

STABLE BUT SITE-DEPENDENT OAK REGENERATION FOLLOWING CONSERVATION THINNING

Evidence from a 22-year study in western Sweden



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Table of contents

Abstract	2
Sammanfattning	3
Introduction	4
Aim	5
Materials and methods	6
Area description	6
Measurements	7
Statistical analysis	8
Results	9
Long-term effects of thinning	11
The effects of environmental variables	11
The effect of competition	14
Discussion	17
Long-term effects of thinning	17
The effects of environmental variables	18
The effect of competition	19
Management implications	21
Limitations	21
Conclusions	22
Acknowledgements	23
References	24
Appendix 1: Popular science summary	30
Appendix 2: List of all packages used in the analysis	31
Appendix 3: List of all analyses reported in the text	32

Abstract

The native oaks in Sweden (*Quercus robur* and *Q. petraea*) are keystone species that support high biodiversity, which is why maintaining healthy oak ecosystems is of great importance. However, oak regeneration has declined across Europe due to increased competition and reduced light availability following changes in land use and forest management. As part of the Swedish Oak Project in 2003, conservation thinning was applied in oak-rich forests in southern Sweden to improve oak regeneration by increasing canopy openness. Short-term surveys indicated positive effects on oak seedling density, but the long-term effects remained unclear. This study evaluated oak regeneration 22 years after thinning in five experimental forest sites in western Sweden. This was done by measuring oak seedling density and height, tree basal area, canopy openness and competing woody vegetation in 2025 and comparing with data collected in 2003 and 2005. Generalised linear mixed models were used to analyse the effects of thinning, environmental variables and competition on oak regeneration. Spatial variation among sites and subplots explained a substantially larger proportion of variance in oak regeneration than the measured environmental variables, competition and treatment effects, indicating that local site conditions strongly influenced regeneration dynamics. Oak seedling density declined by 54% in control plots over the two decades, while densities in thinned plots remained more stable. However, differences between treatments were generally not statistically significant. Total basal area was negatively associated with oak seedling density, whereas canopy openness did not significantly predict regeneration. Competition analyses provided no clear evidence that competitor species suppressed oak regeneration. Thinning was associated with greater individual seedling heights and higher variation in oak height, suggesting heterogeneous growth responses following thinning. Overall, the results suggest that conservation thinning may contribute to maintaining oak regeneration over long time periods, although effects appear modest, strongly site dependent and unlikely to persist without repeated intervention. These findings highlight the importance of targeting conservation thinning at sites with intrinsic regeneration potential and of adaptive long-term management approaches in oak conservation.

Sammanfattning

De inhemska ekarna i Sverige (*Quercus robur* och *Q. petraea*) är nyckelarter, som stödjer hög biologisk mångfald, vilket gör det viktigt att upprätthålla friska ekosystem med ek. Dessvärre har ekföryngringen minskat i Europa till följd av ökad konkurrens och minskad ljustillgång efter förändringar i markanvändning och skogsbruk. Som en del av Ekprojektet utfördes naturvårdsgallring år 2003 i ekrika blandskogar i södra Sverige för att förbättra ekföryngringen genom att öka ljustillgången. Korttidsstudier visade positiva effekter på tätheten av ekplantor, men långtids-effekterna förblev oklara. Denna studie utvärderade ekföryngringen 22 år efter gallringen på fem lokaler i västra Sverige. Data om täthet och höjd av ekplantor och konkurrerande vedarter, trädens grundyta och kronöppning samlades in 2025 och jämfördes med data från 2003 och 2005. Generaliserade linjära modeller med blandade effekter användes för att analysera effekterna av gallring, miljövariabler och konkurrens på ekföryngringen. Spatial variation mellan lokaler och mätytor förklarade större andel av variansen i ekföryngringen än uppmätta miljövariabler, konkurrens och behandlingseffekter, vilket tyder på att lokala förhållanden hade stort inflytande på föryngringsdynamiken. Tätheten av ekplantor minskade med 54% i referensytorna under de två årtiondena, medan tätheten i gallrade ytor förblev mer stabil. Skillnaderna mellan behandlingarna var dock generellt inte statistiskt signifikanta. Trädgrundyta var negativt associerad med tätheten av ekplantor, medan kronöppning inte hade någon signifikant effekt på föryngringen. Konkurrensanalyserna gav inget tydligt stöd för att konkurrerande arter hämmade ekföryngringen. Gallring var associerad med högre individuella planthöjder och högre variation i ekhöjd, vilket tyder på heterogena tillväxtresponser efter gallringen. Sammantaget tyder resultaten på att naturvårdsgallring kan bidra till att upprätthålla ekföryngring över lång tid, även om effekterna verkar måttliga, starkt platsberoende och osannolika att bestå utan upprepade åtgärder. Dessa fynd understryker vikten av att rikta naturvårdsgallring mot lokaler med naturlig föryngringspotential och av adaptiva och långsiktiga förvaltningsstrategier vid bevarande av ek.

Introduction

Broadleaved trees like oaks (*Quercus* spp.) only make up a small proportion of the forest area in Sweden and are often threatened by spruce encroachment, as production forests of Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) dominate Swedish forests, resulting in reduced biodiversity (Royal Swedish Academy of Agriculture and Forestry, 2024). Forests are nevertheless critical habitats for a large proportion of Sweden's red-listed species (SLU Artdatabanken, 2020), which is why restoration and conservation of mixed forests with higher structural and species diversity is of great importance for protecting biodiversity and preserving forest continuity.

Especially large and old broadleaved trees support high biodiversity through tree-related microhabitats (Kozák et al., 2023; Larrieu & Cabanettes, 2012; Paillet et al., 2019), and contribute disproportionately to reproduction (Andrus et al., 2020; S. J. Smith et al., 2022). Among temperate broadleaved trees, oaks stand out as keystone species. Pedunculate oak (*Quercus robur*) and sessile oak (*Quercus petraea*) constitute habitat and food source for a wide range of organisms, including birds (Bossema, 1979; Carlson et al., 1998), saproxylic beetles (Ranius & Jansson, 2000), spiders (Mupepele et al., 2014), lichens (Paltto et al., 2010) and fungi (Antonsson & Jansson, 2001). In Sweden, oaks occur mainly in mixed broadleaved forests of the boreonemoral zone in the southern part of the country, where they make up only 4.5% of tree volume in the Götaland region (SLU Institutionen för skoglig resurshushållning, 2025).

Historically, oaks were more abundant in open landscapes like wood pastures maintained by grazing, but during the 18th and 19th centuries, oak populations declined across much of Europe (Lindbladh & Foster, 2010; Vera, 2000). While climatic change influenced forest composition to some extent, land use changes, particularly the abandonment of traditional pasture management and shift to modern forestry and agriculture, were the main drivers of this decline, by promoting forest succession that disadvantaged oaks (Lindbladh & Foster, 2010; Vera, 2000). As a result, many formerly open oak habitats became dense closed forests dominated by shade-tolerant species such as beech (*Fagus sylvatica*) and Norway spruce (*Picea abies*), which have outcompeted oaks and hindered their regeneration (Lindbladh & Foster, 2010; Vera, 2000).

Large and old trees are declining globally (Lindenmayer et al., 2012), with oak decline particularly well-documented across Europe and North America, expressed through increased mortality, crown and root damage, foliage discolouration, and poor regeneration (Kelly, 2002; Oliver et al., 2005; Sonesson, 1999; Thomas et al., 2002; Vera, 2000). Crucially, maintaining successful regeneration is essential for the persistence of oak and associated species, as well as for their ability to adapt to changing environmental conditions, such as climate change (Cannon et al., 2022). Limited regeneration not only risks creating an age gap between old and young trees but can also lead to a gradual decline or even local disappearance of oaks that are not replaced by new trees (Lindenmayer et al., 2012; Vera, 2000). This loss could eventually lead to local extinctions of other species dependent on large, old oaks, as the much younger oaks or other tree species cannot take on the same ecological role (Antonsson & Jansson, 2001; Lindenmayer et al., 2012).

Insufficient regeneration has been observed in southern Sweden, where it has been reported that oaks often do not reach the tall sapling stage of over 130 cm (Leonardsson et al., 2015). This pattern is partly attributed to browsing by ungulates, as intense browsing pressure limits the survival and growth of seedlings, either killing them or keeping them in the seedling stage (Annighöfer et al., 2015; Götmark, Berglund, et al., 2005; Leonardsson et al., 2015; Petersson et al., 2019). Other biotic factors limiting oak regeneration could be predation on acorns by insects and smaller mammals, such as mice and rabbits (Crawley & Long, 1995). Wild boars also eat acorns and roots, and can kill seedlings and saplings by uprooting them while foraging (Bruinderink & Hazebroek, 1996; Gómez & Hódar, 2008).

Competition and light availability are major factors affecting oak regeneration. Oak seedling density generally increases with basal area of oak but decreases with basal area of other species (Annighöfer et al., 2015). A decline in mature oaks thus inevitably reduces the number of seedlings, while a higher abundance of other tree species increases competition among seedlings. Because oaks are relatively light-demanding and slow-growing, they are particularly sensitive to shading and competition from faster-growing, more shade-tolerant species that can overtop oak seedlings over time (Götmark, Berglund, et al., 2005; Kelly, 2002; Leonardsson et al., 2015; Oliver et al., 2005). These two factors are important especially when combined, as canopy gaps that benefit oak seedlings and saplings also favour other species, leading to strong competition even under improved light conditions (Annighöfer et al., 2015). However, surrounding vegetation does not always hinder seedling survival but can even improve it, for example by protecting seedlings from browsing (Crawley & Long, 1995; Jensen et al., 2012; Kelly, 2002). Oak regeneration is thus shaped by interacting biotic and abiotic factors, many of which can be influenced by forest management.

