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Effects of stand structural attributes on oak recruitment in mixed temperate forests

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ABSTRACT

Oak-dominated forests worldwide support high levels of biodiversity and provide many important ecosystem services. However, oak forest sustainability is challenged by unsuccessful recruitment of oaks into the overstory. It is debated whether relatively shade-intolerant oaks can maintain dominance under continuous cover forestry and examples of successful recruitment of oak into the overstory in mixed, uneven-aged forests are rare. This study, set in southern Sweden, investigated the effects of selective cutting on stand structure and oak recruits and how stand density, canopy openness, and a tree species-specific shade casting index relates to the density of oak recruits. We focused on oak recruitment from the lower and middle canopy (dbh 5–10, 10–20 cm), i.e. trees that were beyond browsing height. Our findings indicate that a lower stand density was positively related to recruitment density of the smaller diameter size class, and as an indirect effect that a higher canopy openness with a lower shade-casting index was positively (but not significantly) associated with oak recruitment. Selective cutting decreased stand basal area and stand density while it increased canopy openness, but it did not have a direct short term effect on oak recruitment. These results indicate that stand structures obtained through continuous cover forestry may benefit recruiting oaks and that stand density, canopy openness and a canopy composition with high light transmission may need to be considered when ensuring the continuity of mixed, uneven-aged oak forests.

1. Introduction

Oak-dominated forests in Eurasia and North America support high levels of biodiversity and provide many important ecosystem services including timber and fuelwood, recreation and aesthetic values, and they offer an opportunity for adaptation of forest management to climate change because of their high resilience to disturbance and environmental stress (Norman et al., 2010, Gil-Pelegrín et al., 2017, Johnson et al., 2019, Harvey et al., 2020, Stavi et al., 2022, Chakraborty et al., 2024). For example, pedunculate oak (*Quercus robur* L.) and sessile oak (*Q. petraea* (Matt.) Liebl.) are foundation species ranking among the most important trees associated with endangered invertebrates, lichens, fungi, and birds in Europe (Lindbladh and Foster, 2010). During the last 300 years, large areas of the once widespread mixed and multi-aged oak-dominated forest type has been degraded by deforestation for agriculture and for conversion to conifer plantations (Lindbladh et al., 2014, Bobiec et al., 2018). The remaining fragmented oak forests support much higher levels of biodiversity than conifer plantations (Berg et al., 1994, Sundberg et al., 2019). Ensuring the continuity of these remaining oak forests is critical to safeguarding biodiversity and ecosystem services, and many oak-dominated forests have been designated for nature conservation and restoration in Scandinavia (Götmark, 2013, Mölder et al., 2019).

However, many oak forests are still managed fully or partly for timber production, and it is a great challenge to conserve and restore biodiversity rich oak-dominated habitats while also maintaining the economic viability of forestry (Stimm et al., 2022). Such multi-purpose forest management may best be obtained within the framework of an

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integrative oak forest management approach such as continuous cover forestry (Mölder et al., 2019, Mason et al., 2022). Continuous cover forestry includes creating and managing structurally diverse mixed forests that promote native tree species while sustaining wood production (Pommerening and Murphy, 2004). The silvicultural focus lies therein on selective cutting and natural regeneration (Pommerening and Murphy, 2004, Mason et al., 2022). There is, however, limited practical experience with continuous cover forestry methods in many countries, including Sweden (Mason et al., 2022). This is especially true in structurally diverse temperate forests, where there is a lack of knowledge on which stand structural attributes favor oak recruits, and how selective cutting impacts stand structure and oak recruitment. Hence, it is not currently clear how to sustain oak dominated stands under continuous forest cover (Pommerening and Murphy, 2004, Ligot et al., 2013, Petersson et al., 2019) and whether less shade-tolerant oaks can attain dominance in these stands. Some previous studies supported management solutions that combine oak regeneration with selective cutting or gap cutting (e.g. Stahl-Streit, 2004, Király and Ódor, 2010, Leonardsson et al., 2015, Petersson et al., 2020), but light requirements of oak saplings together with competition from relatively more shade-tolerant co-occurring woody species complicates such approaches. Oaks typically require a minimum of 15–20 % of full light for sustained growth (von Lüpke, 1998, Löf et al., 2007), however studies have shown that shrubs can still outcompete oak saplings at these light levels (Kohler et al., 2020, Leonardsson et al., 2015). Thus, even where oak seedlings establish, recruitment into the overstory is typically limited (Petersson et al., 2019). According to the literature review of Kohler et al. (2020), the main factors influencing successful oak regeneration are light availability, competing vegetation, browsing, initial oak seedling density and intensity of tending efforts. However, oak trees in diameter classes ranging from 5 to 20 cm have been largely understudied. Success in manipulating stand structure to benefit the recruitment of these oak trees into the overstory has been inconsistent. This is likely due to a lack knowledge of how different stand structural attributes and the timing of canopy cover changes influence the necessary light availability for oak development (Mölder et al., 2019, Stimm et al., 2022). This knowledge gap hinders advancement of sound and reliable management strategies in mixed temperate forests.

The goal of this study was to inform practical silviculture and restoration of structurally diverse forest habitats with a high proportion of oak. Specifically, we examined (1) which specific stand structural attributes favor oak recruits (here defined as oak trees with a diameter of 5.0–19.9 cm); (2) how selective cutting influences stand structural attributes; and (3) the effects of selective cutting on oak recruitment. We hypothesized that stand structural attributes that influence the oak regeneration layer will also play an important role for oak recruitment. For this, we included the first two factors (light availability, competing vegetation) of (Kohler et al., 2020) and tested the effects of stand density, canopy openness and shade-casting index on oak recruitment. As the selective cutting will lead to an increase in canopy openness and a decrease in density of competing trees, we anticipated that plots with selective cutting will have a higher oak recruitment than plots without

