor of 13 megapixels, a Super Fish Eye lens objective 5.6 mm and a self-leveling function. The indirect site factor (ISF) (percentage of above canopy light based on diffuse radiation), the direct

site factor (DSF) (relative amount of incident direct radiation which penetrates below canopy), the total site factor (TSF) (relative amount of total (diffuse and direct) incident radiation which penetrates below canopy), and the canopy openness (openness) are calculated by processing the hemispherical photos with the WinScanopy Pro b software package (Regents Instruments Inc. and Sainte-Foy 2012).

The ground vegetation and the deadwood cover were visually assessed in each plot and recorded as a percentage of the sampled plot area. All overstory surrounding trees bordering the expanded gaps were recorded by species and their DBH was measured. The DBH of all gap-fillers (young trees with a DBH greater than 7 cm but less than 20 m in height) in each expanded gap was measured and their basal area per hectare was calculated.

Data analysis

The oak regeneration was analyzed for seedlings/sapling density per total (oak), per different development stages (oak1, oak2, oak3, oak4) and for estimated cumulative biomass (biomass_oak) per ground area (m²), a roughly measure, which combine information on plant density and height in a single number (Feldmann et al. 2020). Similarly, to Annighöfer et al. (2015), the oak regeneration was grouped into four development stages according to their height: oak1—small seedlings with a height of 4–20 cm, oak2—tall seedlings with a height of 21–50 cm, oak3—small saplings with a height of 51–130 cm and oak4—tall saplings with a height of more than 130 cm and a DBH of less than 7 cm (see Table S1). The biomass of oak regeneration, as well as the biomass of the seedlings/saplings of beech and of the other species together was estimated using the allometric equation proposed by Annighöfer et al. (2016).

Different explanatory variables were calculated, grouped as: (i) stand parameters (number or basal area of the surrounding overstory trees, basal area of the gap-fillers); (ii) neighborhood at regeneration level (the density and biomass of beech, the other main tree species in regeneration, and of the other species considered together (due to their low proportion in the regeneration), some diversity indices (species richness and Shannon index), the percentage of browsed saplings and the cover of the ground vegetation, respectively of the *Rubus* spp.), percentage of deadwood in the sampled plot and (iii) environmental factors (light conditions and, slope, elevation) (Table 1).

To reveal general patterns in dependence of all recorded variables, a principal component analysis (PCA) was conducted. However, due to the limited range of variation in altitude and in slope, both environmental variables were excluded from the analysis. Also plot position along the cardinal directions and the distance of each plot from the

Table 1 Explanatory variables for the oak regeneration

Explanatory variables	Abreviations	Unit	Mean (min–max)
<i>Stand parameters</i>			
% of oak in the number of surrounding overstory trees	No_OAK	%	42 (0–86)
% of beech in the number of surrounding overstory trees	No_BEECH	%	56 (14–100)
% of oak in the basal area of surrounding overstory trees	BA_OAK	%	44 (0–95)
% of beech in the basal area of surrounding overstory trees	BA_OAK	%	54 (4–100)
Basal area of the gap-fillers	BA_Gapfillers	m ² ha ⁻¹	4.7 (0.4–11.2)
<i>Neighborhood at regeneration level</i>			
Beech density	Beech	No. m ⁻²	0.6 (0–10.8)
Beech biomass	biomass_beech	g m ⁻²	72.9 (0–872.5)
Other species density	Other	No. m ⁻²	0.1 (0–2.4)
Other species biomass	biomass_other	g m ⁻²	6.2 (0–196.7)
Species richness	Richness	No. m ⁻²	0.2 (0.1–0.6)
Shannon index	Shannon		0.4 (0–1.5)
Percentage of browsed saplings	Browsing	%	10 (0–73)
Ground vegetation cover	Vegetation	%	42 (0–100)
<i>Rubus</i> sp. Cover	Rubus	%	18 (0–100)
Percentage of deadwood	Deadwood	%	7 (0–90)
<i>Environmental factors</i>			
Total site factor	TSF	%	21 (2–68)
Canopy openness	Openness	%	12 (3–29)
Slope	Slope	°	16 (3–24)
Elevation	Elevation	m	569 (446–680)

Species in the regeneration were written with the lower case letters

gap's centre (gap centre, gap edge and intermediate position within each gap) were removed from PCA because the large variation of gap size and the pronounced irregularity of gap's shape conducted to a reduction in the importance of such environmental factors in explaining tree regeneration patterns.

The Spearman's rank correlations or Pearson coefficients for linear correlations were used to identify the highly correlated variables ($r \geq 0.85$). Highly correlated variables included: total site factor with direct site factor ($r = 0.99$, $p < 0.05$) and indirect site factor ($r = 0.87$, $p < 0.05$); beech regeneration density with the regeneration density of beech and other species combined ($r = 0.97$, $p < 0.05$); beech regeneration biomass with the combined regeneration biomass of beech and other species ($r = 0.98$, $p < 0.05$), due to the very small proportion of other species; No_OAK with BA_OAK ($r = 0.91$, $p < 0.05$) and No_BEECH with BA_BEECH ($r = 0.86$, $p < 0.05$). Therefore, the indirect and direct site

factors, BA_OAK and BA_BEECH, as well as the combined regeneration density and biomass of beech and other species, were excluded from the subsequent analyses.

Before to start the regression analysis, in order to reduce the number of explanatory variables, a Boruta analysis was performed to identify the most important variables for oak regeneration (R package “Boruta”, version 8.0.0). All considered variables were classified as relevant, tentative and irrelevant variables based on comparison of each variable's importance value assessed by the random forest algorithm (mean importance, Table 2) with that of a shadow variable created by 100 randomly permutating the variable's values (Kursa and Rudnicki 2010). Variables with an importance value greater than the highest shadow values were categorized as relevant variables and were ranked based on the proportion of random forest iterations in which the variable was more important than the most important shadow variable (Norm hits, Table 2). Boruta analysis was performed separately for the total regeneration density of oak (oak) and of each development stage (oak1-oak4), as well as for its total biomass (biomass_oak). In the case when the number of relevant variables was greater than 5, the five most important variables were kept for the linear regression analysis. If Boruta algorithm found fewer than 5 relevant variables, all these variables were included in the regression analysis. Prior to apply the multiple regression analysis, the Shapiro–Wilk test was performed to check the normality of the response variables data. In order to normalize them, the response variables were transformed logarithmically. All combinations of full potentially models (containing all relevant predictor variables indicated by Boruta and their interactions) were simplified using the function “selMod” from “pgirmess” R package, version 2.0.3 and the best model was selected based on corrected AIC values from the models with $\Delta AIC_c < 3$. In the final analysis's step, the best model found for each response variable was further simplified by removing the non-significant variables and interactions according to their p-values applying stepwise deletion (backward selection). It should be mentioned out that for the best model for each response variable, the variance inflation factor (VIF) was calculated to check the collinearity among the variables included in model and thus to assess how much the variance of a regression coefficient in model is inflated by the multicollinearity. When was meet a $VIF > 3$, an additionally simplification of the model by removing the variable or interaction that generated such high VIF values was conducted.

