ACTA UNIVERSITATIS AGRICULTURAE SUECIAE

SLU

DOCTORAL THESIS NO. 2026:9
FACULTY OF FOREST SCIENCES

Oaks under continuous cover forestry

Recruitment challenges and biodiversity implications

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SWEDISH UNIVERSITY
OF AGRICULTURAL
SCIENCES

DOCTORAL THESIS
Alnarp 2026

Acta Universitatis Agriculturae Sueciae
2026:9

Cover: Oak mixed forest, adapted from Appl (n.d.). *Architectural drawings, minimal style CAD tree with roots line drawing and tree grunge vector: view, set of section wetland forest outline for landscape design drawing*. Adobe Stock (asset no. 1668585402).

ISSN 1652-6880
ISBN (print version) 978-91-8124-206-5
ISBN (electronic version) 978-91-8124-226-3
https//doi.org/10.54612/a.3jm1o6aoal

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Print: SLU Grafisk service, Alnarp 2026

Oaks under continuous cover forestry – Recruitment challenges and biodiversity implications

Abstract

Oak forests provide essential ecosystem services and support a disproportionate share of forest biodiversity in temperate regions, yet their long-term persistence is increasingly limited by insufficient recruitment. Although regeneration failure is well documented, comparatively little is known about growth of oak recruits in intermediate size classes (dbh 5–20 cm), particularly near the northern distribution limit. Continuous cover forestry (CCF) is increasingly promoted as a management approach to reconcile timber production, biodiversity conservation, and climate adaptation, with selective cutting as a management tool. This thesis investigated how selective cutting, stand structure, and climate affect oak recruitment and oak-associated biodiversity by combining long-term observational data from the Swedish National Forest Inventory with field experiments across southern Sweden. Across studies, oak recruitment was consistently constrained by competitive stand conditions, particularly high stand basal area, stem density, and proportions of shade-tolerant species. Selective cutting showed no short-term effect on oak recruit density but was associated with increased diameter growth of oak recruits after a sixteen-year period. Selective cutting also supported epiphytic lichen species richness and evenness, while unmanaged stands showed declines, although foliose lichens decreased across treatments which could not be fully explained. Long-term inventory data further revealed a pronounced decline in growth of oak recruits over the past four decades that persisted even after accounting for stand structure, site conditions, and climatic variability. Overall, our results show that successful oak recruitment under CCF requires balancing continuous forest cover with sufficiently strong or repeated interventions to reduce competition and maintain light availability. Integrating recruitment objectives with biodiversity goals is therefore essential to ensure the long-term persistence of oak-dominated forests under ongoing climate change.

Keywords: *Quercus*, pedunculate oak, sessile oak, oak recruitment, selective cutting, national forest inventory, stand structure, epiphytes, temperate forests

Ekar under kontinuitetsskogsbruk – utmaningar för rekrytering av unga ekar och konsekvenser för biologisk mångfald

Abstract

Skogar dominerade av ek tillhandahåller viktiga ekosystemtjänster och hyser en oproportionerligt stor andel av den biologiska mångfalden i tempererade regioner, men deras långsiktiga fortlevnad begränsas i allt högre grad av bristande föryngring och rekrytering. Trots att misslyckad föryngring är väl dokumenterad är kunskapen fortfarande begränsad om tillväxten hos unga ekar i mellanliggande storleksklasser, så kallade rekryter (dbh 5–20 cm), särskilt nära ekens nordliga utbredningsgräns. Kontinuitetsskogsbruk lyfts allt oftare fram som ett sätt att förena virkesproduktion, biologisk mångfald och klimatanpassning, där plockhuggning utgör ett centralt verktyg. Denna avhandling undersöker hur plockhuggning, beståndsstruktur och klimat påverkar rekrytering av ek och associerad biologisk mångfald genom att kombinera långsiktiga data från Riksskogstaxeringen med fältexperiment i södra Sverige. Sammantaget begränsades rekryteringen av ek konsekvent av konkurrens i bestånden, särskilt vid hög grundyta, hög stamantalstäthet och en stor andel skuggtoleranta trädslag. Plockhuggning gav inga kortsiktiga effekter på tätheten av rekryter av ek, men var kopplad till ökad diametertillväxt efter sexton år. Samtidigt gynnade plockhuggning artrikedom och jämnhet hos epifytiska lavar, medan minskningar observerades i obehandlade bestånd, även om foliosa lavar minskade i båda behandlingarna av orsaker som inte fullt ut kunde förklaras. Långsiktiga data från Riksskogstaxeringen visade dessutom en tydlig nedgång i tillväxten hos rekryter av ek under de senaste fyra decennierna, som kvarstod även efter att beståndsstruktur, ståndortsförhållanden och klimatvariation beaktats. Sammantaget visar resultaten att framgångsrik rekrytering av ek under kontinuitetsskogsbruk kräver en avvägning mellan att bibehålla krontäckning och att genomföra tillräckligt kraftiga eller upprepade åtgärder för att minska konkurrens och säkerställa goda ljusförhållanden. Att integrera mål för rekrytering av ekmed mål för biologisk mångfald är därför avgörande för att säkerställa den långsiktiga fortlevnaden av skogar dominerade av ek i ett föränderligt klimat.