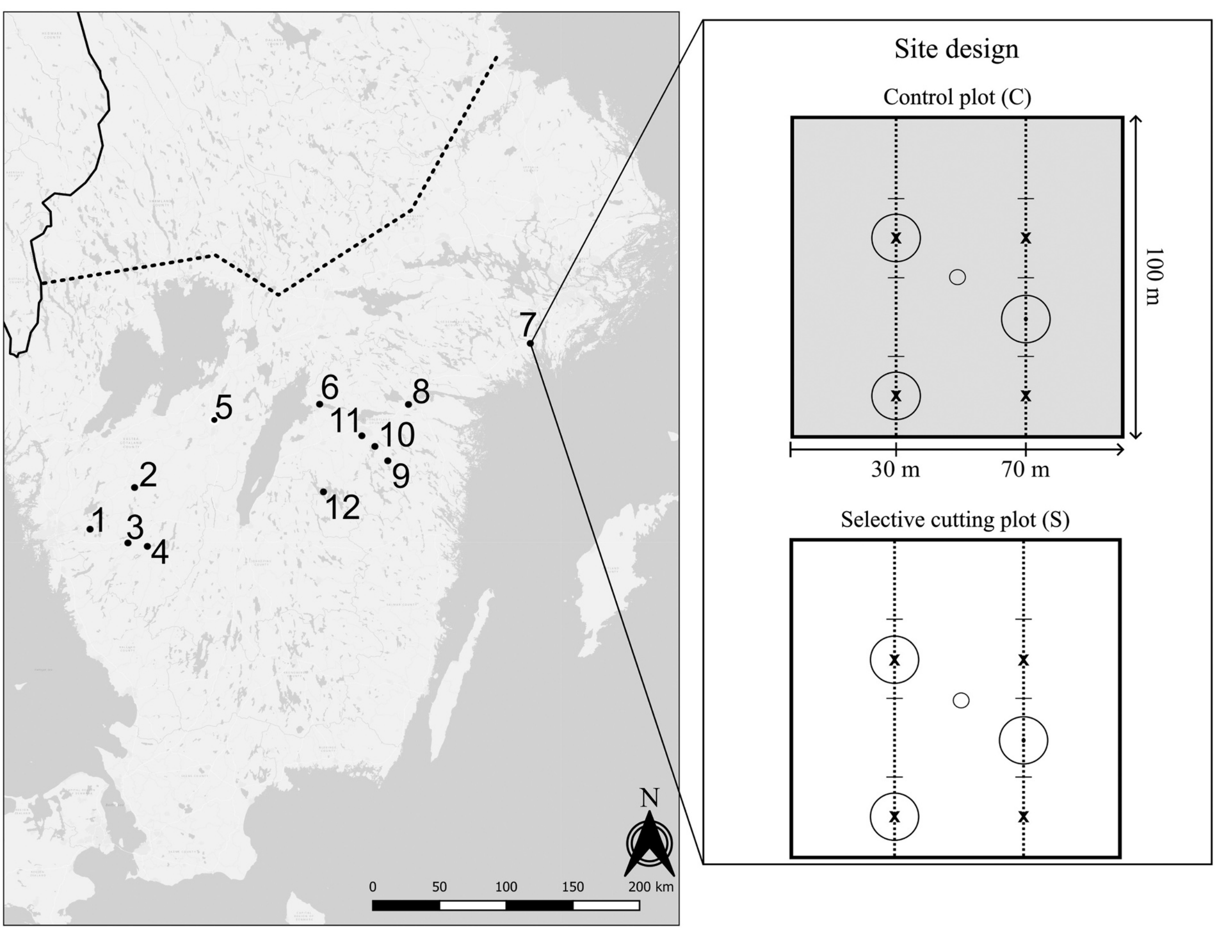

Fig. 1. Study region in Sweden and the location of the 12 experimental sites established in 2016 (left) south of "Limes Norrlandicus" (denoted by dashed line, Sjörs, 1999), with an example of the experimental design (right). Numbers 1–12 in the map correspond to the site numbers in Table 1. The experimental design at each site and treatment plot shows the four sections (separated with horizontal lines) along each of the two transects (at 30 m (T30) and 70 m (T70)). There were three circular subplots (radius 10 m, open circles) for tree measurements in each treatment plot, and four sample points for estimates of canopy cover with hemispherical photographs (marked with an 'x').

selective cutting. For this study, we used 12 experimental sites in mixed, uneven-aged temperate forests located across southern Sweden.

2. Methods

2.1. Description of the region and climate

In Sweden, pedunculate oak and sessile oak reach their northern distribution limit at the *Limes Norrlandicus* (Fig. 1, Sjörs, 1999). The forest in this area consists mostly of conifer-dominated production forests, while oaks account for 4 % of the total standing volume (SLU, 2020). In this region, oaks commonly occur in tree species mixtures with Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.), along with broadleaves such as birch (*Betula pendula* Roth. and *B. pubescens* Ehrh.), European aspen (*Populus tremula* L.), small-leaved lime (*Tilia cordata* Mill.), rowan (*Sorbus aucuparia L.*) and European hazel (*Corylus avellana* L.) in the understory (Drössler et al., 2012).

Climatic conditions differ among the 12 experimental sites with decreasing precipitation from the west to the east (Table 1). Along the west coast, the mean annual (2000–2022) temperature and precipitation were 7.2°C and 980 mm, respectively. In comparison, the mean annual temperature and precipitation on the east coast were 7.4°C and 708 mm (Hersbach et al., 2023). Most years within the experimental period (2016–2022) experienced relatively normal precipitation and temperatures except for 2018, which was a dry year with precipitation up to 50 % lower than average and temperatures 2–4 ℃ higher than average (Wilcke et al., 2020, SMHI, 2024).