All statistical analyses were performed in R Statistical Software (v 4.1.2, R Core Team 2024) using R Studio 2024.04.2.

Table 2 Variables detected as important by Boruta analysis for predicting the density of the total oak regeneration (oak) and of each development stage (oak1-oak4), as well as the total biomass of oak regeneration (biomass_oak)

Regeneration development stage	Identified variables	Mean importance	Norm hits
Oak (total)	Browsing	10.84	1.00
	No_OAK	7.01	0.98
	No_BEECH	6.85	0.98
	Richness	4.09	0.93
	Biomass_beech	3.64	0.87
Oak1 (4–20 cm in height)	Browsing	10.77	1.00
	Biomass_beech	9.08	0.99
	Vegetation	7.60	0.98
	Beech	7.34	0.97
	No_OAK	6.71	0.94
Oak2 (21–50 cm in height)	Browsing	8.26	0.99
	No_OAK	6.61	0.98
	No_BEECH	5.79	0.96
	Richness	3.69	0.93
	TSF	2.45	0.65
Oak3 (51–130 cm in height)	Openness	2.12	0.57
	Richness	1.71	0.55
oak4 (0.1–6.9 cm in DBH)	Openness	5.35	0.98
	TSF	5.12	0.97
Biom_oak (total)	TSF	3.83	0.88
	Openness	3.51	0.85
	Shannon	2.89	0.74
	No_OAK	2.93	0.73
	Browsing	1.96	0.50

Their mean importance value (Mean Importance) and their percentage of random forest iterations (Norm Hits) in which their importance was greater than that of the most important shadow variable are presented

Results

On the 204 surveyed plots, with a total area of 2255 m², 3738 seedlings and saplings were recorded. Regeneration was found on 91% of the plots, with oak regeneration present on a total of 139 plots (68%). Of the total oak regeneration, about half of the seedlings belongs to the first regeneration development stage—oak1 (48%), 40% belongs to the second regeneration development stage (oak2), 11% to oak3 and only 1% to oak4.

However, the sessile oak was the species with the highest density in the regeneration, with an average of 1.0 individual m⁻². In comparison, the other main species in the regeneration, European beech, was presented with a lower density (0.6 individuals m⁻²), while all other species combined accounted only 0.07 individuals per m² (Fig. 2a). On average, sessile oak accounted for 48% of the total regeneration density at the plot level, followed by beech with 41%. A contrasting pattern in regeneration biomass was observed, with the highest average biomass found for beech (72.9 g m⁻²), followed by oak (9.3 g m⁻²) and other species (6.2 g m⁻²) (Fig. 2b). The average proportion of each species in the total plot regeneration biomass was 55% for beech, 34% for sessile oak, and 11% for other species.

The average browsing rate at the regeneration level was approximately 12%. However, sessile oak was disproportionately affected, accounting for 88% of the all-browsed individuals within regeneration layer. The percentage of browsed all seedlings and saplings was highly correlated with the proportion of browsed oak individuals ($r=0.88$, $p<0.0001$). Among oak regeneration, about 20% of seedlings and saplings were affected by browsing, with the highest

rate observed in the second development stage oak2 (24%), followed by oak1 (17%) and oak3 (16%).

The PCA of the all-recorded variables explained only 42.3% of the variance (Fig. 3). The oak density in the first development stage (oak1) was very closely related to the percentage of browsing (browsing), the proportion of oak in the overstory trees surrounding the gap (No_OAK), and the basal area of oak in the same layer (BA_OAK). It was negatively related to the density and biomass of beech in the regeneration layer (beech, biomass_beech), as well as to the number and basal area of beech in the gap surrounding overstory trees (No_BEECH, BA_BEECH). Also, the *Rubus* spp. cover percentage (Rubus) and Shannon diversity index of regeneration (Shannon) were negatively related to oak1. Oak total abundance (oak) and oak2 keep the browsing percentage as explanatory variables.

Regarding the total oak regeneration density, Boruta analysis indicated that the percentage of browsing, the proportion of oak and beech among gap surrounding overstory trees, the species richness in the regeneration layer and the biomass of beech regeneration, were all closely associated with oak regeneration density (Table 2).

When focusing on the four development stages, the importance of explanatory variables differed substantially among them. For the first stage (oak1), browsing percentage, biomass of beech regeneration (biomass_beech), vegetation cover, the density of beech regeneration (beech) and the proportion of oak among surrounding overstory trees (No_OAK) were identified as important variables for the abundance of oak regeneration. For the second stage (oak2), browsing percentage (browsing), the proportion of oak (No_OAK) and beech (No_BEECH) in the surrounding

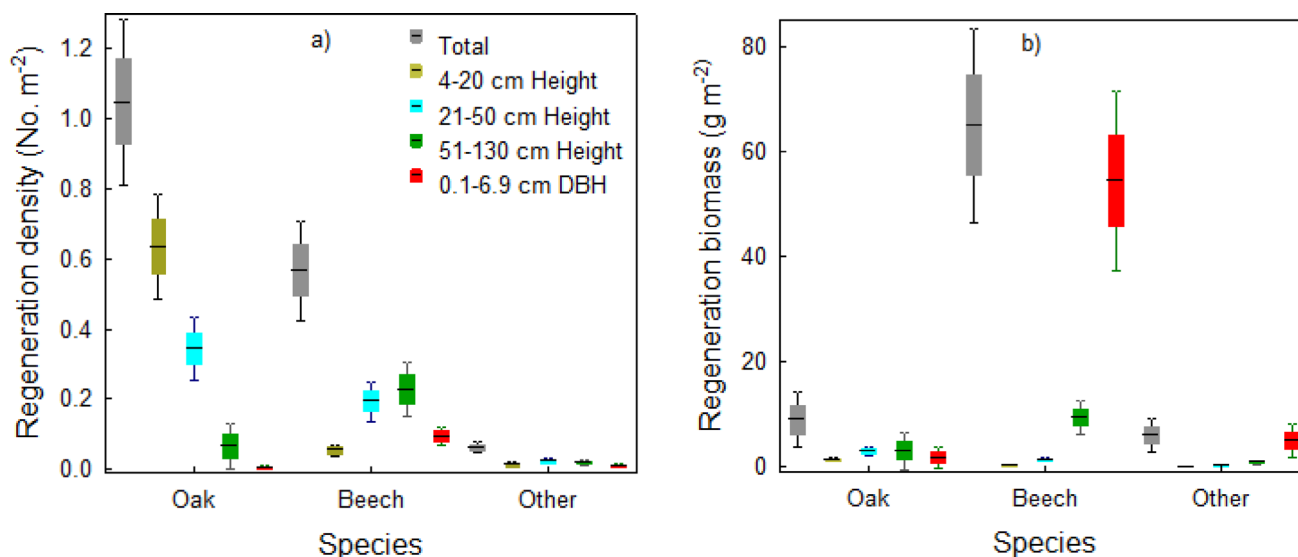


Fig. 2 The average regeneration density and biomass by species per total and by the for developmental stages (small seedlings: 4–20 cm height, tall seedlings: 21–50 cm height, small saplings: 51–130 cm

height and tall saplings: >130 cm in height and a DBH <7 cm (0.1–6.9 cm DBH). Mean; Box: Mean $\pm$ SE; Whisker: Mean $\pm$ 0.95 Conf. Interval. (Color figure online)