Management approaches aimed at promoting healthy oak ecosystems and successful regeneration range from passive to active methods. Protected areas with minimal intervention are a common approach, where natural processes are allowed to shape forest dynamics (Götmark, 2013). Active methods include reintroduction of traditional management, like wood pastures or controlled burning to limit competing vegetation, as well as silvicultural practices, such as enrichment planting and partial cutting to limit competition, create canopy gaps or more space for individual oak crowns (Götmark, 2013; Mölder et al., 2019).

The Swedish Oak Project is a long-term research project studying partial cuttings of oak-rich mixed forests (*The Swedish Oak Project*, 2024). The project includes 25 sites in southern Sweden, each with two plots of approximately 1 ha: one undisturbed control plot and one experimental plot treated with conservation-oriented thinning in the winter of 2002/2003, removing on average 23% of the basal area. The sites have been surveyed both before and after thinning to assess its effects on biodiversity, growth and vitality of large oaks, and oak regeneration (Franc & Götmark, 2008; Götmark, 2009; Götmark, Paltto, et al., 2005; Paltto et al., 2008). Two years after thinning, Götmark (2007) reported increased oak seedling density in the experimental plots, and concluded that conservation thinning favours oak regeneration in short term by opening the canopy. However, these thinning effects may fade over time, as the canopy can gradually close again, and other species may eventually benefit more than oak. This was observed ten years after the thinning, when Leonardsson et al. (2015) reported that oak seedling density had not increased in the thinned plots. Instead, they found that other broadleaves and shrubs had increased more in density and height than oaks, possibly reflecting oaks' slower growth and susceptibility to competition from faster-growing species. However, Leonardsson et al. (2015) did not compare thinned and control plots, leaving the overall effects of thinning unknown.

Aim

Most studies on oak regeneration cover only short periods of 3–10 years (Götmark, 2007; Leonardsson et al., 2015; Sonesson, 1999), while few have followed regeneration for more than 20 years (Kelly, 2002). Understanding long-term dynamics is critical for effective management of oak-rich forests, since regeneration failure combined with the ongoing decline of large and old trees can lead to degradation of these ecosystems. The aim of this study was therefore to evaluate if conservation thinning affects oak regeneration in the long term, through its structural and environmental drivers. This was done by comparing present data from experimental plots to data from control plots, as well as to similar data collected in 2003 and 2005.

The research questions are:

1. How has oak seedling density changed over 22 years, and how has this change been influenced by conservation thinning?
2. How do total basal area, oak basal area and canopy openness influence oak seedling density, and do these effects differ between thinned and control plots?
3. How do competitor density and height influence oak seedling density and height, and how does conservation thinning affect the height of oak and competitor seedlings?

Materials and methods

Area description

Five of the 25 sites were selected for this study due to accessibility. The sites are located in western Sweden, with Skölvne in Herrljunga, Karla in Vara, Östadkulle in Vårgårda, and Sandviksås and Rya åsar in Borås municipalities (Figure 1). The sites were originally selected for the project because they were oak-rich, with varying proportions of other broadleaves and conifers (Table 1). The control and experimental plots were initially similar in forest structure. The sites are within the boreonemoral zone, a transition zone between the temperate deciduous forests of southern Europe and the boreal forests of northern Europe. The soils are mainly mesic moraines, with brown earth soils dominating at most sites. Roe deer (*Capreolus capreolus*) and moose (*Alces alces*) are the most common browsing ungulates in the region. Rya åsar is formally protected as a nature reserve, while the other sites are classified as woodland key habitats, forest areas with high conservation values that provide suitable habitat for red-listed species (Roberge et al., 2020).

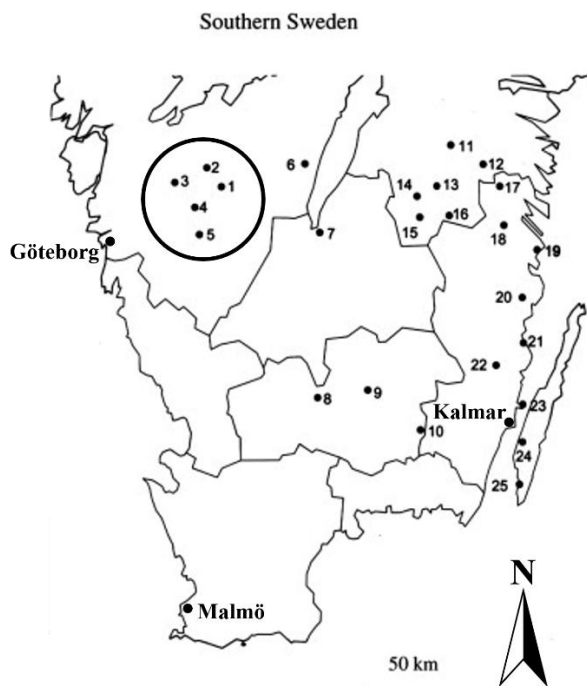


Figure 1. Map of the five study sites in southwestern Sweden: Skölvne (1), Karla (2), Östadkulle (3), Sandviksås (4), and Rya åsar (5). Modified from Götmark (2007).

Table 1. Description of the five study sites, including basal area (m²/ha) for different tree groups before thinning, percentage of overall basal area removed, and other abundant broadleaved tree species. Modified from Götmark (2007).

Site ^a	Basal area (m ² /ha) of trees > 5 cm in diameter at 130 cm			Basal area removed in the thinning (%)	Other abundant broadleaved species
	Oaks	Other broadleaves	Conifers		
1. Skölvene	18.2	9.0	1.2	20.3	<i>Alnus glutinosa</i> , <i>Betula</i> spp.
2. Karla	13.1	6.7	0.3	28.1	<i>Betula</i> spp., <i>Populus tremula</i>
3. Östadkulle	15.1	14.4	1.6	26.5	<i>Fraxinus excelsior</i> , <i>Populus tremula</i>
4. Sandviksås	10.2	5.5	15.1 ^b	31.2	<i>Betula</i> spp.
5. Rya åsar	22.8	7.9	1.3	15.6	<i>Betula</i> spp., <i>Sorbus aucuparia</i>

^a Site numbers correspond to locations in Figure 1.

^b Mainly *Picea abies*.

Measurements

Seedling data were collected during September and October 2025. Following Götmark (2007), two transects were established on a central part of each plot. To ensure representative locations of the subplots for this study, the transects were divided into 4 equal sections, in which the position of one subplot each was randomised. Along each transect, four 5 m² (1×5 m) subplots were marked, resulting in eight subplots (40 m²) per plot and 16 subplots (80 m²) per site (Figure 2). Inside the subplots, all woody species were identified, and the height of seedlings and saplings shorter than 130 cm was measured. For saplings taller than 130 cm, the girth at breast height (130 cm; girth < 15.7 cm, corresponding to 5 cm diameter) was measured.

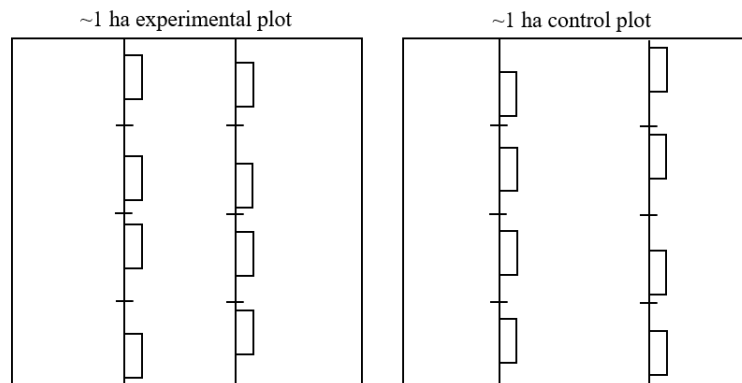


Figure 2. Example of a site with an experimental plot (thinned) and a control plot, each including two transects divided in 4 sections with one 5 m² subplot in each (not in scale).

Two topsoil samples (0–7 cm depth) per subplot were collected using a metal core. The soil was wrapped in plastic film and stored frozen. The two samples were separated, and one was randomly selected for analysis. The samples were dried at 40°C until constant mass, which for most samples was 72 hours. Dry samples were crushed in a mortar and sieved to 2 mm, removing roots, stones and larger particles. Then, 10 g of soil and 25 ml of distilled water were mixed in a beaker. Some samples required 50 ml of water since 25 ml was not enough to form a slurry. The samples were stirred for 30 minutes on a magnetic stirrer, after which they were allowed to equilibrate with atmospheric CO₂ for 30 minutes. Finally, pH was measured with a Mettler Toledo pH meter at room temperature (~21°C), by gently swirling the electrode in the soil slurry.

To measure canopy openness, four upward-facing photos at breast height per subplot were taken on an ultrawide 12 MP smartphone camera. The images were analysed in ImageJ (Schneider et al., 2012) by converting to binary black and white pixels, where black pixels accounted for canopy cover and white pixels for open sky. Canopy openness was calculated as the proportion of white pixels in each image. Prior to thresholding, images were standardised to improve contrast between canopy elements and sky. In photographs where backlit foliage reduced contrast, colour channels were separated and the blue channel was selected for analysis, as it provided the clearest distinction between vegetation and sky. Minor image corrections, including sharpening and manual correction of overexposed trunk surfaces, were applied when necessary to avoid misclassification of canopy cover. Threshold values were adjusted manually while visually comparing binary and original images to ensure consistent classification across photographs.

Tree data were collected in November and December 2025. The girth of all trees larger than 15.7 cm (corresponding to 5 cm diameter at breast height) was measured within a central area of 0.1 ha, that included one of the transects. The girth was then converted to diameter, which was used to calculate tree basal area.