2.2. Experimental design

In 2016, 12 experimental sites were established in ca 40–80 year old, mixed broadleaved forest stands across the study region (Table 1, Fig. 1). These stands showed few signs of management for timber production or grazing but only five were in parts formally protected. All stands had regenerated naturally from abandoned pastures and hay meadows (Nordén et al., 2019) and most sites were dominated by oak (*Q. robur and/or Q. petraea)*. Some old trees, mostly oaks, were still present but most trees were in a younger age range as mentioned above. At each site we established two, 1-ha treatment plots (100 ×100 m) spaced 25–125 m apart. Plots were randomly assigned as control treatment (C) which did not receive cutting, or a selective cutting treatment (S) which received cutting across the whole 1-ha plot in the winter 2016/2017. The main aim was to alter stand structure to increase the density of young oak trees for recruitment into the overstory and ensuring continuity of biodiversity rich oak-dominated habitats. Therefore, selective tree harvesting targeted Norway spruce, birch and dense patches of hazel as potentially strong competitors of oak recruitment. Some oaks were removed in some stands but most trees of temperate broadleaved tree species and especially trees considered valuable for biodiversity (with cavities, injuries and dead wood) were always retained. The selective tree harvesting was done using combinations of harvester, forwarder, chain saw, tractor and ATV (Nordén et al., 2019). On average, cutting removed about 25–30 % of the basal area from plots receiving the S treatment.

In each treatment plot, two parallel transects were positioned 30 m and 70 m from the south-west corner of the plot (Fig. 1). From hereon we refer to these transects as T30 and T70. Each transect was divided into four sections of 25 m (Sections 1–4) with a total length of 100 m. A 10-m radius circular sub-plot was delineated in the centre of Sections 1 and 3 of T30 and 2 of T70 (3 sub-plots per treatment plot) to conduct tree measurements (see below). We call these subplots semi-permanent because their centre was not monumented, centres were relocated by measuring the distance along the transects.

Table 1
Characteristics of 12 sites and control (C) and selective cutting (S) treatments (one C and one S per site). Site numbers correspond with numbering in Fig. 1. Site coordinates of latitude (lat) and longitude (long) correspond with the C plot of each site. Initial stand basal area (m^2 ha^{-1}) in 2016. The percentage of oak is based on the share of oak of stand basal area in 2022. The mean diameter of the overstory (cm) is based on overstory trees in 2022 (3 subplots per treatment plot). Composition indicated the three most common species based on their basal area in the control plot in 2022. The mean annual temperature and the mean annual precipitation derived from ERA5 data (Hersbach et al. 2023) from 2000 to 2022.

Site number	Site name	Site coordinates		Initial stand basal area [m^2 ha^{-1}]		Percentage Oak [%]		Mean diameter of overstory [cm]		Composition	Temperature [℃]	Precipitation [mm]
		Lat	Long	C	S	C	S	C	S			
1	Tvärsjönäs	57.76	12.40	27.4	27.0	71.5	74.8	19.6	24.1	Oak-Spruce-Aspen	7.5	986
2	Remmene	58.03	12.92	16.5	19.6	22.0	75.0	15.8	33.6	Spruce-Oak-Aspen	7.2	898
3	Bosnäs	57.67	12.84	20.0	17.6	60.9	56.6	28.4	23.7	Oak-Birch-Spruce	7.2	1008
4	Aplared	57.65	13.07	17.7	22.4	38.8	63.8	17.7	23.4	Oak-Aspen-Beech	6.9	1029
5	Stöpen	58.47	13.86	40.2	29.9	19.3	70.4	19.9	29.6	Spruce-Oak-Hazel	7.4	787
6	Motala	58.57	15.09	26.6	25.2	7.9	35.3	18.3	17.2	Spruce-Alder-Oak	7.3	733
7	Tullgarn	58.96	17.56	17.8	13.4	58.3	74.1	23.9	28.3	Oak-Aspen-Birch	7.3	688
8	Klockaretorpet	58.57	16.13	24.7	23.9	38.0	58.2	22.0	27.4	Oak-Aspen-Pine	7.5	693
9	Kvarntorp	58.20	15.90	19.0	17.6	32.5	36.9	20.9	26.9	Oak-Aspen-Hazel	7.4	722
10	Hovetorp	58.30	15.74	15.3	17.7	53.2	63.1	13.7	19.7	Oak-Maple-Pine	7.3	727
11	Slaka	58.37	15.58	13.1	17.2	3.5	17.2	15.0	14.7	Pine-Birch-Aspen	7.1	729
12	Aspenäs	58.00	15.30	22.2	24.8	42.1	72.8	23.3	23.4	Oak-Aspen-Spruce	7.0	740

2.3. Data collection and statistical analysis

Data were collected in the summer of 2016 (pre-treatment) and six growing seasons later in the summer of 2022 (post-treatment). In each sub-plot, diameter (cm) at breast height (dbh) was measured on all living trees dbh $\geq$ 5 cm, and this was recorded by species. We did not distinguish between the two oak species since both species are ecologically overlapping and the objective was to promote oak recruitment regardless of species. Measurements were done in all three sub-plots per treatment plot.

Canopy openness, as a proxy for measuring light availability, was estimated with hemispherical photography. Images were collected at four sample points per treatment plot in the summers of 2016 and 2022 with a Nikon D5300 fitted with a Canon 15 mm fish-eye lens. The photographs were taken in the centre of the first and third section in both transects with a distance of 50 m along the same transect and 40 m between transects (Fig. 1). This sampling was conducted with the camera and lens held 1.3 m above the forest floor by a tripod (Hale and Edwards, 2002). Sampling occurred early in the morning to avoid direct sunlight on canopy foliage and the lens. The hemispherical photographs were analysed using the "Hemiphot.R" package (ter Steege, 2018) to calculate the percentage of canopy openness.

Oak recruitment was assessed by analysing oak density by diameter class (stems ha^{-1}). Our analysis focused on trees in the diameter range of 5.0–19.9 cm because we were interested in oak recruitment. This range was chosen to analyse the effect of selective cutting on oaks in the lower and middle canopy that have grown out of browsing height. For the analysis, we sorted oaks to two classes: 5.0–9.9 cm as diameter class 'A' in the lower canopy and 10.0–19.9 cm as diameter class 'B' in the middle canopy.