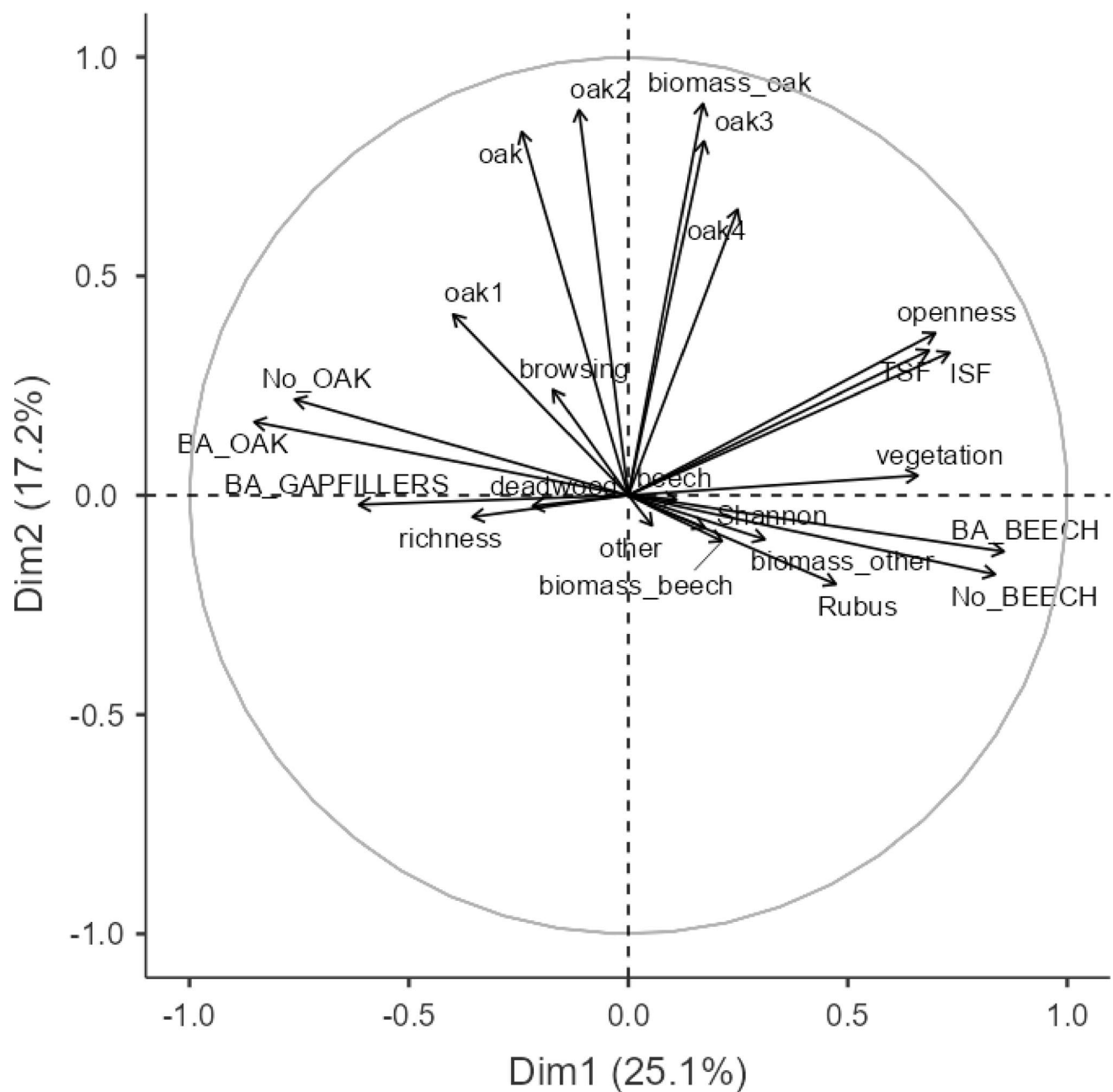


Fig. 3 Principal component analysis (PCA) for the 204 plots. The total regeneration biomass of oak is labeled as biomass_oak, the total density of oak and of each development stages as oak1, oak2, oak3 and oak4, the explanatory variables were labeled as in Table 1

overstory trees, the richness of the regeneration layer (richness) and the total site factor (TSF) were detected as the most five important variables.

For oak 3, the canopy openness and the regeneration richness were important, whereas for oak4, only the light variables (canopy openness and total site factor) remained as important variables. For the total oak regeneration biomass (biomass_oak), the most important five explanatory variables indicated by Boruta algorithm were the total site factor (TSF), canopy openness (openness), diversity of

regeneration (Shannon), the browsing percentage (browsing) and the percentage of oak (No_OAK) in the number of surrounding overstory trees (Table 2).

The multiple linear regression models revealed higher adjusted R^2 values for oak1, oak 2 and oak than for oak3 and oak4 (Table 3). The removing of non-significant variables and interactions led to models with only one explanatory variable in the case of oak3 and oak4. For oak1, the percentage of browsed seedlings and the percentage of oak in the number of surrounding overstory trees (No_OAK)

Table 3 Best model fit using multiple linear regression (estimated coefficients, standard error, t-value and *p*-values of the regression models) for regeneration density in each development stages (oak1–oak4) and for total oak regeneration density (oak) (n m⁻²)