Statistical analysis

Data cleaning and analyses were conducted in R (version 4.5.2; R Core Team, 2025), using the {tidyverse} collection of packages (Wickham et al., 2019). Graphs were created using the {ggplot2} package (Wickham, 2016). Data from 2003 and 2005 were collected by Götmark (2007). Not all environmental variables were consistently recorded across all subplots in both early years, which is why 2003 and 2005 were combined into an early period after thinning, with basal area values from 2003, pH values from 2005, and canopy openness averaged across both. Year 2025 was designated as the late period. Period was treated as a factor rather than a continuous variable to account for the large temporal gap between early years and 2025. Soil pH was excluded from the final models, because the values were not directly comparable between years, as pH was measured using different methods in 2005 (field meter, pH range 5.40–6.60) and 2025 (soil slurry, pH range 3.61–5.49). Only data from 2025 were used for height analyses, as seedling heights were recorded as exact measurements, while data from 2003 and 2005 were categorised (< 20 cm and 20–130 cm). Height analyses were restricted to seedlings (≤ 130 cm), but sapling data (> 130 cm, DBH < 5 cm) were collected and included in density analyses. For simplicity, all individuals included in the density analyses (seedlings and saplings) are referred to as seedlings throughout. Competitor species occurring in more than 10% of the subplots across all survey years were chosen as the competitor species (*Sorbus aucuparia*, *Corylus avellana*, *Frangula alnus*, *Populus tremula*, *Fraxinus excelsior*, *Picea abies* and merged *Betula* spp.).

Mixed models were used due to the hierarchical data structure, with subplots nested within transects within plots within sites. The full random-effects structure was used in most analyses but simplified, when necessary, because of model convergence issues (Appendix 3). Models with oak seedling density as the response variable were fitted using the {glmmTMB} package (Brooks et

al., 2017; McGillicuddy et al., 2025), with subplot area included as a log-transformed offset to standardise counts to density per m². Negative binomial distribution (nbinom2) was used to account for overdispersed count data. Post-hoc tests were performed on the oak density models using the {emmeans} package (Lenth et al., 2026), to test differences between periods and treatments and to obtain estimated marginal means standardised to density per m². The significance of treatment-specific basal area effects was obtained using the *emtrends* function. Correlation between total basal area and canopy openness was assessed using Pearson's correlation tests.

Mean oak height was modelled as a function of mean competitor height, treatment, and total competitor density using linear mixed models ({lme4} and {lmerTest} packages; Bates et al., 2015; Kuznetsova et al., 2017), with log-transformed response variables due to non-normal residuals. Individual oak and competitor seedling heights were modelled as a function of treatment using {glmmTMB}, with a log-linked Gamma distribution to better handle positive continuous data where variance scales with the mean. A dispersion formula (~treatment) was included to allow variance to differ between treatments. The height ratio between mean competitor height and mean oak height was modelled as a function of treatment and competitor density using log-transformed linear mixed models ({lme4} and {lmerTest}). Logarithmic estimates were back-transformed to obtain percentage changes for interpretation.

Model fit was assessed using {DHARMA} and {performance} packages (Hartig et al., 2024; Lüdecke et al., 2021), including tests for residual patterns and overdispersion. Models were compared using Akaike Information Criterion (AIC). All models reported were run on datasets excluding trunk shoots, as they do not represent true regeneration. Sensitivity analyses were conducted to test if including shoots or basal area measurements from survey areas larger than the standard 0.3 ha (in 2003) affected the results. All packages used are listed in Appendix 2, and all models that are reported in the results are listed in Appendix 3.

Results

Stand conditions changed over the two decades (Table 2). Between 2003 and 2025, mean total basal area increased from 31.3 m²/ha to 40.9 m²/ha in control plots and from 23.4 m²/ha to 24.9 m²/ha in thinned plots. At the plot level, basal area generally increased over time, except in Skölvne and Östadkulle thinned plots in which mean basal area decreased. Mean oak basal area increased from 16.8 m²/ha to 22.0 m²/ha in control plots, driven by all sites except Rya åsar. In thinned plots, oak basal area decreased from 15.0 m²/ha to 14.7 m²/ha over time, with all sites except Karla and Rya åsar showing decreases. Canopy openness decreased from the early to the late period across most sites and treatments. Mean canopy openness decreased from 26.5% to 16.1% in control plots and from 51.6% to 17.2% in thinned plots. More variation was observed in the early period, while by the late period, values were more similar between treatments at most sites, apart from Sandviksås where the thinned plot remained more open.

Table 2. Total basal area (m²/ha), oak basal area (m²/ha), and mean canopy openness (mean $\pm$ SD%) across sites, treatments and periods.

Site	Treatment	Total BA (m ² /ha)		Oak BA (m ² /ha)		Canopy openness (mean $\pm$ SD%)	
		Early	Late	Early	Late	Early	Late
Skölvene	control	34.7	39.9	20.7	23.5	35.6 $\pm$ 17.8	13.5 $\pm$ 2.1
	thinned	22.9	22.2	17.7	13.9	55.0 $\pm$ 0.0	12.3 $\pm$ 4.9
Karla	control	26.3	26.9	20.0	20.1	25.5 $\pm$ 4.5	23.4 $\pm$ 4.9
	thinned	16.2	31.0	8.8	13.3	55.0 $\pm$ 17.5	15.8 $\pm$ 4.2
Östadkulle	control	32.5	43.4	15.6	25.6	12.5 $\pm$ 2.3	11.0 $\pm$ 2.7
	thinned	28.4	18.3	14.3	10.6	39.6 $\pm$ 5.9	10.8 $\pm$ 6.8
Sandviksås	control	31.7	59.4	10.9	25.5	34.0 $\pm$ 14.3	15.3 $\pm$ 2.6
	thinned	22.2	22.5	9.7	9.3	62.0 $\pm$ 9.6	33.8 $\pm$ 10.9
Rya åsar	control	31.2	35.0	16.9	15.1	25.0 $\pm$ 3.5	17.4 $\pm$ 5.7
	thinned	27.4	30.3	24.6	26.2	46.3 $\pm$ 6.5	13.4 $\pm$ 1.6

Mean oak seedling densities varied substantially among sites, treatments and years (Table 3). Karla showed the highest seedling densities overall and Sandviksås the lowest. Considerable variation between subplots within sites and plots was observed, reflected by the relatively large standard deviations.

Table 3. Mean oak seedling densities (mean $\pm$ SD seedlings per m²) across sites, treatments and years.

Site	Treatment	2003 (mean $\pm$ SD)	2005 (mean $\pm$ SD)	2025 (mean $\pm$ SD)
Skölvene	control	1.00 $\pm$ 0.65	0.80 $\pm$ 0.65	0.50 $\pm$ 0.64
	thinned	1.06 $\pm$ 0.57	0.80 $\pm$ 0.61	1.88 $\pm$ 1.43
Karla	control	11.84 $\pm$ 6.52	7.44 $\pm$ 5.62	4.60 $\pm$ 3.85
	thinned	2.83 $\pm$ 2.77	1.67 $\pm$ 1.30	5.22 $\pm$ 7.13
Östadkulle	control	1.20 $\pm$ 1.34	1.38 $\pm$ 1.07	0.50 $\pm$ 0.60
	thinned	0.57 $\pm$ 0.80	1.28 $\pm$ 1.30	0.22 $\pm$ 0.42
Sandviksås	control	0.85 $\pm$ 0.78	0.68 $\pm$ 0.55	0.48 $\pm$ 1.38
	thinned	0.15 $\pm$ 0.14	0.30 $\pm$ 0.26	1.52 $\pm$ 2.25
Rya åsar	control	1.80 $\pm$ 1.92	1.07 $\pm$ 1.06	1.40 $\pm$ 3.03
	thinned	8.40 $\pm$ 6.82	7.10 $\pm$ 6.40	0.82 $\pm$ 1.54

Long-term effects of thinning

Oak seedling density was significantly lower in the late period overall ($\beta = -0.778 \pm 0.212$, $p < 0.001$). Oak density decreased by 54% in control plots between the early and late period ($p < 0.001$; Figure 3). In contrast, oak density in thinned plots showed no significant change (20% increase, $p = 0.444$). This difference in temporal patterns was reflected in a significant interaction between treatment and period ($\beta = 0.961 \pm 0.322$, $p = 0.003$). In the early period, mean density was 1.28 seedlings/m² in control plots, and 1.08 seedlings/m² in thinned plots, with no statistically significant difference between treatments ($p = 0.687$). A separate analysis of 2005 data showed no significant difference between treatments either ($p = 0.938$). In the late period, mean density was 0.59 seedlings/m² in control plots, and 1.3 seedlings/m² in thinned plots, with no significant difference between treatments ($p = 0.064$). Treatment and period together explained only 3.6% of the variance in oak seedling density, while random effects explained 65.1%.

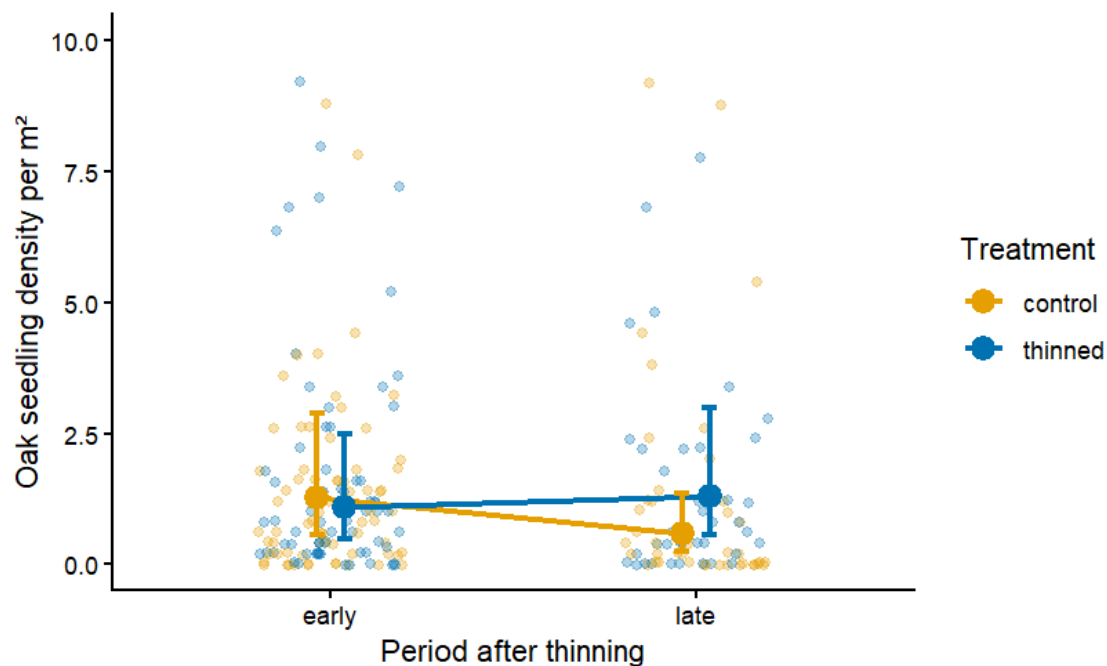


Figure 3. Oak seedling density in control and thinned plots during early (2003, 2005) and late (2025) periods after conservation thinning. Large points represent estimated marginal means $\pm$ 95% confidence intervals, while small points represent observed subplot densities. Y-axis is limited to 10 seedlings/m² for readability, and 9 data points above this threshold are not shown (control early: 5, control late: 1, thinned early: 2, thinned late: 1).