Oak trees with a dbh greater than the recruitment size and other tree species (independent of size) were classified as overstory trees while European hazel constituted the shrub layer (no other shrub species present). This classification was defined to separately evaluate the influence of overstory trees and the shrub layer on oak recruitment.

Using the collected data from 2022, we calculated density and stand basal area (m^2 ha^{-1}) for the overstory and shrub layers separately. As an estimate of species-specific influence on light availability, we used the shade-casting ability (SCA) of each overstory tree species as a qualitative index. We included this index for better representation of the subplot canopy since the canopy openness derived from the hemispherical photographs provided us with a mean canopy openness value per plot. The index is based on expert knowledge from Ellenberg et al. (1992) and assigns each species a score from 1 (very low shade-casting ability) to 5 (very high shade-casting ability) (Table S1; see also Verheyen et al., 2012; De Lombaerde et al., 2019; Depauw et al., 2020). Using this scoring, we calculated a weighted average for each subplot by multiplying the basal area for each tree species with its shade-casting ability and then dividing the sum of these products with the total basal area. A relatively high SCA index value corresponds with tree species having a high shade casting ability comprising a relatively high proportion of the basal area. In our study, we found three SCA index ranges that were each dominated by two genera. Pine and birch dominated the SCA index range 1.0–1.9, oak and aspen in the range 2.0–2.9 and oak and spruce dominated the range 3.0–3.9. Trees that were considered oak recruits were not included in the SCA index calculation.

We used Generalized Linear Mixed-effects Model (GLMM) for all our statistical analyses. The GLMMs were created using the "glmmTMB" package (Brooks et al., 2017) and post-hoc test were calculated by the "emmeans" and "multcomp" package (Lenth, 2023, Hothorn et al., 2008). For model selection in the first part of the analysis, we used the 'AIC' function in the "stats" package (R Core Team, 2023). For model evaluation, we used the 'simulateResiduals' function and 'testDispersion' function from the "DHARMa" package to look at the QQ-plot based on simulated residuals, for patterns in the residuals and heteroscedasticity in residual plots and to test for over- and underdispersion (Hartig, 2022). Additionally, we performed tests for zero-inflation with the 'testZeroInflation' function of this package. For visualization of model predictions, the 'plot_model' function from the "sjPlot" package was used ((Lüdecke, 2023)). When a model included an interaction term, we used the mean of the moderator term with one standard deviation above and below. All analyses were carried out with R version R 4.3.2 (R Core Team, 2023).

First, we evaluated the effect of stand structural attributes on the response variable oak recruit density in two separate models. We analysed the data on subplot level since stand structure has a greater variation among the subplots in contrast to the treatment. The first model, included diameter class, stand density from 2022 and their interaction as fixed effects (model 1). For the second model, we compared three different candidate models: 1) including diameter class, canopy openness and SCA, their three-way interaction and all two-way interactions (model 2), 2) diameter class, canopy openness and SCA, as well as the two-way interaction between the latter two variables (model 3), 3) the main effects of diameter class, canopy openness and SCA as fixed effects (model 4). All models included subplot within site as random effect, a negative binomial distribution with a log link, taking zero-inflation into account by modelling the probability of zeros by a ziformula including the intercept and the variable diameter class. To better differentiate among stand structural variables, we did not include the fixed effect 'treatment'. An overview of the models can be found in Table S2.

Second, we tested the effect of the selective cutting treatment on the following four stand structural attributes as response variables: stand basal area (m^2 ha^{-1}) (model 5), stand density (stems ha^{-1}) (model 6), number of tree or shrub species (model 7), all separately for the overstory and shrub layers, and canopy openness (model 8). Because the treatment was applied across the whole hectare, we analysed the data on plot level and not on subplot level. For these models, we included the interaction of sampling year (a factorial variable with two levels) and treatment (a factorial variable with two levels) as fixed effects and site as random effect. We used a Gaussian distribution with identity link for the models for stand basal area and a negative binomial distribution with a log link in the models for stand density and number of tree or shrub species. For modelling canopy openness, we used a beta distribution with a logit link. An overview of the models can be found in Table S3.

Third, we evaluated the effect of selective cutting on oak recruitment in the two diameter classes on plot level. As response variables, we used the proportion of oak recruits (model 9) and the density of oak recruits (stems ha^{-1}) (model 10) in 2022. For the proportion of oak recruits, we included diameter class, treatment (C versus S) and their interaction as fixed effects, and the pre-treatment proportion of oak recruits as an offset (Buckley, 2015). We used a beta distribution with a logit link, site as a random factor and a ziformula (as above) to account for zero-inflation. For oak recruit density, we included diameter class, treatment and their interaction, and the pre-treatment oak recruit density as fixed effects and site as a random factor. We used a negative binomial distribution with a log link and the same ziformula for zero-inflation as above. An overview of the models can be found in Table S4.

3. Results

In 2016, 1589 stems of all woody species were measured of which 1024 were classified as overstory trees and 565 were in the shrub layer (European hazel). Of the overstory trees, 172 were oak. The average stem number per site, excluding oak recruits, was 662 $\pm$ 277 stems per ha^{-1} with 427 $\pm$ 122 overstory stems and 235 $\pm$ 283 shrub layer stems. An overview of the initial diameter distribution can be found in Figure S1. In 2022, we measured 2116 stems of which 1218 were classified as overstory trees of which 240 were oak. In this sampling year, the shrub layer consisted of 898 European hazel stems and the average stem number per sites was 882 $\pm$ 439 stems per ha^{-1} with 508 $\pm$ 194 overstory stems and 374 $\pm$ 444 shrub layer stems.