Model	Variable	Estimated coefficient	Std. error	t-value	<i>p</i> -value	Adjusted R ²
Log (oak1)	(Intercept)	1.821×10^{-1}	3.460×10^{-2}	5.263	<0.001	0.281
	Browsing	1.817×10^{-3}	8.140×10^{-4}	2.233	0.027	
	No_OAK	1.615×10^{-3}	5.418×10^{-4}	2.980	0.003	
	Biomass_beech	-2.456×10^{-4}	8.589×10^{-5}	-2.859	0.005	
	Vegetation	-1.834×10^{-3}	3.479×10^{-4}	-5.272	<0.001	
Log (oak2)	(Intercept)	-2.811×10^{-2}	1.817×10^{-2}	-1.547	0.123	0.301
	Browsing: No_OAK	3.108×10^{-5}	9.720×10^{-5}	3.197	0.001	
	No_OAK: richness	3.096×10^{-3}	1.268×10^{-3}	2.442	0.015	
	No_OAK: TSF	5.193×10^{-5}	1.650×10^{-5}	3.131	0.002	
	Richness: TSF	1.075×10^{-2}	3.730×10^{-3}	2.881	0.004	
Log (oak3)	(Intercept)	-2.881×10^{-2}	1.143×10^{-2}	-2.518	0.012	0.181
	Openness	3.798×10^{-3}	8.779×10^{-4}	4.327	<0.001	
Log (oak4)	(Intercept)	-3.139×10^{-3}	1.588×10^{-3}	-2.015	0.045	0.138
	TSF	2.405×10^{-4}	6.258×10^{-5}	3.843	<0.001	
Log (oak)	(Intercept)	-4.139×10^{-2}	4.247×10^{-2}	-0.975	0.331	0.254
	Browsing	3.582×10^{-3}	1.012×10^{-3}	3.539	<0.001	
	No_OAK	3.244×10^{-3}	6.443×10^{-4}	5.036	<0.001	
	Richness	4.714×10^{-1}	1.311×10^{-1}	3.596	<0.001	
Biomass_oak	(Intercept)	-5.816	4.813	-1.208	0.228	0.154
	TSF	7.212×10^{-1}	1.933×10^{-1}	3.731	<0.001	

showed a significant positive effect on oak abundance (Fig. 3a), whereas the biomass of beech in regeneration (biomass_beech) and the percent of vegetation cover (vegetation) indicated a significant negative effect (Fig. 4b, c). The *p*-values of the explanatory variables of oak2 kept in the best model only the interactions of the number of surrounding overstory trees (No_OAK) (Fig. 4d) with browsing percentage, regeneration richness and total site factor (TSF) but also interaction between light parameter (TSF) and richness as positive significant effect on the response variables, showing a higher effect of mature oak trees as the higher TSF and the species diversity of regeneration are. However, the light conditions were not significant alone for oak2. For the two latest regeneration stages, only the light variables are found as significant explanatory variables for oak regeneration abundance: canopy openness (openness) in oak 3 (Fig. 4e), respectively total site factor in oak4.

The browsing percentage, the number of surrounding overstory trees (No_OAK) and the species richness of regeneration were significant for the total oak abundance. The total oak regeneration biomass (biomass_oak) presented the light parameter (TSF) as single significant explanatory variable, light having a significant positive effect on oak biomass (Fig. 4f, Table 3).

Discussion

Regeneration is a key process in forest stand dynamics, often acting as a bottleneck to the successful establishment of tree species in mixed forests (Nakashizuka 2001). In this context, the present study primarily aimed to assess whether sessile oak is truly regenerating in one of Europe's best-preserved old-growth forest dominated by this species, given its near absence in the gap-fillers layer (Petrutan et al. 2013).

Our detailed inventory revealed that sessile oak is indeed regenerating and currently represents the dominant species in the regeneration layer, with an average density of 1.0 individuals per m² and an average relative share of 48%. However, the majority of oak regeneration (88%) was concentrated in the early regeneration development stages (oak1 and oak2), with nearly half of individuals less than 20 cm in height (oak1). A similar pattern was observed in a large-scale study of managed oak stands in Germany (Anni-ghöfer et al. 2015), where oak regeneration also occurred predominantly in the early stages. Despite the investigated stands are managed to promote oak regeneration, the average density of oak seedlings and saplings in those stands was only slightly higher (1.6 individuals m⁻²), and the distribution across development stages closely mirrored our findings, with 61% classified as oak1, 28% as oak2, 9% as oak3, and only 1% reaching oak4. In contrast, oak regeneration in the unmanaged forests of Białowieża National Park was significantly lower, with densities ranging from 0.01 to 0.04 individuals per m², and slightly higher values (up to 0.1 individuals per m²) recorded only in large gaps (Bobiec et