The effects of environmental variables

Total basal area had a significant negative effect on oak seedling density, with a 4.8% decrease per 1 m²/ha increase in total basal area ($\beta = -0.049 \pm 0.022$, $p = 0.025$). Oak basal area did not have a significant effect overall ($\beta = -0.092 \pm 0.048$, $p = 0.057$). The negative effect of total basal area remained significant after controlling for canopy openness and period (5.8% decrease per 1 m²/ha, $\beta = -0.059 \pm 0.021$, $p = 0.004$, Figure 4). There was no significant difference in oak seedling density between the two periods after controlling for total basal area ($\beta = -0.288 \pm 0.248$, $p = 0.246$), but when controlling for total basal area and canopy openness, oak seedling density was 61.5% lower in the late period compared to the early period ($\beta = -0.955 \pm 0.326$, $p = 0.003$). Basal area and period together explained 11.1% of the variance in oak seedling density, while random effects explained 52.7%. Basal area, canopy and period together explained 19.8% of the variance, whereas random effects explained 46.6%.

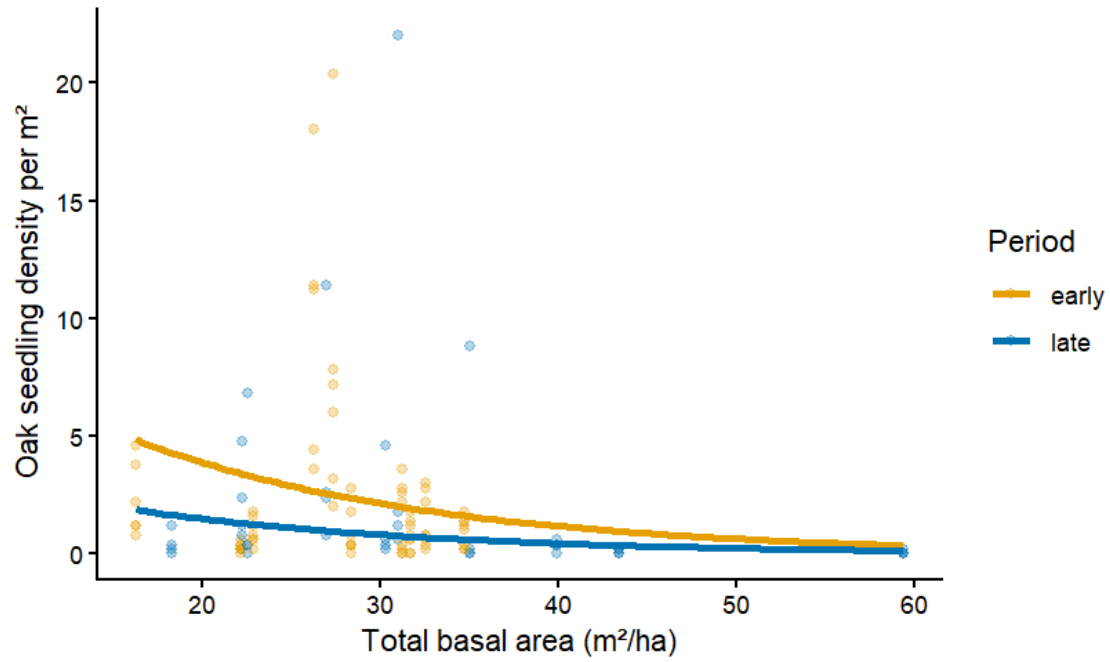


Figure 4. The relationship between total basal area (m²/ha) and oak seedling density across early (2003, 2005) and late (2025) periods. Points represent observed subplot densities, while lines represent model predictions.

The effect of total basal area on oak seedling density differed significantly between thinned and control plots, as indicated by the significant interaction between treatment and total basal area ($\beta = 0.154 \pm 0.059$, $p = 0.009$, Figure 5). In control plots, oak density decreased by 11.9% per 1 m²/ha increase in total basal area ($\beta = -0.127 \pm 0.041$, $p = 0.002$), while no significant effect was observed in thinned plots ($\beta = 0.027 \pm 0.040$, $p = 0.495$). Similarly, the effect of oak basal area differed between treatments ($\beta = 0.206 \pm 0.067$, $p = 0.002$), with a 13.0% decrease in oak seedling density per 1 m²/ha increase in control plots ($\beta = -0.140 \pm 0.050$, $p = 0.005$) and no significant effect in thinned plots ($\beta = 0.066 \pm 0.041$, $p = 0.104$). The interaction between treatment and total basal area, together with canopy openness and period, explained 38.3% of the variance in oak seedling density, whereas random effects explained 30.2%. The interaction between treatment and oak basal area, together with canopy openness and period, explained 21.6% of the variance, while random effects explained 49.5%.

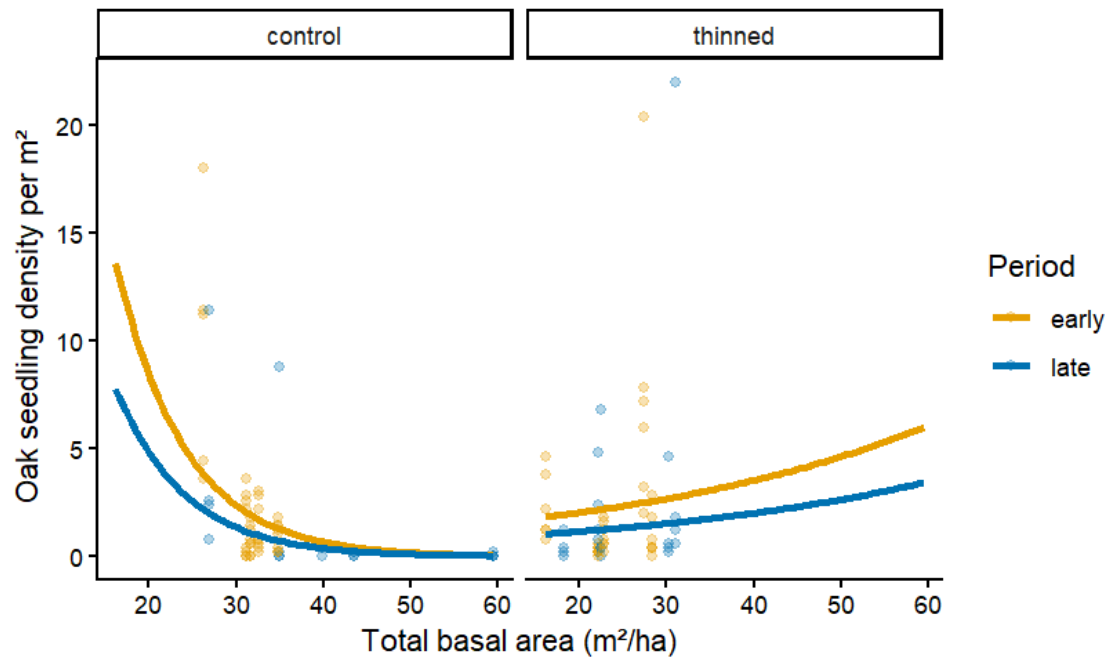


Figure 5. The relationship between total basal area (m^2/ha) and oak seedling density in control and thinned plots across early (2003, 2005) and late (2025) periods. Points represent observed subplot densities, while lines represent model predictions.

Neither canopy openness ($\beta = 0.006 \pm 0.010$, $p = 0.556$) nor pH ($\beta = -0.119 \pm 0.419$, $p = 0.778$) had a significant effect on oak seedling density. The effect of canopy openness remained non-significant after accounting for total basal area and period ($\beta = -0.017 \pm 0.010$, $p = 0.096$, Figure 6). Total basal area and canopy openness were moderately negatively correlated ($r = -0.420$, $p < 0.001$). After controlling for canopy openness, oak seedling density was 50.1% lower in the late period compared to the early period ($\beta = -0.696 \pm 0.282$, $p = 0.014$).