3.1. Stand structural attributes and oak recruitment

Regardless of treatment (S or C), using data from subplots, we found that density of oak recruits decreased with increasing stand density (P = 0.004) (Fig. 2a). This effect was significant for diameter class 'A' (P = 0.006) but not for diameter class 'B' (P = 0.392). For diameter class 'A', model 1 predicted a 42 % decrease from 50 stems ha^{-1} at a stem density of 1000 stems ha^{-1} to 29 stems ha^{-1} at a stem density of 2000 stems ha^{-1}. This response by diameter class 'A' was consistent when effects of overstory density (P = 0.009) and shrub layer density (P = 0.016) were analysed separately. The best of our candidate models for the density of oak recruits depending on canopy openness and shade casting index was model 3 which (ΔAIC = −5.2 and −1.1 for model 2 and 4, respectively) included diameter class (P = 0.088), canopy openness (P = 0.053), the SCA index term (P = 0.270) and the interaction (P = 0.071) between the two latter (Table S2, S5). There was a tendency towards a larger number of oak recruits with higher canopy openness and lower shade-casting index (Fig. 2b). At a canopy openness of 65 %, model 3 predicted an oak recruit density of 104 stems ha^{-1} at a SCA index of 2.08 compared to 26 stems ha^{-1} at a SCA index of 3.29. However, as the P-values of canopy openness and the interaction was > 0.05, and the difference in AIC towards the simpler model (model 4), without any interaction, was small (ΔAIC = −1.1), these effects need to be interpreted with care.

3.2. Effects of selective cutting on stand structural attributes

The average stand basal area of overstory trees did not differ between the two treatments before selective cutting in 2016 (Fig. 3a). However, in the C treatment stand basal area increased by 15 % from 26 m^2 ha^{-1} in 2016–30 m^2 ha^{-1} in 2022 (P = 0.013). In the S treatment, the stand basal area decreased by 21 % from 24 m^2 ha^{-1} in 2016–19 m^2 ha^{-1} in 2022 (P = 0.003). Thus, in 2022 the C treatment had a higher basal area than the S treatment (P < 0.001). The stand basal area of the shrub layer did not differ significantly before and after selective cutting in any of the treatments (P = 0.353 and P = 0.328, respectively). In the C treatment, the stand basal area of shrubs was 0.9 m^2 ha^{-1} in 2016 and 1.6 m^2 ha^{-1} in 2022 (P = 0.106) and in the S treatment 1.3 m^2 ha^{-1} and 1.2 m^2 ha^{-1}, respectively (P = 0.783).

Stem density of overstory trees trended similarly to stand basal area (Fig. 3b). There was no difference in stem density between C (595 stems ha^{-1}) and S (550 stems ha^{-1}) treatments before selective cutting (P = 0.541). Six years after the establishment of the experiment, the stem density in the C treatment was 730 stems ha^{-1}, although the difference to the pre-treatment stem density was not significant (P = 0.110). In 2022, the S treatment had a 37 % lower (P < 0.001) stem density (345 stems ha^{-1}), compared to 2016. Shrub layer stem density showed no difference between the years (C treatment P = 0.313, S treatment P = 0.596) and between treatments (2016 P = 0.461, 2022 P = 0.526).

Selective cutting had a positive effect on canopy openness (Fig. 3c). After six years, selective cutting increased (P = 0.006) the canopy openness from 25 % to 32 %. In the C treatment, canopy openness did not change (P = 0.587). Accordingly, canopy openness differed between C and S plots in 2022 (P < 0.001). The mean number of tree species was not affected by treatment (C treatment P = 0.334, S treatment = 0.682) and there was no change over time (2016 P = 0.622, 2022 P = 0.377) (Fig. 3d). In total, we identified 23 different tree species (listed in Table S1) with an average of 6 species in S treatment and 7 in C treatment in 2022.

3.3. Effects of selective cutting on oak recruitment

In total, we measured 145 oak recruits in 2022 of which 58 were categorized as diameter class 'A' and 87 as diameter class 'B'. The share of oak recruits of the total stem density in diameter class 'A' was not significantly different with 1.7 % in the C treatment compared to 2.5 % in the S treatment (P = 0.175) (Fig. 4a). For diameter class 'B', the share was higher in the S treatment with 4.1 % as compared to 2.3 % in the C treatment (P = 0.013). However, selective cutting had no effect on mean recruitment stem density of diameter class 'A' (P = 0.673) or B (P = 0.669) in 2022 (Fig. 4b). For diameter class 'A', the mean stem density in C and S treatments were 19 and 20 stems ha^{-1}, and for diameter class 'B', 41 and 38 stems ha^{-1}, respectively.

4. Discussion

Our first hypothesis was that stand structural attributes that influence the oak regeneration layer would also play an important role for oak recruitment. In our study, we focused on the two structural attributes light availability and competing vegetation and made predictions using variables such as stand density, canopy openness and shade-casting index. The key finding of our study was that stand density, comprised of overstory tree density and shrub density, had a negative effect on oak recruit density of diameter class 'A' (5–9.9 cm diameter) but not of diameter class 'B' (10–19.9 cm diameter). For diameter class