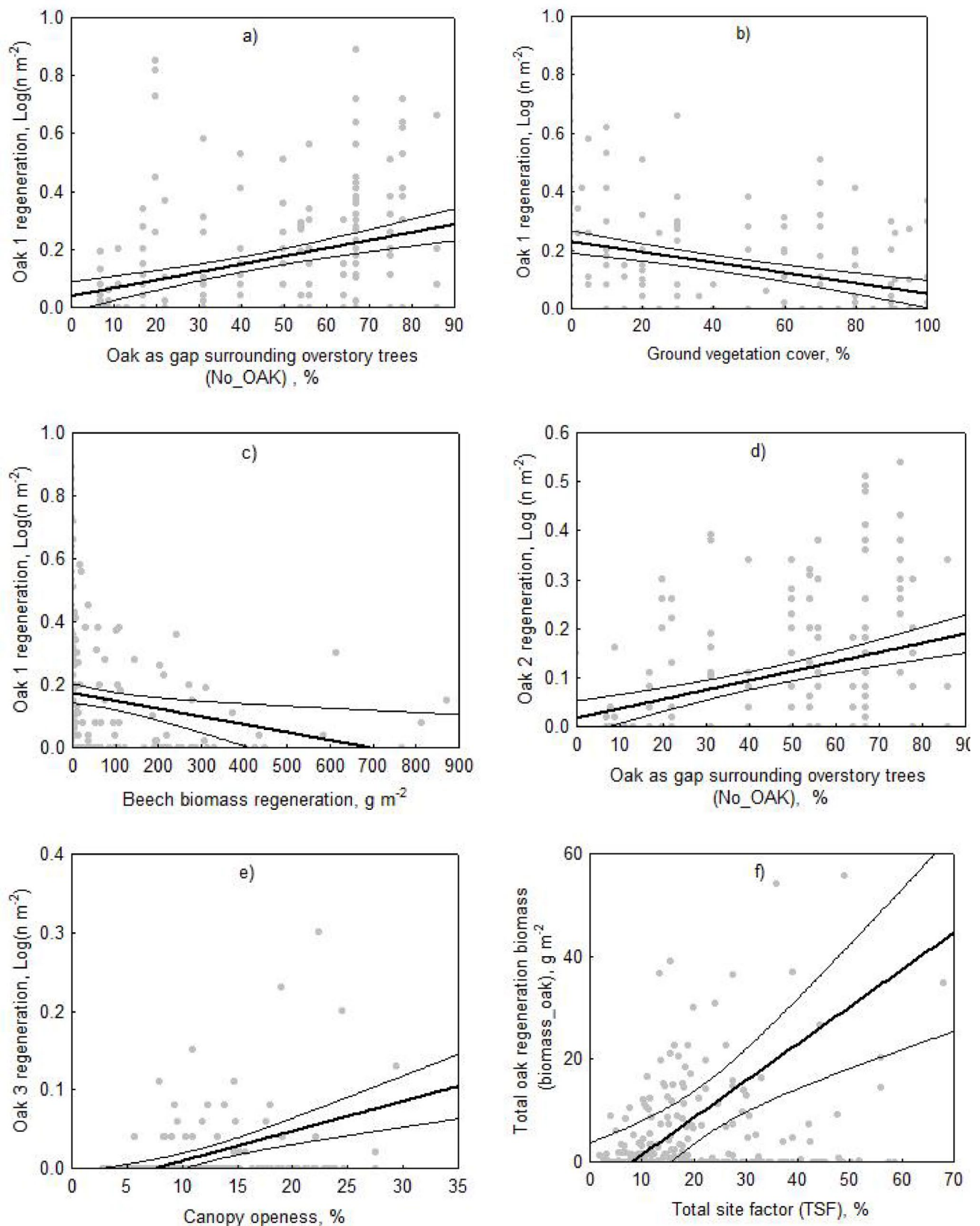


Fig. 4 The most important variables explaining sessile oak regeneration density in various development stages (oak1—4a, 4b, 4c, oak2—4d, oak3—4e) and total sessile oak regeneration biomass (4f). Each graph shows the significant regression line ($p < 0.05$), with the 95%

confidence interval. The regression line indicates the partial effect of significant predictor while holding other variables constant. The entire model based on multiple linear regression is showed in Table 3

al. 2011). Similarly, Dobrowolska et al. (2022) found in the Polish part of Białowieża forest very low number of the oak trees in the regeneration, varied from 0.05 individuals per m² in the small gaps to 0.09. Even within the largest gaps, taller oak saplings (oak4, higher than 1.3 m) accounted lower than 5% of total oak regeneration (Bobiec et al. 2011), Dobrowolska et al. 2022). An even more pronounced regeneration failure was reported in one of the few remaining old-growth multi-species beech-oak forests, the Sitno Reserve, in Slovakia. There, despite sessile oak contributing 9.2% of the basal area and 3.4% of the tree number in the main canopy tree layer, it was nearly absent in regeneration, with only 25 saplings per hectare recorded in canopy gaps.

The regeneration pattern observed in our study suggests that the mature oak trees are producing viable acorns, which germinates successfully and establish as seedlings. Therefore, the initial phases of the regeneration process—seed production, dispersal, germination, and early seedling establishment (Clark et al. 1999)—appear to be functioning effectively in this old-growth forest. However, the subsequent stages, growth and recruitment, which are essential for successful regeneration, appear to be limited.

Our analysis confirmed that the performance of oak natural regeneration is governed by multiple interacting factors, which vary depending on the developmental stage of regeneration cohort (Annighöfer et al. 2015; Mölder et al. 2019; Axer et al. 2023). Among these, light availability emerges as a critical factor. Increased canopy openness has consistently been associated with improved relative height growth and survival of oak regeneration (i.e. Diaci et al. 2008; Ligot et al. 2013; Annighöfer et al. 2015; Kuehne et al. 2020; Petersson et al. 2020; Dobrowolska et al. 2022; Tinya et al. 2025). This was confirmed by our study, in which variables describing light availability are significant predictors of oak biomass, composite metric integrating both regeneration density and height (Feldmann et al. 2020). In contrast to Dobrowolska (2006), light conditions did not significantly influence the overall density of oak regeneration (oak) and the abundance of the small seedlings (oak1). However, light availability became a significant factor for the abundance of taller seedlings (oak2), and especially of saplings (oak3 and oak4). The findings derived from the old-growth forest conditions, align closely with results from managed oak stands reported by Annighöfer et al. (2015).

The light requirements of young deciduous trees typically increase with plant size (Valladares and Niinemets 2008). This is particularly true for oak seedlings, which exhibit a relatively high degree of shade tolerance during their initial years (Valladares et al. 2002). This early-stage tolerance is partly attributed to the substantial nutrient reserves stored in the acorn (Grime 1966; Ziegenhagen and Kausch 1995). However, once these seed reserves are exhausted, adequate

light levels become essential for continued growth and survival (Tinya et al. 2020).

Empirical studies have attempted to quantify these light thresholds, providing insight into the minimum and optimal conditions for oak regeneration success. According to von Lüpke (1998) and Röhrig et al. (2006), oak regeneration can persist in shaded forest understories at light levels as low as 15% of above canopy light for several years. However, continuous height growth typically requires levels exceeding 20% of open-field conditions (Röhrig et al. 2006; Ligot et al. 2013). Light levels above 50% are considered particularly favorable for the growth and successful establishment of oak regeneration (Kuehne et al. 2020; Modrow et al. 2020), which was generally not the case in our study (Table 1; Fig. 4).

Nevertheless, in their comprehensive review, Kohler et al. (2020) emphasized that there is still a lack of long-term studies covering a broad gradient of light conditions. As a result, our understanding of how light requirements shift throughout the ontogeny of young oaks remains incomplete. Further research is needed to clarify the dynamic relationship between developmental stage and light demand over time.

High initial seedling densities appear to be a crucial factor for successful oak regeneration (Wallraf and Wagner 2019; Kuehne et al. 2020). In our study, a high density of initial oak seedlings (oak1) was closely associated with a high proportion of oak in the overstory (No_OAK), as shown by our explanatory models (Table 3; Fig. 4) as well as with a high proportion of the sessile oak in the basal area of gap surrounding trees (BA_OAK, Fig. 4). This finding supports the idea that a sufficient number of mature, seed-producing trees (i.e. mother trees) is necessary to initiate regeneration, in agreement with observations by Tinya et al. (2019). Previous studies have likewise demonstrated a positive relationship between oak basal area of overstory trees and regeneration density (Annighöfer et al. 2015; Axer et al. 2023), with the highest regeneration densities occurred when oak basal area exceeded 25–30 m² ha⁻¹.

Beyond overstory composition, the competition from ground vegetation (Mölder et al. 2019) or other woody species, particularly the shade-tolerant European beech can hinder the oak regeneration success (Ammer and Dingel 1997; Collet et al. 1996; Ligot et al. 2013; Mölder et al. 2019; Jaloviar et al. 2020; Tinya et al. 2025). Our study found significant negative effects of both ground vegetation cover (veg) and beech biomass in the regeneration layer (biom-beech) on the density of small seedlings (oak1), confirming these interactions.

Browsing pressure also emerged as crucial factor influencing regeneration dynamics (Harmer and Morgan 2007). In our study, browsing rate was found as a significant

explanatory variable for oak density in both first and second development stages (Table 3). Similarly, browsing was identified as one of the most influential variables affecting the presence of short saplings in the Białowieża Forest (Dobrowolska et al. 2022) and in managed forests in Germany (Annighöfer et al. 2015). Interestingly, the relationship between the percentage of the browsed tree species in regeneration and oak seedlings/saplings density was positive similar to findings by Annighöfer et al. (2015) in managed oak stands. This counterintuitive result may be due to the high browsing preference for sessile oak, which represented 88% of all browsed individuals and to the highly correlation between the percentage of browsed oak individuals and the overall browsing rate (browsing). As oak density increases, so too does the number of browsed individuals.