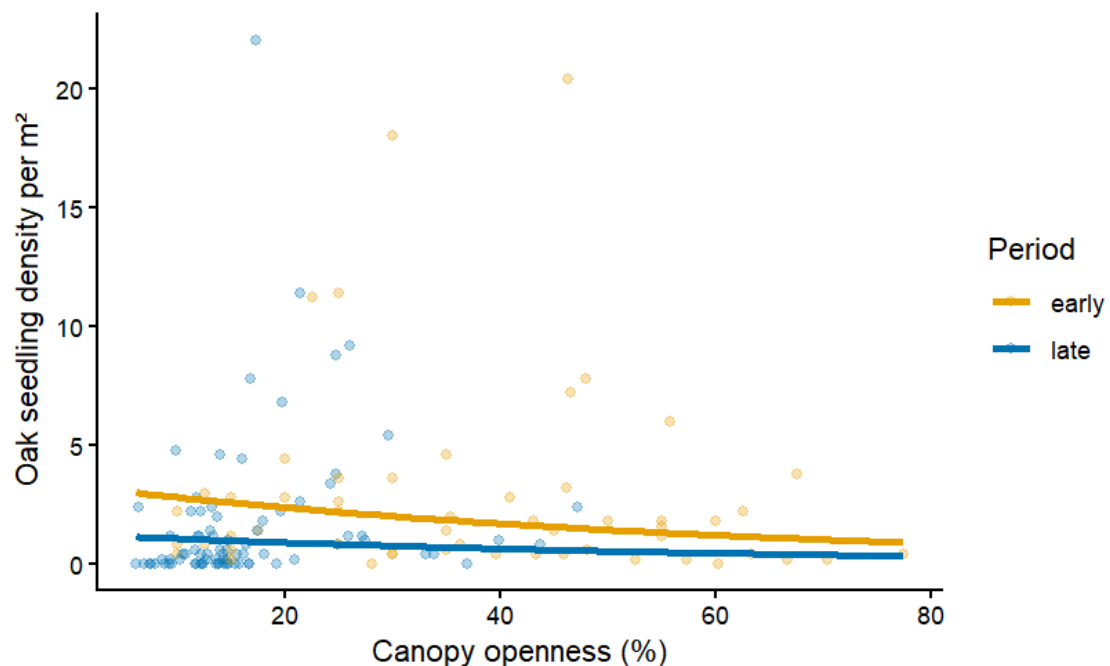


Figure 6. The relationship between canopy openness (%) and oak seedling density across early (2003, 2005) and late (2025) periods. Points represent observed subplot densities, while lines represent model predictions.

The effect of competition

Total competitor density had a significant, slightly positive effect on oak seedling density ($\beta = 0.011 \pm 0.005$, $p = 0.017$, Figure 7). The effect did not differ between treatments or periods, as neither interaction was significant ($p = 0.122$ and $p = 0.930$, respectively). Oak density was 67.3% lower in the late period, although this effect was only marginally significant ($\beta = -0.396 \pm 0.207$, $p = 0.055$). Total competitor density and period explained 7.87% of the variance in oak seedling density and random effects explained 49.9%. After accounting for total competitor density and period, treatment had no significant effect on oak seedling density ($\beta = 0.298 \pm 0.250$, $p = 0.233$). Competitor species richness did not have a significant effect on oak density either ($\beta = 0.194 \pm 0.107$, $p = 0.070$).

At the species level, only *Fraxinus excelsior* ($\beta = 0.011 \pm 0.005$, $p = 0.028$) and *Betula* spp. ($\beta = -0.119 \pm 0.054$, $p = 0.027$) had significant effects on oak seedling density. Both species were unevenly distributed across sites and highly concentrated at one site and plot (Table 4).

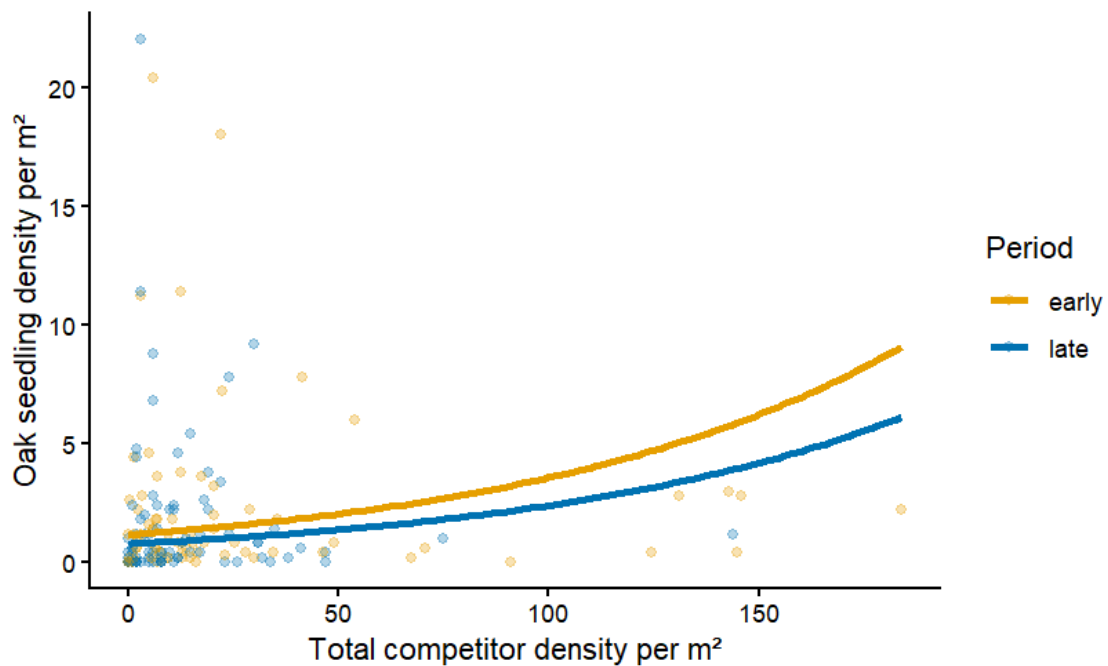


Figure 7. The relationship between total competitor seedling density and oak seedling density, across early (2003, 2005) and late (2025) periods. Points represent observed subplot densities, while lines represent model predictions.

Table 4. Total seedling counts of *Fraxinus excelsior*, *Betula* spp. and *Quercus* spp. by site and treatment. Early period counts (2003, 2005) were averaged before summing. Oak counts were rounded to the nearest integer.

Site	Treatment	<i>Fraxinus excelsior</i>	<i>Betula</i> spp.	<i>Quercus</i> spp.
Karla	control	0	0	427
	thinned	0	2.5	278
Rya åsar	control	0	0	115
	thinned	0	0	266
Sandviksås	control	0	0.5	56
	thinned	0	104.5	72
Skölvene	control	1	0.5	58
	thinned	1.5	5	109
Östadkulle	control	1015	0	74
	thinned	520.5	4	43

Total competitor density did not have a significant effect on mean oak height ($\beta = 0.002 \pm 0.003$, $p = 0.449$). In contrast, mean competitor height did have a significant positive effect ($\beta = 0.007 \pm 0.002$, $p = 0.002$). On average, a 1 cm increase in mean competitor height was associated with a 0.67% relative increase in mean oak seedling height. For example, predicted mean oak height was 13.8 cm in subplots where competitors were on average 20 cm tall, compared to a mean oak height of 20.6 cm where competitors were on average 80 cm tall. Mean competitor height explained 9.66% of the variance in mean oak height, while random effects explained 61.6%.

Mean oak seedling height did not differ significantly between treatments ($\beta = 0.390 \pm 0.264$, $p = 0.174$). In contrast, individual oak height was significantly higher in thinned plots, with 37.4% taller oak seedlings compared to control plots ($\beta = 0.317 \pm 0.100$, $p = 0.001$, Figure 8a). Individual competitor height showed a similar pattern, with 52.2% taller competitor seedlings in thinned plots ($\beta = 0.420 \pm 0.156$, $p = 0.007$, Figure 8b). Oak heights were 65.5% more variable in thinned plots ($p < 0.001$), while competitor heights were 25.3% more variable ($p = 0.019$). Treatment explained 4.7% and 6.4% of the variance in oak and competitor height, respectively, while random effects explained 51.3% and 48.5%.

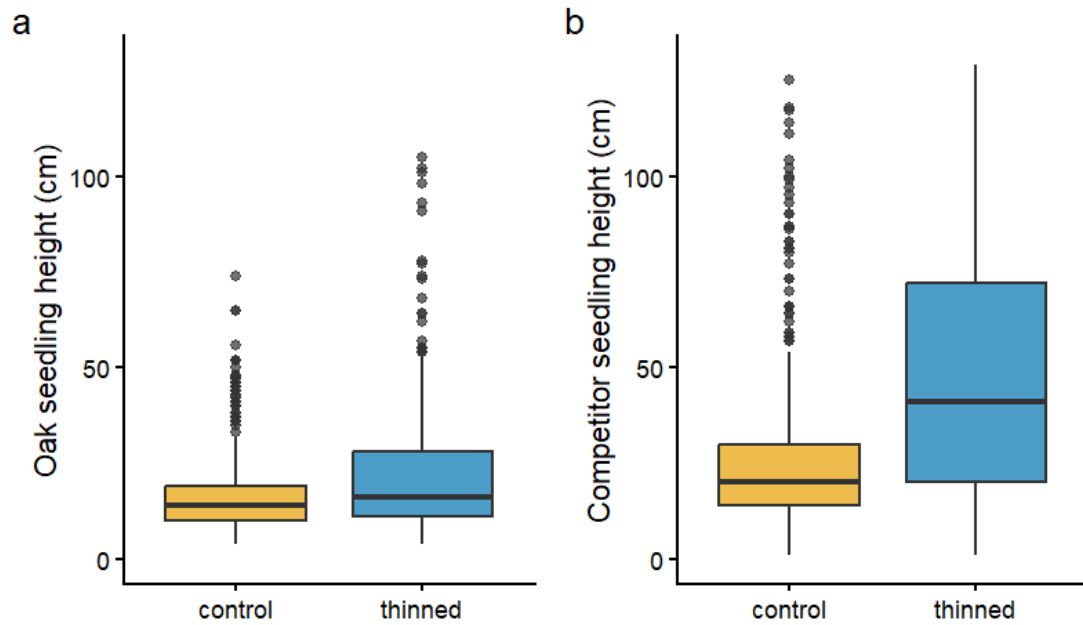


Figure 8. Individual seedling heights of oak and competitor species in control and thinned plots in 2025. Boxes show the interquartile range, whiskers extend to 1.5 times the interquartile range and points show outliers.

Treatment did not have a significant effect on the height ratio between mean competitor height and mean oak height ($\beta = 0.220 \pm 0.384$, $p = 0.588$), and neither did total competitor density ($\beta = 0.002 \pm 0.004$, $p = 0.700$). Height ratio did not have a significant effect on oak seedling density ($\beta = 0.160 \pm 0.122$, $p = 0.191$, Figure 9).