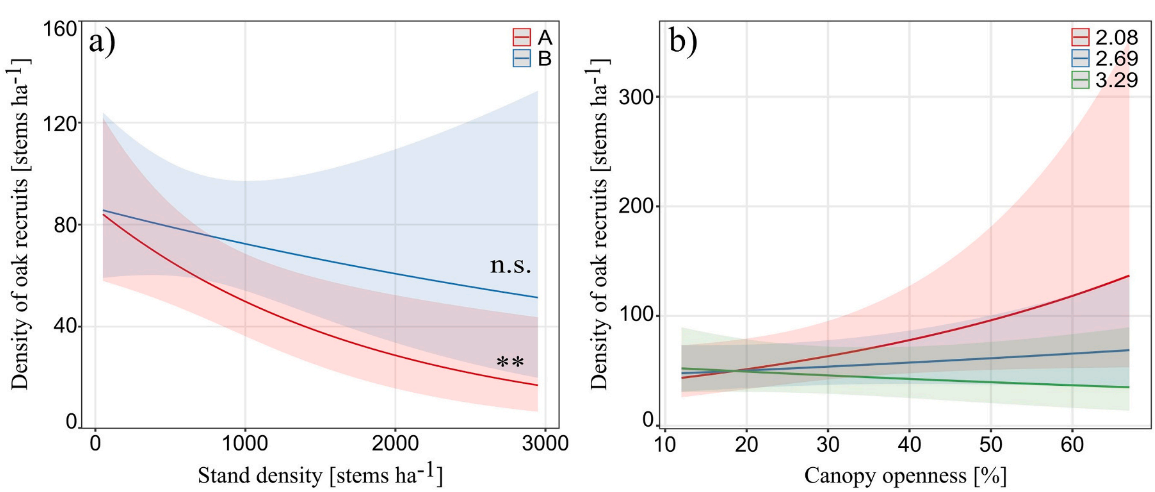

Fig. 2. Density of oak recruits in diameter class A and B as a function of stand density (a). Combined effect of the shade-casting index and canopy openness on density of oak recruits (b). Lines represent model predictions within the continuous variable range (a) and the other continuous variable set to its mean (2.69) ± standard deviation (2.08, 3.29) (b). Shaded areas around the lines represent the confidence intervals of the predictions. Oak recruit diameter class "A" 5.0–9.9 cm and "B" 10.0–19.9 cm. "* *" P ≤ 0.01 and "n.s." P > 0.05. Note that the interaction terms illustrated in (b) were non-significant (P = 0.071), see Table S3.

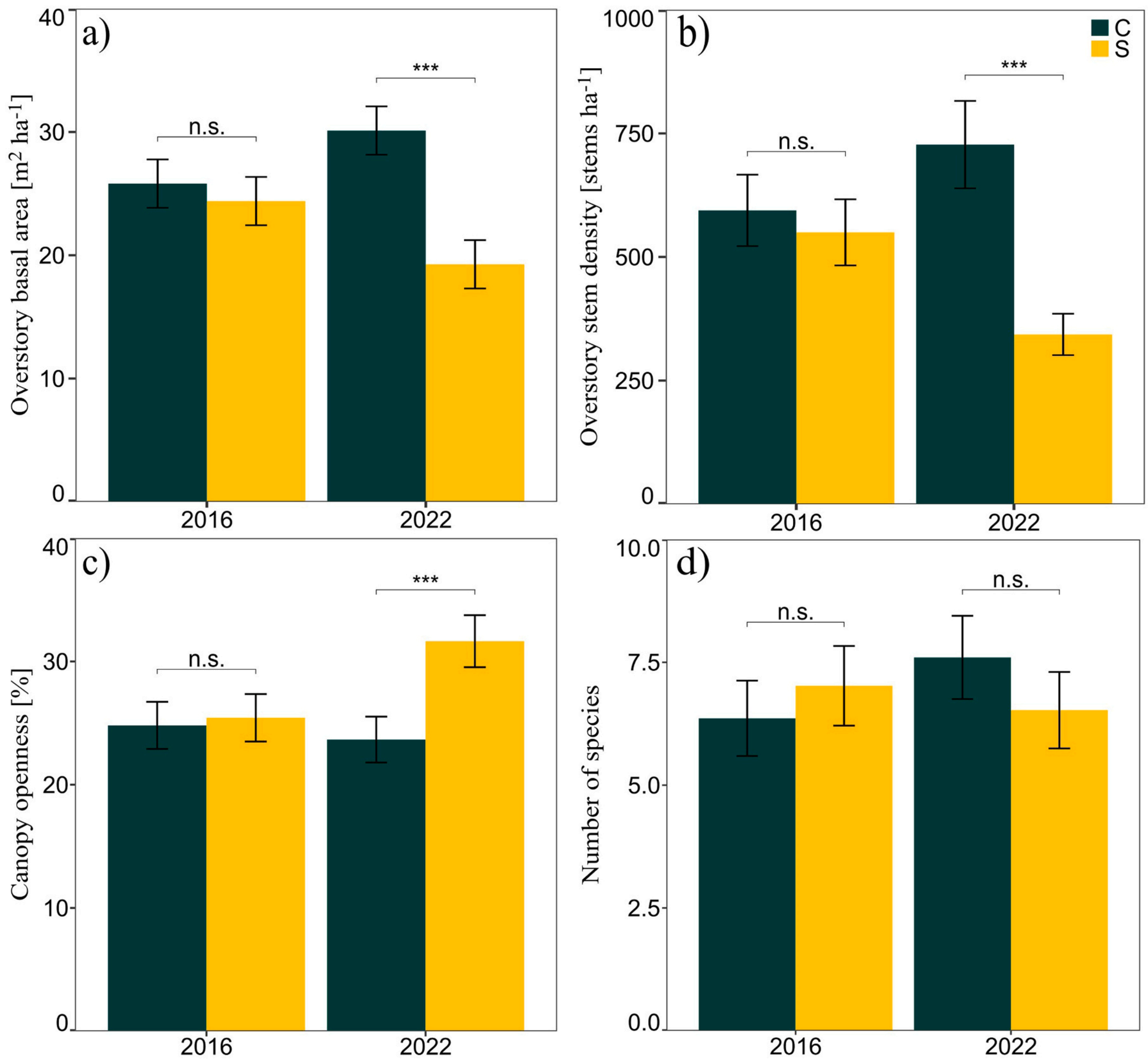

Fig. 3. Comparison of four stand structural attributes in control (C, green) and selective cutting (S, yellow) treatments. (a) mean basal area of overstory trees; (b) mean stem density of overstory trees; (c) mean canopy openness; and (d) mean number of tree species before (2016) and six years after selective cutting (2022). Error bars represent ± SE for the treatments. “* ** ” is $P \leq 0.001$ and “n.s.” is $P > 0.05$. An overview of the P-values can be found in Table S6.