However, this does not imply that browsing has no negative effect. In some stands, oak regeneration may have been entirely absent due to repeated browsing, with seedlings eliminated before establishing or not even reached the sapling stage (Reimoser and Gossow 1996; Harmer and Morgan 2007; Borderieux et al. 2021). Our findings support the view that sessile oak is more palatable to deer than other species (Berquist et al. 2009; Borkowski et al. 2017) included European beech, which is less frequently browsed and can survive repeated herbivory without significant mortality (Rozenbergar and Diaci 2014; Petritan et al. 2015). This differential palatability may further disadvantage oak in contribute to its failure in the late developmental stages of the regeneration. Harmer (1999) found that the combination of shading and browsing had a greater negative impact on oak seedling biomass than on beech or other competing species. To better isolate browsing effects from other variables, paired fenced and unfenced plots will be helpful.

Although these findings offer valuable insights into the drivers of oak regeneration, several limitations should be acknowledged, as they affect the interpretation of our results and their broader applicability. First, our study is based on a single old-growth forest site, and while it captures detailed local dynamics, caution must be exercised in generalizing the patterns observed. Other factors such as microclimatic variation or soil traits (e.g., soil pH and iron content—see Annighöfer et al. 2015) may influence regeneration success across different forest types or regions. Furthermore, some of the models presented, particularly those explaining advanced regeneration stages (e.g., oak3 and oak4), showed relatively low explanatory power (R^2 values), mainly due to the few oaks reached these late developmental stages. This suggests that other unmeasured ecological factors—such as soil nutrient availability, moisture conditions, or biotic interactions—may play critical roles in shaping outcomes. The cross-sectional nature of our study also prevents us from capturing temporal dynamics, such as the influence of

past years, seedling survival variability across growing seasons, or long-term recruitment trends under climate change.

These limitations underscore the need for future studies to incorporate broader spatial replication, additional environmental variables, and temporal data to improve the mechanistic understanding of sessile oak regeneration in natural and managed systems.

Conclusion and practical implications

Our study provides clear evidence that sessile oak retains the capacity to naturally regenerate in the studied old-growth forest. High densities of seedlings confirm that key early processes—seed production, dispersal, and initial establishment—are functioning effectively. However, the sharp decline of oak individuals at later developmental stages highlights a critical bottleneck, where limited light availability, competition from shade-tolerant species such as European beech, and high browsing pressure collectively constrain recruitment into the taller saplings layer.

Light availability emerged as a principal driver of oak regeneration success, particularly in the transition from seedling to sapling stages, underscoring the importance of canopy openness for oak recruitment. Instead, ground vegetation competition, beech regeneration biomass, and selective browsing disproportionately affected smaller oak individuals, increasing mortality risks during early growth. In the absence of sufficient natural disturbance creating adequate canopy openings, sessile oak regeneration is unlikely to sustain its dominance, threatening the future resilience and biodiversity of these forest systems.

These findings carry important practical and policy implications. They align closely with the goals of the New EU Forest Strategy for 2030, which emphasizes promoting resilient forest ecosystems through natural regeneration and biodiversity enhancement, and the EU Biodiversity Strategy for 2030, which calls for the restoration of dynamic, self-sustaining forest ecosystems.

From a practical perspective, ensuring a sufficient number of seed-bearing oak trees is a foundational step for initiating regeneration. Management interventions should maintain or enhance the reproductive oaks, particularly around regeneration gaps. However, this must be complemented by canopy interventions that increase light availability, particularly in later regeneration development stages. Moreover, effective control of competing vegetation—especially beech—and strategies to mitigate browsing pressure (e.g. temporary fencing, population management of ungulates) are essential. Given the increasing challenges facing oak-dominated forests under changing climate, active monitoring and adaptive management will be crucial for maintaining their ecological

and silvicultural value. By integrating these actions, forest managers and conservation planners can support the natural resilience of oak-dominated ecosystems while contributing to the broader European and global efforts toward sustainable forest management and biodiversity conservation.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10342-025-01815-z>.

Acknowledgements This project was financed by the Romanian National Authority for Scientific Research and Innovation, project number PN-II-RU-TE-2011-3-0075; and by project PN23090301, within the FORCLIMSOC nucleu program. We appreciate the permission and logistic support given by staff of the Barzava Forest District, we are grateful especially to eng. Gheorghe Marc, the forest district leader.

Author contributions A.M. Petritan: Conceptualization, Investigation, Methodology, Validation, Data curation, Formal analysis, Funding acquisition, Project administration, Resources, Writing – original draft. F.L. Toiu: Investigation, Writing – review & editing. N.C. Tudose: Investigation, Validation, Formal analysis, Writing – review & editing. I.C. Petritan: Conceptualization, Investigation, Methodology, Formal analysis, Data curation, Writing – review & editing.

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

Declarations

Conflict of interest The authors declare no competing interests.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Ammer C, Dingel C (1997) Untersuchungen über den Einfluss starker Weichlaubholzkonzurrenz auf das Wachstum und die Qualität junger Stieleichen. Forstw. Cbl. 116: S-346.
- Annighöfer P, Beckschäfer P, Vor T, Ammer C (2015) Regeneration patterns of European oak species (*Quercus petraea* (Matt.) Liebl., *Quercus robur* L.) in dependence of environment and neighborhood. PLoS ONE 10(8):e0134935. <https://doi.org/10.1371/journal.pone.0134935>
- Annighöfer P, Ameztegui A, Ammer C, Balandier P, Bartsch N, Bolte A, Coll L, Collet C, Ewald J, Frischbier N et al (2016)