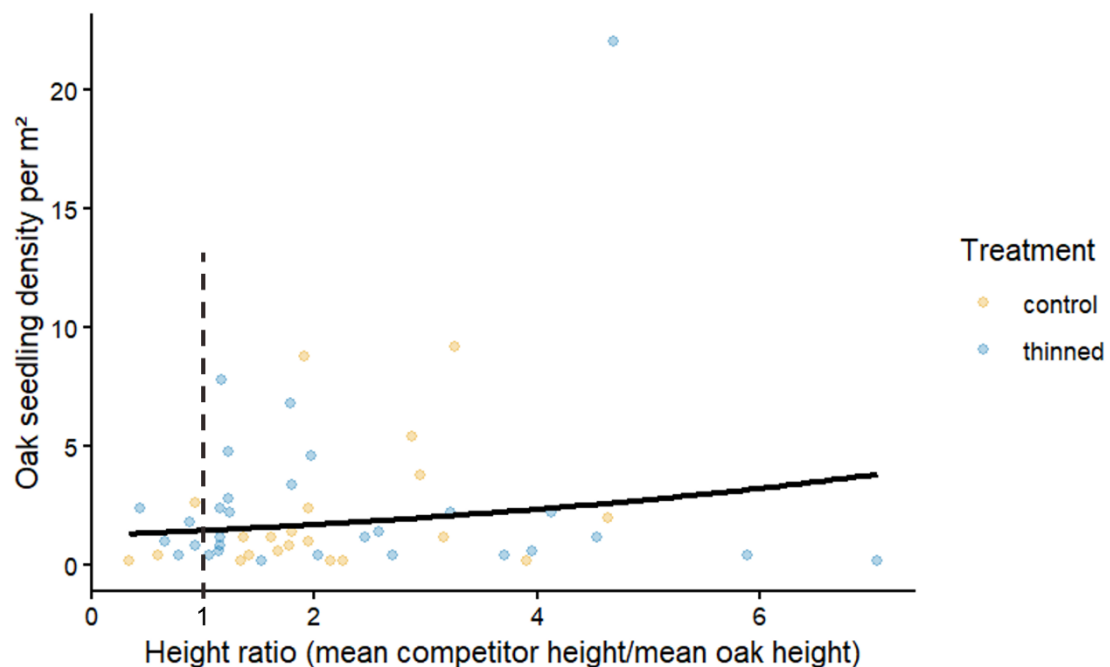


Figure 9. The relationship between height ratio (mean competitor seedling height/mean oak seedling height) and oak seedling density. Points represent observed subplot densities, while the line represents model prediction. A height ratio below one indicates oaks being relatively taller than competitors, while a ratio above one indicates competitors being relatively taller.

Discussion

A key finding of this study was that variation in oak regeneration was largely driven by spatial heterogeneity among sites and subplots rather than by the measured fixed effects alone. Across the analyses, fixed effects explained only small to modest proportions of the observed variance (4–22%), while random effects accounted for substantially larger proportions (47–65%). The only exception was the model including the interaction between treatment and total basal area, in which fixed effects explained more variance than random effects (38.3% vs. 30.2%), suggesting that stand structural conditions may partly explain variation in oak regeneration among sites.

Variance components indicated that both site- and subplot-level variation was important, with neither level consistently explaining more variance across models (Appendix 3). Site-level variation likely reflects broader differences between forests in stand structure and growing conditions, such as soil characteristics and browsing pressure. Subplot-level variation may reflect smaller-scale differences in microhabitat conditions, such as light availability, subplot productivity and soil moisture. At Sandviksås for example, subplots varied between lower-lying wetter areas and elevated drier ground, from open to denser canopy, demonstrating the kind of within-plot heterogeneity captured by the subplot random effect. Taken together, these results emphasize the importance of underlying spatial variation among sites and subplots in mediating regeneration outcomes and suggest that management effects cannot be fully understood without considering the spatial context in which they occur.

Long-term effects of thinning

Period showed a consistent negative effect on oak seedling density, and several models indicated significantly lower densities in the late period, suggesting an overall decline of oak density over the two decades. In control plots, oak seedling density decreased by 54% between the early and late period, suggesting that leaving these forests for free development does not improve oak regeneration. Density remained more stable in thinned plots, with a non-significant 20% increase over time. However, density in thinned plots increased to 1.3 seedlings/m² over time, which was similar to the 1.28 seedlings/m² observed in control plots during the early period. These results suggest that conservation thinning did not produce a significant long-term increase in oak seedling density but may have contributed to delaying the decline observed in control plots.

Götmark (2007) reported significantly higher mean seedling density in thinned plots compared to control plots, using data from 2005. In contrast, the analyses in the present study did not detect significant differences between treatments, neither in the merged early period, nor in 2005. This inconsistency in results is likely due to the different number of sites, as the previous study surveyed 25 sites, compared to the subset of five sites in this study. Götmark (2007) included sites across southern Sweden, with more sites in the eastern part (Figure 1, sites 6–25), while this study only focused on the western sites. Therefore, the results of this study cannot be generalised to the broader region of southern Sweden, but further replication is needed to assess the generality of these patterns. Regional variation in forest conditions, such as differing browsing pressure, stand structure and soil conditions might have influenced the thinning response, making direct comparison with Götmark (2007) difficult. Most variation in oak seedling density was explained by spatial structure on site and especially subplot level, rather than treatment. Overall, these results neither directly support nor contradict the earlier findings of positive thinning effects on oak regeneration but suggest that thinning may have helped maintain a relatively stable level of oak regeneration, with responses varying considerably among sites and regions.

The effects of environmental variables

Total basal area increased in control plots (31.3 to 40.9 m²/ha) but barely recovered in thinned plots (23.4 to 24.9 m²/ha). Mortality of the remaining trees likely contributed to this pattern, especially at Östadkulle, where mean total basal area declined by 10 m²/ha (Table 2). While oak basal area accounted for part of this decrease, mortality of *Fraxinus excelsior* likely explains much of it, as several dead ashes were observed in the thinned plot during fieldwork. This mortality is likely due to ash dieback caused by the fungus *Hymenoscyphus fraxineus* (Bengtsson et al., 2021). However, measurement differences might also partly explain this pattern. In the early period, basal area was measured across a 0.3 ha area, while measurements in this study were done in a 0.1 ha area due to time constraints. Although this smaller area was within the previously measured area, it may not fully represent the broader stand structure, meaning the extrapolated values should be interpreted with some caution.

Total basal area was the only environmental variable that significantly predicted oak seedling density overall, with higher total basal area associated with lower density. Similarly, Petersson et al. (2019) observed oak sapling density decreasing with basal area, which they attributed to reduced understory light availability. However, the effect differed between treatments, as oak density decreased significantly with increasing total basal area in control plots, while no significant effect was observed in thinned plots. Parker & Dey (2008) found that reducing basal area increased oak seedling survival through improved photosynthetic potential, suggesting that the negative effect of basal area on oak density observed in control plots may operate through light limitation. Higher basal area is generally associated with lower light availability (Comeau, 2002; Comeau & Heineman, 2003; Hale et al., 2009; Sonohat et al., 2004), which is also supported by the moderate negative correlation between total basal area and canopy openness observed in this study. The weaker relationship observed in thinned plots may indicate that thinning reduced light limitation enough to prevent the shading effect. However, because the range of basal area values was narrower in thinned plots than in control plots, it remains unclear whether the weaker relationship reflects a biological effect of thinning reducing shading, or simply the lower variation in basal area within thinned plots.

Oak basal area was not associated with higher oak seedling density overall, which is consistent with the results of Götmark (2007), who found no effect of oak basal area on oak seedling survival and growth. In control plots, oak basal area was associated with lower seedling density, while there was no significant effect in thinned plots, mirroring the pattern observed for total basal area, as oak basal area is already captured within total basal area. These results contrast with Annighöfer et al. (2015), who found that oak basal area was associated with higher density of oak seedlings in an early development stage. Such classification of seedlings in different stages was not done in this study, which could explain the difference, as the density of young seedlings may be more dependent on seed source proximity. The sites in this study were initially chosen for the project because they are oak-rich, suggesting that mature oaks as a seed source may not have been limiting for seedling establishment. This may indicate that the negative effects associated with higher oak basal area, such as increased shading, were more influential than any positive seed source effect.

Despite the expected importance of light availability for oak regeneration, canopy openness did not predict oak seedling density in this study, contrasting findings from previous studies (Götmark, 2007; Leonardsson et al., 2015). Over the two decades, mean canopy openness values decreased from 24.6% to 16.1% in control plots, and from 51.1% to 17.2% in thinned plots, resulting in canopy openness being very similar between treatments in 2025. Although oak seedling density did not differ significantly between treatments in the late period, density declined in control plots while remaining relatively stable in thinned plots. Given that there is still a marginally significant difference in oak density in the late period despite a minor difference in canopy openness, it is

unlikely that the mechanism behind the oak regeneration difference is the current light availability alone. Instead, regeneration dynamics may partly reflect legacy effects of the initially more open conditions following thinning, such as enhanced seedling establishment during the early period or altered competition dynamics that persisted after canopy closure.

Methodological factors may have partly contributed to the weak relationship between canopy openness and oak seedling density. Although canopy openness is a commonly used proxy, it is not a perfect measurement of light availability in the understory, and smartphone photography combined with ImageJ analysis does not provide an absolute measurement of canopy openness (Smith & Ramsay, 2018). In some of the studied forests, species such as *Corylus avellana* and *Frangula alnus* had formed dense subcanopy patches, and photographs taken at breast height may therefore have underestimated canopy openness due to these leaves appearing larger near the camera, which could partly explain the weak relationship. Canopy measurements differed slightly between survey years. While canopy was estimated using image analysis in 2003 and 2025, it was visually estimated in 2005. The photos were taken at seedling height in 2003 and at breast height in 2025, and image analysis likely also differed between these years. These inconsistencies may have introduced noise into canopy comparisons across time but are unlikely to explain the absence of the expected relationship between canopy openness and oak density, as this relationship was also weak within individual survey periods.