’A’, our model predicted a 42 % decrease in oak recruit density from 50 stems ha^{-1} at a stand density of 1000 stems ha^{-1} to 29 stems ha^{-1} at a stand density of 2000 stems ha^{-1}. Additionally, increasing canopy openness combined with a lower shade-casting index of the overstory tended to favor oak recruit density compared to a similar canopy openness with a higher shade-casting index of the overstory. At a canopy openness of 65 %, our model predicted an oak recruit density of 104 stems ha^{-1} at a SCA index of 2.08 compared to 26 stems ha^{-1} at a SCA index of 3.29. Selective cutting did not directly promote increased density of oak recruits in the short time span of our study (six years) (hypothesis 3). However, selective cutting may still affect stand structural attributes which in-turn may create more favorable conditions for the long-term recruitment of oak regeneration into the overstory in mixed, uneven-aged temperate forests (hypothesis 2). In the following, we will discuss our findings in relation to our hypotheses and other studies.

Following our results, management of stand density plays an important role for achieving successful oak recruitment. This is supported by Aussenac (2000) who found that reduced stand density led to lower competitive effects above- and belowground through increases in canopy openness and improving soil water availability. An additional effect of decreasing stand density was found by Schmitt et al. (2020) who showed that, regardless of the trees̓ social status, decreasing stand density mitigated the effects of drought and increased resistance, resilience and recovery of the individual tree. Considering the climate projections for Europe with an increase in the probability of summer droughts (Bolte et al., 2009), a decrease in stand density might increase the chance of oak recruits to tolerate these stressors. This might be especially important for sites along the west coast where oaks are not acclimated to dry conditions because of higher precipitation (Trouvé et al. 2017). Several studies further recommend that, for successful regeneration of oak, it is necessary to control competing vegetation in the shrub layer if overstory canopy openness is increased (Ligot et al., 2013, Modrow et al., 2019, Mölder et al., 2019, Petersson et al., 2020). In our study, we did not see a difference in shrub layer density between the control and selective cutting plots. However, our results show that shrub layer density, regardless of selective cutting treatment, had a negative effect on oak recruit density. Further, competing vegetation in the shrub layer and initial seedling density have been shown to be important factors influencing the success of oak regeneration (Kohler et al., 2020). Since a successful oak regeneration influences oak recruitment, it is important to take the influence of shrub layer vegetation into account.

Additionally, we found canopy openness and SCA index to be influencing factors on oak recruit density. Annighöfer et al. (2015) found that increasing light availability had a stronger effect on

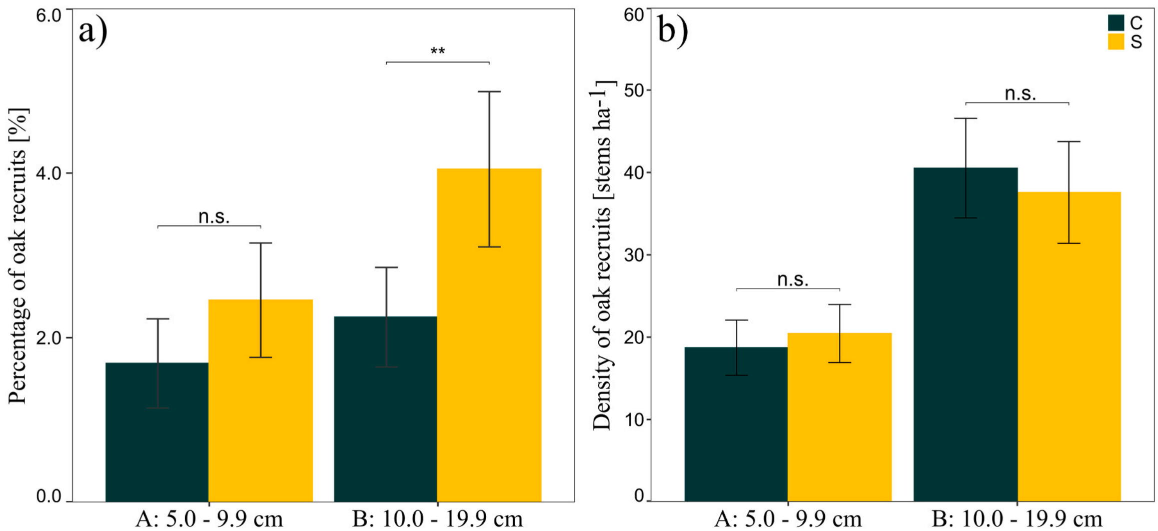

Fig. 4. Mean proportion of oak recruits relative to the total number of stems ha^{-1} (a), and mean stem density of oak recruits (b). The x-axis shows the two diameter classes 'A' (5.0–9.9 cm dbh) and 'B' (10.0–19.9 cm dbh) and the two treatments control (C) in green and selective cutting (S) in yellow in 2022. Error bars represent ± SE. "* *" $P \leq 0.01$ and "n.s." $P > 0.05$. An overview of the P-values can be found in Table S7.

abundance of smaller oak recruits than a decrease in basal area of other tree species. In their study, the maximum light availability was 36 % and canopy openness ranged between 2 % and 51 % which is similar to the range in our study (13–67 % canopy openness). However, it is possible that the larger oak recruits in our study might benefit more from an even higher light availability because the light requirement of oak increases with age and size (von Lüpke and Hauskeller-Bullerjahn, 1999). This partially aligns with the positive tendency we found, of an increase in oak recruits in stands with lower shade-casting index and higher canopy openness. A lower shade-casting index is found in stands with a higher proportion of tree species with a crown of higher light transmission, e.g. pioneer species such as pine and birch. Natural regeneration of oak under a pine canopy has been shown to be successful (Mosandl and Kleinert, 1998) which can be due to the relatively higher shade-tolerance of oak compared to pine, and the high light transmission of a pine canopy (von Lüpke, 1998, Forrester et al., 2017). However, a pine density over 1500 pines ha^{-1} has been shown to negatively impact the successful transition from oak regeneration stage to oak recruitment stage (Navarro-González et al., 2013). Birch has a higher competitive strength due to its relatively faster growth potential, however Götmark and Kiffer (2014) as well as Brunet et al. (2014) found that oak was able to develop alongside pioneer species birch and ash after catastrophic disturbances such as windthrow and Dutch elm disease.