- Species-specific and generic biomass equations for seedlings and saplings of European tree species. Eur J for Res 135:313–329
- Axer M, Martens S, Schlicht R, Wagner S (2021) Modelling natural regeneration of European beech in Saxony, Germany: identifying factors influencing the occurrence and density of regeneration. Eur J Res 140:947–968
- Axer M, Martens S, Schlicht R, Eisenhauer DR, Wagner S (2023) Modelling natural regeneration of oak in Saxony, Germany: identifying factors influencing the occurrence and density of regeneration. iForest-BiogeoSci for 16(1):47. <https://doi.org/10.3832/for4064-015>
- Bauhus J, Puettmann KJ, Kühne C (2013) Close-to-nature forest management in Europe: Does it support complexity and adaptability of forest ecosystems? In: Messier C, Puettmann KJ, Coates KD (eds) Managing forests as complex adaptive systems: building resilience to the challenge of global change. Routledge, The Earthscan forest Library, pp 187–213
- Bergquist J, Löf M, Örlander G (2009) Effects of roe deer browsing and site preparation on performance of planted broadleaved and conifer seedlings when using temporary fences. Scand J for Res 24:308–317. <https://doi.org/10.1080/02827580903117420>
- Bobiec A, Jaszcz E, Wojtunik K (2011) Oak (*Quercus robur* L.) regeneration as a response to natural dynamics of stands in European hemiboreal zone. Eur J Forest Res 130:785–797
- Borderieux J, Paillet Y, Dalmasso M, Mârell A, Perot T, Vallet P (2021) The presence of shade-intolerant conifers facilitates the regeneration of *Quercus petraea* in mixed stands. For Ecol Manage 491:119189. <https://doi.org/10.1016/j.foreco.2021.119189>
- Borkowski J, Dobrowolska D, Dąbrowski W, Banul R, Żalwski D (2017) Young conifer stands form a deer browsing refuge for an oak admixture: silvicultural implications for forest regeneration under herbivore pressure. Eur J for Res 136:787–800. <https://doi.org/10.1007/s10342-017-1070-3>
- Brang P, Spathelf P, Larsen JB, Bauhus J, Boncina A, Chauvin C, Drossler L, Garcia-Guemes C, Heiri C, Kerr G et al (2014) Suitability of close-to-nature silviculture for adapting temperate European forests to climate change. Forestry 87:492–503. <https://doi.org/10.1093/forestry/cpu018>
- Brzeziecki B, Pommerening A, Miśicki S, Drozdowski S, Żybura H (2016) A common lack of demographic equilibrium among tree species in Białowieża National Park (NE Poland): evidence from long-term plots. J Veg Sci 27:460–469
- Clark JS, Beckage B, Camill P, Cleveland B, Hille Ris Lambers J, Lichter J, McLachlan J, Mohan J, Wyckoff PH (1999) Interpreting recruitment limitation in forests. Am J Bot 86:1–16
- Collet C, Guehl JM, Frochot H, Ferhi A (1996) Effect of two forest grasses differing in their growth dynamics on the water relations and the growth of *Quercus petraea* seedlings. Can J Bot 74:1562–1571. <https://doi.org/10.1139/b96-189>
- Demeter L, Molnár AP, Öllerer K, Csóka G, Kiš A, Vadász C, Horváth F, Molnár Z (2021) Rethinking the natural regeneration failure of pedunculate oak: The pathogen mildew hypothesis. Biol Conserv 253:108928. <https://doi.org/10.1016/j.biocon.2020.108928>
- Diaci J, Györek N, Gliha J, Nagel TA (2008) Response of *Quercus robur* L. seedlings to north-south asymmetry of light within gaps in floodplain forests of Slovenia. Ann Sci 65:105
- Diaci J, Adamic T, Rozman A (2012) Gap recruitment and partitioning in an old-growth beech forest of the Dinaric Mountains: influences of light regime, herb competition and browsing. For Ecol Manage 285:20–28. <https://doi.org/10.1016/j.foreco.2012.08.010>
- Dobrowolska D (2006) Oak natural regeneration and conversion processes in mixed Scots pine stands. Forestry 79:503–513. <https://doi.org/10.1093/forestry/cpl034>
- Dobrowolska D, Piasecka Ż, Stereńczak K (2022) Canopy gap characteristics and regeneration patterns in the Białowieża forest based