McCarthy & Robison (2003) found no relationship between light and oak regeneration in mixed-oak forests and discussed that light might not be a limiting factor for oak establishment and growth in their study system. Other possible factors affecting oak regeneration in the studied forests include browsing pressure and soil conditions. Many studies have linked browsing by deer and moose to the decline of oak regeneration (Annighöfer et al., 2015; Götmark, Berglund, et al., 2005; Leonardsson et al., 2015; Petersson et al., 2019), and browsing damage was frequently observed on oak seedlings during fieldwork, suggesting that browsing may have been an important confounding factor. Soil pH did not predict oak seedling density, consistent with Götmark (2007), although these results are not fully independent, as the early period measurements in this study overlap with those of Götmark (2007). However, these results are reasonable, as *Quercus robur* and *Q. petraea* are tolerant across the pH range (3.61–6.60) observed (Ducousso & Bordacs, 2003). Annighöfer et al. (2015) observed higher seedling densities on sites with lower nutrient availability and pH, conditions they considered unfavourable and therefore associated with less competition. Similarly, Kelly (2002) reported increased mortality when seedlings in a clearing were fertilised with nitrogen only, and Franzén et al. (2024) found that oak regeneration decreased with increasing nitrogen levels, likely due to higher competition.

Below-ground competition could also play an important role that this study did not assess. Shading could make oak seedlings more susceptible to root competition, as it tends to shift resource allocation from root to shoot growth (van Hees, 1997). Götmark (2007) noted that apart from increased light, thinning might have improved seedling survival due to reduced below-ground competition from cut trees and shrubs. This mechanism could partly explain the differing basal area effects between treatments observed in this study. In control plots, higher basal area might not only reflect greater shading but also stronger below-ground competition, amplifying the negative effect on oak seedling density. In thinned plots, removal of competing trees and shrubs may have reduced root competition, possibly weakening the relationship between basal area and oak density, and facilitating seedling establishment.

The effect of competition

Competitor seedling density was associated with higher oak density, with one possible explanation for this being co-occurrence in productive subplots, where favourable conditions may support

higher densities of both oaks and competitor species. Although facilitation of oak seedlings by other species protecting them from browsing and therefore improving their survival has been observed in other studies (Jensen et al., 2012; Kelly, 2002), this mechanism could not be assessed in the present study. Competitor density and period explained little of the observed pattern in oak seedling density, while spatial heterogeneity accounted for a substantially larger share of the variance. The effect of competitor density did not differ between treatments or periods, suggesting that the relationship may reflect a general site productivity pattern rather than a treatment-specific response. Of the individual competitor species, only densities of *Fraxinus excelsior* and *Betula* spp. appeared to predict oak seedling density. However, these species were highly concentrated at single sites and plots, suggesting that these effects reflect site-level variation rather than real species effects.

Total competitor density did not predict mean oak height, suggesting that the number of competitors in the subplots does not hinder oak growth. This is contrasting the findings of Jensen & Löf (2017), who observed interspecific competition restricting oak height growth after four growing seasons. Mean competitor height was positively associated with mean oak height, although this effect was not large, and may also reflect co-occurrence in subplots with favourable conditions.

Mean oak height at subplot level did not differ between treatments, whereas individual seedling heights did. While individual seedling height captures variation within subplots, this variability is smoothed out when oak height is averaged at subplot level. The absence of a difference on subplot level likely also reflects the small sample size of 51 subplots compared to 687 individual height observations. In thinned plots, individual oak seedlings were 37.4% taller and individual competitors 52.2% taller compared to control plots, suggesting that thinning may have benefitted the growth of both oak and competitor seedlings, while the reduced light availability may have limited seedling growth in control plots.

Oak height variability was 65.5% greater in thinned plots, indicating a heterogeneous growth response to thinning. This suggests that some individuals could have benefitted strongly from increased light or growing space, while others showed more limited growth responses. For example, seedlings already growing in more open or more shaded microsites may have responded differently, as thinning could have amplified these existing differences. Another possible explanation is differences in establishment timing, where seedlings established before thinning may have been more adapted to shaded conditions and therefore grown more slowly, while seedlings established after thinning may have benefitted from higher light availability and grown faster. The height variation between treatments was greater for oak than for competitor species, suggesting that oak seedlings responded more variably to thinning. Competitor seedling heights appeared less variable, although this should be interpreted with caution, as competitor species were generally taller than oaks and the 130 cm seedling threshold likely excluded taller individuals from the dataset, reducing the observed variation.

Treatment did not affect the ratio between mean competitor height and mean oak height, implying that thinning did not alter how oaks are keeping up with competitors. Jensen & Löf (2017) similarly observed that oaks initially kept up with the growth of competitors, but this effect faded after just four growing seasons. In this study, competitor density did not affect height ratio, suggesting that competitors were not relatively taller in denser subplots. Furthermore, height ratio did not predict oak seedling density, suggesting that subplots with relatively taller competitors were not associated with lower oak seedling densities. Together, these results provide no clear evidence of competitive suppression of oak seedlings by competitor species. However, height analyses were restricted to individuals shorter than 130 cm, as exact heights were not recorded for taller individuals, but seedling densities included individuals taller than 130 cm (DBH < 5 cm). This could have led to

uncertainty in the results, as the height ratio likely underestimates the competitive height advantage of the tallest competitors. The result of competitor density not affecting height ratio should therefore be interpreted with caution, as subplots with many tall competitors would show high density but the height ratio cannot capture those individuals, potentially masking a relationship.

Management implications

The most important practical finding of this study is that while thinning might help maintain more stable oak regeneration compared to leaving a forest for free development, site selection matters most. The conservation thinning did not produce consistent results across all sites, neither in the short term nor the long term. Of the five sites included in this study, Karla showed the best oak regeneration, while other sites such as Sandviksås showed poor regeneration throughout the study period (Table 3). Field observations suggested that this difference might have been apparent before thinning, as Karla had some oak regeneration even in the control plot, while the control plot at Sandviksås was dominated by spruce and had very few oak seedlings, suggesting that these sites might not respond similarly to thinning. Therefore, conservation thinning efforts should be targeted at sites with intrinsic regeneration potential, like Karla. Knowing other site characteristics, such as browsing pressure, is also important for informing management decisions.

The results of this study suggest that the effects of a single thinning on light availability did not persist over 22 years, as canopy openness had converged between treatments by the late period. This indicates that repeated thinning at shorter intervals may be needed. Although this study did not find evidence for competitive suppression of oak seedlings, other studies have highlighted the importance of continuously controlling competitor density (Annighöfer et al., 2015; Humphrey & Swaine, 1997; Leonardsson et al., 2015), and of applying repeated disturbances, such as partial harvest and prescribed burning (Iverson et al., 2017). Therefore, additional thinning at these sites should be considered, and future long-term studies with more frequent measurements would help determine the optimal thinning interval. In addition, removing some of the understory trees for biofuel could make conservation thinning more worthwhile for individual forest owners (Lennartsson et al., 2017).

Limitations

This study would have benefitted from a larger sample size. A higher number of study sites would have improved the statistical power to detect treatment effects, which was limited by the inclusion of only five sites. In addition, the relatively large number of predictors and interactions may have been high for the available dataset, especially because some models' sample size was further reduced due to missing environmental data. This was mainly a limitation of the historical data, since most environmental variables were measured across all subplots in 2025. However, it would have been ideal if basal area had been measured in the full 0.3 ha area that included both transects in 2025, allowing the basal area analyses to use all subplot data. Exact seedling height measurements were only available for 2025, preventing temporal comparisons of height development. Restricting competitor density analyses to individuals shorter than 130 cm would have ensured consistency with the height analyses and enabled more reliable interpretation of models where density and height ratio were analysed together. Had distances between seedlings been measured, competitor indices could have been used to analyse competition effects in more detail.

A larger dataset would also have enabled more detailed ecological analyses. For example, competitor species could have been divided into functional groups (e.g. shade-tolerant and light-demanding species, or shrubs, broadleaves and conifers), which could have revealed whether different competitor types responded differently to thinning and whether the positive relationship

between competitor and oak density was driven by specific functional groups. This information would help inform future management decisions. Analysing the effects of environmental variables on oak seedling height, competitor seedling height and density, as well as separating oak seedlings into different size or age classes, could also have provided additional ecological insight.

Several ecological processes not accounted for in this study might have influenced the results. Ungulate browsing is a major factor affecting oak regeneration and has been reported in the same study areas (Götmark, Berglund, et al., 2005; Leonardsson et al., 2015), but no browsing data were collected in this study. This is a meaningful limitation because browsing shapes both seedling density and height, and these effects are difficult to separate from competition effects without enclosure data. Leonardsson et al. (2015) demonstrated that enclosures promoted oak regeneration after conservation thinning at the same sites, suggesting that the thinning effects measured in this study may represent a net outcome after browsing suppression, potentially underestimating the true regeneration response to thinning. Browsing also tends to maintain seedlings in a stunted state, which likely contributed to the low height values recorded, as browsing damage was observed on several seedlings during fieldwork. Oak regeneration is also strongly affected by masting years. Götmark (2007) reported that a masting year in 2000 had produced many oak seedlings that were still dominating after thinning. This could have influenced differences in seedling density between periods, as no information on mast events closer to 2025 was available. Climate warming and drought events during the study period may also have affected acorn production, seedling establishment, survival and growth in ways that could not be accounted for in this study.

Conclusions

This study evaluated whether conservation thinning promotes oak regeneration over a 22-year period. Overall, the results suggest that thinning helped maintain oak seedling densities rather than increase them, with densities remaining relatively stable in thinned plots, while declining substantially in control plots. However, these effects were modest, differences between treatments were generally not statistically significant and responses varied considerably among sites. The strong influence of site- and subplot-level variation suggests that local environmental conditions are key determinants of oak regeneration dynamics and can strongly mediate the outcomes of management interventions. The convergence of canopy openness between treatments over time suggests that the benefits of a single thinning intervention may diminish as stands develop. These findings highlight the importance of adaptive, site-specific management and suggest that repeated interventions may be necessary to support the long-term conservation of oak populations.