Together with findings of Stimm et al. (2022) and Bobiec et al. (2018), this suggests that mixed forests with a canopy that is more open and composed of species that have a crown that allows for higher light transmission might be more suitable for recruitment of oak trees. Our results align with their findings and thus indicate a higher density of oak recruits at lower shade-casting index values. The importance of the shade-casting attributes of a canopy to tree recruits is supported by Canham et al. (1994) who found that crown geometry of the various tree species played an important role in determining understory light availability. Shade-tolerant tree species were found to cast heavy shade because of their deep crowns which could have an influence in a mixed forest of shade-tolerant and shade-intolerant species. Thus, a shift of canopy dominance to shade-tolerant species likely negatively affects the regeneration and recruitment processes of shade-intolerant species. Hence, it is necessary to include species composition in stand management decision-making if oak continuity is the objective.

Our results in combination with previously mentioned studies suggest that silviculture aimed at reducing competition and increasing canopy openness is necessary to promote recruitment of oaks into the overstory. Additional factors to consider are the intensity and timing of silvicultural activities within the stand so that competing tree species are not further promoted. According to Zenner et al. (2012) oaks with a slower height growth at age 15 than their neighboring competitors would likely be subordinate trees by age 30, and in jeopardy of being permanently overtopped. This suggests that silvicultural measures should be taken earlier than in our study or be more intensive to promote oak recruitment towards a favorable position in the canopy. Considering the findings of Zenner et al. (2012), our findings strengthen the argument to decrease competition, increase canopy openness, and favor competing tree species with a lower shade-casting index to advance oak recruits of the diameter classes studied in this research. Thus, repeated or more intensive selective cutting would likely be necessary to favor oak recruitment – repeated or more intensive selective cutting could accomplish this by increasing canopy openness, shifting canopy composition towards higher light transmission, and by decreasing mid-story competition that might be at risk of overtopping and outcompeting the oak recruits.

Plots that were selectively harvested did not show higher oak recruitment than untreated plots. There are several possible reasons why selective cutting did not increase recruit density for either diameter class. First, few or no oak seedlings and saplings were observed (although not recorded) in the regeneration pool at some sites prior to the selective cutting, which decreases the probability of ingrowth into recruit diameter class 'A' at those sites. This can be partially explained by the weak competitive ability of oak seedlings under dense canopies such as before treatment in 2016 (Kanjevac et al., 2021) and the observed (although not recorded) browsing of oak seedlings. Six years after the selective cut, a high number of oak seedlings was observed across all plots, especially on the western sites. A second possible factor could be the relatively short experimental period. Six years might not have been enough time to see significant ingrowth (Shifley, 2004). While the potential ingrowth from oak saplings to diameter class 'A' and from diameter class 'A' to diameter class 'B' is theoretically possible (Fahlvik and Johansson, 2021), it depends heavily on density of oak saplings and oak trees in diameter class 'A'. Third, it should be considered that many overstory tree species, especially birch and aspen, are pioneer species and might respond quicker to the increase in canopy openness, thus resulting in increased competition. Additionally a methodological consideration should be taken since we did not measure the study sites post-treatment in 2017. This would have made it possible to assess the direct effect of the selective cutting on oak recruit density.

However, we chose the difference of oak recruit density between the treated plot and the untreated control plot. We included the oak recruit density from 2016 in our model to account for pre-treatment oak recruit density.

5. Implications for forest management

The successful recruitment of oak in mixed, uneven-aged forests requires the consideration of multiple factors. In our study, we identified stand density as an important stand structural variable, and a potentially positive effect of canopy openness with low shade-casting capacity of the tree species in the overstory. This aligns with multiple studies in which competition by other tree species, low light availability and light transmission of the canopy have been identified as common issues (Canham et al., 1994, Aussenac, 2000, Ligot et al., 2013, Modrow et al., 2019). Further, a decrease in stand density might positively affect oak recruits by increasing their resistance, resilience and recovery from drought (Schmitt et al., 2020).

Our study provides an important piece of information for the successful recruitment of oak trees in a largely understudied diameter size class. If the aim is to ensure oak continuity, it is essential to put management efforts into oak recruitment size classes. For this, overall stand density should be kept below 1000 stems ha^{-1} since a 50 % increase of stand density was predicted to decrease oak recruit density of the smaller size class by 42 %. Further, a higher canopy openness with a species composition of tree crowns with higher light transmission (SCA index 2.08) also predicted up to a 400 % increase in oak recruit density. In our study, species with a high shade-casting ability were species such as beech, maple and spruce while species with a low shade-casting ability were birch, pine and aspen. These competitor species are prevalent in many temperate forests and based on our results their management has to be taken into account when the objective is to increase oak recruit development into the overstory.

Additional studies are needed regarding long-term effects of repeated silvicultural measures and how structure can be managed to promote oak development from lower and middle canopies into the overstory. Moreover, further studies are necessary to assess the effect of selective cutting on the response of oak recruits to environmental stressors such as pathogens and repeated droughts.

CRediT authorship contribution statement

Pohl Nora Sophie: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Muraro Luca:** Writing – review & editing, Formal analysis. **Nordén Björn:** Writing – review & editing, Funding acquisition, Conceptualization. **Löf Magnus:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Funding acquisition, Conceptualization. **Hedwall Per-Ola:** Writing – review & editing, Formal analysis. **Aldea Jorge:** Writing – review & editing, Funding acquisition, Formal analysis. **Felton Annika M:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Gardiner Emile S:** Writing – review & editing, Funding acquisition.

Authors' contributions

Primary funding was secured by Magnus Löf, Jorge Aldea, Emile Gardiner and Björn Nordén. Study conception and design were developed by Magnus Löf, Annika M. Felton, Björn Nordén and Nora Pohl. Material preparation and data collection were performed by Nora Pohl. Data analysis was performed by Nora Pohl and supported by Jorge Aldea, Per-Ola Hedwall and Luca Muraro. The first draft of the manuscript was written by Nora Pohl and Magnus Löf, and all authors contributed critically to drafts and gave final approval for publication.

Declaration of Competing 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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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.122721.

Data availability

Data will be made available on request.

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