- on remote sensing data and field measurements. For Ecol Manage 511:120123. <https://doi.org/10.1016/j.foreco.2022.120123>
- Feist MA, Phillippe LR, Busemeyer DT, Ebinger JE (2004) Vegetation survey of dean hills nature preserve, Fayette county, Illinois. Castanea 69:52–66. [https://doi.org/10.2179/0008-7475\(2004\)069%3c0052:VSODHN%3e2.0.CO;2](https://doi.org/10.2179/0008-7475(2004)069%3c0052:VSODHN%3e2.0.CO;2)
- Feldmann E, Glatthorn J, Ammer C, Leuschner C (2020) Regeneration dynamics following the formation of understory gaps in a Slovakian beech virgin forest. Forests 11:585. <https://doi.org/10.3390/f11050585>
- Grime JP (1966) Shade avoidance and shade tolerance in flowering plants. In: Bainbridge G, Evans GC, Rackham O (eds) Light as an ecological factor. Blackwell, Oxford, pp 187–207
- Harmer R (1999) Survival and new shoot production by artificially browsed seedlings of ash, beech, oak and sycamore grown under different levels of shade. Ecol Manage 116:39–50. [https://doi.org/10.1016/S0378-1127\(98\)00459-9](https://doi.org/10.1016/S0378-1127(98)00459-9)
- Harmer R, Morgan G (2007) Development of *Quercus robur* advance regeneration following canopy reduction in an oak woodland. Forestry 80:137–149. <https://doi.org/10.1093/forestry/cpm006>
- Heinrichs S, Walentowski H, Bergmeier E, Mellert KH, Indreica A, Kuzyakov Y, Leuschner C, Petritan AM, Teodosiu M (2016) Forest vegetation in western Romania in relation to climate variables: does community composition reflect modelled tree species distribution? Ann Fo Re. 59:219–236
- Regents Instruments Inc. Sainte-Foy, Québec (2012) WinScanopy Pro b software package for hemispherical image analysis. www.regent-instruments.com
- Jaloviari P, Sedmáková D, Pittner J, Jarčuškova Danková L, Kucbel S, Sedmák R, Saniga M (2020) Gap structure and regeneration in the mixed old-growth forests of National Nature Reserve Sitno, Slovakia. Forests 11:81
- Kasper J, Weigel R, Walentowski H, Gröning A, Petritan AM, Leuschner C (2021) Climate warming-induced replacement of mesic beech by thermophilic oak forests will reduce the carbon storage potential in aboveground biomass and soil. Ann Sci 78:1–34
- Kohler M, Pyttel P, Kuehne C, Modrow T, Bauhus J (2020) On the knowns and unknowns of natural regeneration of silviculturally managed sessile oak (*Quercus petraea* (Matt.) Liebl.) forests—a literature review. Ann Sci 77:1–19
- Kuehne C, Pyttel P, Modrow T, Kohnle U, Bauhus J (2020) Seedling development and regeneration success after 10 years following group selection harvesting in a sessile oak (*Quercus petraea* [Mattuschka] Liebl.) stand. Ann for Sci 77(3):1–13
- Kursa MB (2010) Rudnicki WR 2010 feature selection with the boruta package. J Statist Softw 36:1–13
- Leuschner C (2020) Drought response of European beech (*Fagus sylvatica* L.)—a review. Perspect Plant Ecol Evol Syst 47:125576. <https://doi.org/10.1016/j.ppees.2020.125576>
- Leuschner C, Ellenberg H (2017). Ecology of Central European forests: vegetation ecology of Central Europe (Vol. 1). Springer
- Ligot G, Balandier P, Fayolle A, Lejeune P, Claessens H (2013) Height competition between *Quercus petraea* and *Fagus sylvatica* natural regeneration in mixed and uneven-aged stands. For Ecol Manage 304:391–398. <https://doi.org/10.1016/j.foreco.2013.05.050>
- Lüpke BV (1998) Silvicultural methods of oak regeneration with special respect to shade tolerant mixed species. For Ecol Manage 106:19–26. [https://doi.org/10.1016/S0378-1127\(97\)00235-1](https://doi.org/10.1016/S0378-1127(97)00235-1)
- Modrow T, Kuehne C, Saha S, Bauhus J, Pyttel PL (2020) Photosynthetic performance, height growth, and dominance of naturally regenerated sessile oak (*Quercus petraea* [Mattuschka] Liebl.) seedlings in small-scale canopy openings of varying sizes. Eur J Forest Res 139:41–52
- Mölder A, Sennhenn-Reulen H, Fischer C, Rumpf H, Schönfelder E, Stockmann J, Nagel RV (2019) Success factors for high-quality oak forest (*Quercus robur*, *Q. petraea*) regeneration. For Ecosyst 6(1):49
- Nakashizuka T (2001) Species coexistence in temperate, mixed deciduous forests. Trends Ecol Evol 16:205–210
- Orman O, Wrzesinski P, Dobrowolska D, Szewczyk J (2021) Regeneration growth and crown architecture of European beech and silver fir depend on gap characteristics and light gradient in the mixed montane old-growth stands. For Ecol Manage 482:118866. <https://doi.org/10.1016/j.foreco.2020.118866>
- Petersson LK, Dey DC, Felton AM, Gardiner ES, Löf M (2020) Influence of canopy openness, ungulate exclosure, and low-intensity fire for improved oak regeneration in temperate Europe. Ecol Evol 10:2626–2637. <https://doi.org/10.1002/ece3.6092>
- Petritan AM, Biris IA, Merce O, Turcu D, Petritan IC (2012) Structure and diversity of a natural temperate sessile oak (*Quercus petraea* L.) - European beech (*Fagus sylvatica* L.) forest. For Ecol Manage 280:140–149. <https://doi.org/10.1016/j.foreco.2012.06.007>
- Petritan AM, Nuske RS, Petritan IC, Tudose NC (2013) Gap disturbance patterns in an old-growth sessile oak (*Quercus petraea* L.)—European beech (*Fagus sylvatica* L.) forest remnant in the Carpathian Mountains, Romania. For Ecol Manage 308:67–75. <https://doi.org/10.1016/j.foreco.2013.07.045>
- Petritan IC, Commarmot B, Hobi ML, Petritan AM, Bigler C, Abrudan IV, Rigling A (2015) Structural patterns of beech and silver fir suggest stability and resilience of the virgin forest Sinca in the Southern Carpathians, Romania. For Ecol Manage 356:184–195. <https://doi.org/10.1016/j.foreco.2015.07.015>
- Petrovska R, Bugmann H, Hobi ML, Brang P (2023) Replace me if you can: abundance of advance regeneration under canopy trees in a primeval beech forest. For Ecol Manage 537:120939. <https://doi.org/10.1016/j.foreco.2023.120939>
- R Core Team (2024). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Reimoser F, Gossow H (1996) Impact of ungulates on forest vegetation and its dependence on the silvicultural system. For Ecol Manage 88:107–119. [https://doi.org/10.1016/S0378-1127\(96\)03816-9](https://doi.org/10.1016/S0378-1127(96)03816-9)
- Röhrig E, Bartsch N, von Lüpke B (2006) Waldbau auf ökologischer Grundlage. Eugen Ulmer, Stuttgart
- Rozenberger D, Diaci J (2014) Architecture of *Fagus sylvatica* regeneration improves over time in mixed old-growth and managed forests. For Ecol Manage 318:334–340. <https://doi.org/10.1016/j.foreco.2014.01.037>
- Runkle JR (1992) Guidelines and sample protocol for sampling forest gaps (General technical report No. PNW-GTR-283), General Technical Report. USDA Forest Service
- Saniga M, Balanda M, Kucbel S, Pittner J (2014) Four decades of forest succession in the oak-dominated forest reserves in Slovakia. iForest 7:324–332. <https://doi.org/10.3832/for0996-007>
- Schütz J.-P., Pukkala T, Donoso PJ, von Gadow K (2012) Historical emergence and current application of CCF. In: Pukkala, T., von Gadow, K. (Eds.), Continuous Cover Forestry, second ed. Springer, Dordrecht, pp. 1–29. <https://doi.org/10.1007/978-94-007-2202-6>
- Tinya F, Márialigeti S, Bidló A, Ódor P (2019) Environmental drivers of the forest regeneration in temperate mixed forests. For Ecol Manage 433:720–728. <https://doi.org/10.1016/j.foreco.2018.11.051>
- Tinya F, Kovács B, Aszalos R, Toth B, Csépanyi P, Németh Cs, Ódor P (2020) Initial regeneration success of tree species after different forestry treatments in a sessile oak-hornbeam forest. For Ecol Manage 459:117810. <https://doi.org/10.1016/j.foreco.2019.117810>
- Tinya F, Csépanyi P, Horváth CV, Kovács B, Németh Cs, Ódor P (2025) Fine-scale interventions can reinforce the forest character

- of the understory vegetation – the effects of different artificial gaps in an oak-dominated forest. *For Ecol Manage* 578:122471
- Valladares F, Niinemets Ü (2008) Shade tolerance, a key plant feature of complex nature and consequences. *Annu Rev Ecol Evol Syst* 39:237–257. <https://doi.org/10.1146/annurev.ecolsys.39.110707.173506>
- Valladares F, Chico J, Aranda I, Balaguer L, Dizengremel P, Manrique E, Dreyer E (2002) The greater seedling high-light tolerance of *Quercus robur* over *Fagus sylvatica* is linked to a greater physiological plasticity. *Trees* 16:395–403. <https://doi.org/10.1007/s00468-002-0184-4>
- Van Couwenberghe R, Gegout JC, Lacombe E, Collet C (2013) Light and competition gradients fail to explain the coexistence of shade-tolerant *Fagus sylvatica* and shade intermediate *Quercus petraea* seedlings. *Ann Bot* 112:1421–1430. <https://doi.org/10.1093/aob/mct200>
- Wallraf A, Wagner S (2019) Effects of initial plant density, interspecific competition, tending and age on the survival and quality of oak (*Quercus robur* L.) in young mixed stands in European Russia. *For Ecol Manage* 446:272–284
- Ziegenhagen B, Kausch W (1995) Productivity of young shaded oaks (*Quercus robur* L.) as corresponding to shoot morphology and leaf anatomy. *For Ecol Manage* 72:97–108. [https://doi.org/10.1016/0378-1127\(94\)03482-C](https://doi.org/10.1016/0378-1127(94)03482-C)
- Publisher's note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.