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Appendix 1: Popular science summary

Thinning can slow the decline of oak regeneration – But only in the right forests

Perhaps you have heard about the fact that oaks support a wide range of biodiversity. This means that oaks function as a home or source of food for hundreds of species, such as birds and insects, as well as lichens and fungi. Therefore, oaks are often called keystone species. But have you ever heard of oak decline? It's a phenomenon characterised by damage and mortality of large oaks, as well as poor regeneration. And you can probably imagine the consequences of old oaks disappearing, without enough younger ones taking their place, leading to other tree species slowly replacing them. Eventually, many of the species dependent on oaks could disappear from the landscape entirely.

Thinning as a solution?

To tackle this problem, a group of researchers at the University of Gothenburg started the Swedish Oak Project. Knowing that oaks are light-demanding and therefore sensitive to other competing species that shade them out, they suspected that this could be part of the reason behind poor regeneration. They carried out conservation thinning in oak-rich forests in southern Sweden between 2002–2003, removing a significant portion of the surrounding trees. Each forest had two plots of one hectare, one thinned and the other left untouched for comparison. In the following years, they studied the effects, with promising results. Just two years after thinning, they could see increased numbers of oak seedlings in the thinned plots and concluded that thinning favours oak regeneration by opening the canopy and giving more light to the oaks.

What are the long-term effects?

For my master's thesis, I decided to study if the effects could still be seen 22 years after thinning. I went back to five of the same forests and counted oak seedlings in survey plots, measured surrounding trees and canopy openness.

The key finding was that the effects of thinning varied greatly between the five forests. Some sites, like Karla, showed relatively good oak regeneration throughout the study period, while others, like Sandviksås, had very few oak seedlings in both thinned and unthinned plots. This suggests that thinning is most likely to benefit forests that already have some natural potential for oak regeneration. The results also suggest that thinning has had a lasting stabilising effect. In the unthinned forests, the number of oak seedlings decreased by half since the earlier surveys, while in the thinned forests, seedling numbers remained more stable. In other words, the thinning has not increased oak regeneration in the long term, but it appears to have prevented a decline. Surprisingly, canopy openness did not influence oak seedling density, supporting the idea that other site-specific conditions, rather than light alone, might be the main driver of oak regeneration.

Is one thinning enough?

These findings suggest that while a single thinning can slow the decline, it may not be sufficient in the long term. Over the past two decades, the canopy has closed again in the thinned forests, meaning the more open conditions that thinning originally created have disappeared. Repeated thinning could therefore be necessary to maintain better conditions over time. It might even drive the increase in oak regeneration that a single thinning alone did not achieve. Without such efforts, the stabilising effect of thinning may eventually fade, and the decline in oak regeneration could continue, with consequences for the many species that depend on oak-rich forests.

Appendix 2: List of all packages used in the analysis

Package	Reference
DHARMa	Hartig et al. (2024)
dplyr	Wickham, François, et al. (2026)
emmeans	Lenth et al. (2026)
flextable	Gohel et al. (2026)
ggplot2	Wickham (2016)
glmmTMB	Brooks et al., 2017; McGillicuddy et al. (2025)
Hmisc	Harrell et al. (2026)
lme4	Bates et al. (2015)
lmerTest	Kuznetsova et al. (2017)
MuMIn	Bartoń (2026)
patchwork	Pedersen (2025)
performance	Lüdtke et al. (2021)
readr	Wickham, Hester, et al. (2026)
tidyr	Wickham et al. (2025)

Appendix 3: List of all analyses reported in the text

Model: effect of thinning on oak seedling density through time																																																			
Model formula	glmmTMB(oak_count ~ treatment * period + offset(log(area_m2)) + (1 site/plot/transect/subplot), data = oaks_noshoots, family = nbinom2)																																																		
Model output	Random effects: Conditional model: <table><thead><tr><th>Groups</th><th>Name</th><th>Variance</th><th>Std.Dev.</th></tr></thead><tbody><tr><td>subplot:transect:plot:site</td><td>(Intercept)</td><td>0.83406</td><td>0.9133</td></tr><tr><td>transect:plot:site</td><td>(Intercept)</td><td>0.07776</td><td>0.2789</td></tr><tr><td>plot:site</td><td>(Intercept)</td><td>0.18506</td><td>0.4302</td></tr><tr><td>site</td><td>(Intercept)</td><td>0.44961</td><td>0.6705</td></tr></tbody></table> <table><thead><tr><th></th><th>Estimate</th><th>Std. Error</th><th>z value</th><th>Pr(> z)</th></tr></thead><tbody><tr><td>(Intercept)</td><td>0.2445</td><td>0.4143</td><td>0.590</td><td>0.555063</td></tr><tr><td>treatmentthinned</td><td>-0.1654</td><td>0.4105</td><td>-0.403</td><td>0.687066</td></tr><tr><td>periodlate</td><td>-0.7782</td><td>0.2120</td><td>-3.670</td><td>0.000242 ***</td></tr><tr><td>treatmentthinned:periodlate</td><td>0.9611</td><td>0.3216</td><td>2.988</td><td>0.002806 **</td></tr></tbody></table> Conditional R2: 0.687 Marginal R2: 0.036						Groups	Name	Variance	Std.Dev.	subplot:transect:plot:site	(Intercept)	0.83406	0.9133	transect:plot:site	(Intercept)	0.07776	0.2789	plot:site	(Intercept)	0.18506	0.4302	site	(Intercept)	0.44961	0.6705		Estimate	Std. Error	z value	Pr(> z)	(Intercept)	0.2445	0.4143	0.590	0.555063	treatmentthinned	-0.1654	0.4105	-0.403	0.687066	periodlate	-0.7782	0.2120	-3.670	0.000242 ***	treatmentthinned:periodlate	0.9611	0.3216	2.988	0.002806 **
Groups	Name	Variance	Std.Dev.																																																
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treatmentthinned:periodlate	0.9611	0.3216	2.988	0.002806 **																																															
Post-hoc formula	emm1 <- emmeans(m4_noshoots, ~ treatment period, type = "response", at = list(area_m2 = 1)) pairs(emm1) emm2 <- emmeans(m4_noshoots, ~ period treatment, type = "response", at = list(area_m2 = 1)) pairs(emm2)																																																		
Post-hoc output	period = early: <table><thead><tr><th>treatment</th><th>response</th><th>SE</th><th>df</th><th>asyp.LCL</th><th>asyp.UCL</th></tr></thead><tbody><tr><td>control</td><td>1.277</td><td>0.529</td><td>Inf</td><td>0.567</td><td>2.88</td></tr><tr><td>thinned</td><td>1.082</td><td>0.458</td><td>Inf</td><td>0.472</td><td>2.48</td></tr></tbody></table>						treatment	response	SE	df	asyp.LCL	asyp.UCL	control	1.277	0.529	Inf	0.567	2.88	thinned	1.082	0.458	Inf	0.472	2.48																											
treatment	response	SE	df	asyp.LCL	asyp.UCL																																														
control	1.277	0.529	Inf	0.567	2.88																																														
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	<pre> period = late: treatment response SE df asymp.LCL asymp.UCL control 0.586 0.253 Inf 0.252 1.37 thinned 1.300 0.555 Inf 0.563 3.00 period = early: contrast ratio SE df null z.ratio p.value control / thinned 1.180 0.484 Inf 1 0.403 0.6871 period = late: contrast ratio SE df null z.ratio p.value control / thinned 0.451 0.194 Inf 1 -1.852 0.0641 treatment = control: contrast ratio SE df null z.ratio p.value early / late 2.178 0.462 Inf 1 3.670 0.0002 treatment = thinned: contrast ratio SE df null z.ratio p.value early / late 0.833 0.199 Inf 1 -0.766 0.4439 </pre>
Model: effect of thinning on oak seedling density across inventory years, testing 2005 effects using data only for the five sites included in this study	
Model formula	<pre> glmmTMB(oak_count ~ treatment * factor(year) + offset(log(area_m2)) + (1 site/plot/transect/subplot), data = oaks_noshoots, family = nbinom2) </pre>
Model output	<pre> Random effects: Conditional model: Groups Name Variance Std.Dev. subplot:transect:plot:site (Intercept) 0.83277 0.9126 transect:plot:site (Intercept) 0.08228 0.2868 plot:site (Intercept) 0.18596 0.4312 site (Intercept) 0.44493 0.6670 </pre>

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	<pre> (Intercept) 2.494135 0.154284 14.015724 16.166 1.85e-10 *** mean_competitor_height 0.006664 0.001974 44.698587 3.376 0.00153 ** R2m R2c 0.09659137 0.7129234 </pre>
Model: effects of mean competitor seedling height and thinning on mean oak seedling height	
Model formula	<pre> lmer(log(mean_oak_height) ~ mean_competitor_height + treatment + (1 plot_id), data = height_index) </pre>
Model output	<pre> Random effects: Groups Name Variance Std.Dev. plot_id (Intercept) 0.14753 0.3841 Residual 0.07808 0.2794 Estimate Std. Error df t value Pr(> t) (Intercept) 2.311508 0.192018 9.859695 12.038 3.24e-07*** mean_competitor_height 0.006162 0.002001 43.049076 3.080 0.0036** treatmentthinned 0.390255 0.263899 8.790053 1.479 0.1741 </pre>
Model: effect of thinning on individual oak seedling height	
Model formula	<pre> glmmTMB(height_cm ~ treatment + (1 site/subplot_id), family = Gamma(link = "log"), dispformula = ~treatment, data = oak_heights) </pre>
Model output	<pre> Random effects: Conditional model: Groups Name Variance Std.Dev. subplot_id:site (Intercept) 0.08159 0.2856 site (Intercept) 0.15048 0.3879 Estimate Std. Error z value Pr(> z) (Intercept) 2.69126 0.18852 14.276 < 2e-16 *** </pre>

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