Keywords: *Quercus*, skogsek, bergek, ekrekrytering, selektiv avverkning, Rikskogstaxeringen, beståndstruktur, epifyter, tempererade skogar

Dedication

To Maria Laura. Without you, none of this would have happened.

Yesterday is history, tomorrow is a mystery, but today is a gift –
that's why it's called the present.
Master Oogway

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I. **Pohl, N.S.***, Hedwall, P.O., Aldea, J., Felton, A.M., Gardiner, E.S., Muraro, L., Nordén, B., Löf, M. (2025). Effects of stand structural attributes on oak recruitment in mixed temperate forests. Forest Ecology and Management, Volume 586 (122721), https://doi.org/10.1016/j.foreco.2025.122721

II. Moe, K.T.*, **Pohl, N.S.**, Aldea, J., Löf, M. Effects of target diameter cutting on oak recruitment in a multilayered mixed conifer-broadleaved stand in southern Sweden. Forest Ecology and Management, Volume 604 (123519), https://doi.org/10.1016/j.foreco.2026.123519

III. **Pohl, N.S.***, Hedwall, P.O., Aldea, J., Felton, A.M., Gardiner, E.S., Löf, M., Nordén, B. Selective cutting buffers against long-term decline in epiphytic lichen diversity. (manuscript)

IV. **Pohl, N.S.*,** Hedwall, P.O., Aldea, J., Felton, A.M., Gardiner, E.S., Löf, M. Four decades of declining growth of oak recruits in Sweden: influence of stand structure and climate. (manuscript)

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The contribution of Nora Sophie Pohl to the papers included in this thesis was as follows:

I. **NSP**, ML, AMF, and BN developed the research design and methodology. **NSP** conducted field work for data collection. **NSP**, performed the data analysis together with JA, POH, and ML. **NSP** and ML wrote the first draft of the manuscript and developed it further in collaboration with all other co-authors.

II. KTM, **NSP** and ML developed the research design and methodology. KTM performed the data analysis and wrote the first draft of the manuscript together with **NSP** and ML. All authors developed it further and contributed to the final version.

III. BN developed the research design and methodology. BN and **NSP** conducted field work for data collection. **NSP** and POH performed the data analysis and interpreted the results together with BN, AMF, JA, ML, ESG. **NSP** wrote the first draft of the manuscript and all authors contributed to the final version of this manuscript.

IV. **NSP**, POH, and ML developed the research idea and methodology. **NSP**, POH, and JA performed the data analysis and interpreted the results together with AMF, ESG, and ML. **NSP** wrote the first draft of the manuscript and developed it further with POH, JA, AMF, and ML.

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Abbreviations

BAL	Basal area of larger trees than individual oak recruit
CCF	Continuous cover forestry
GLMM	Generalized Linear Mixed Model
NFI	National Forest Inventory
PBAI	Period Basal Area Increment
SCA	Shade-casting ability
TDC	Target diameter cutting
TDC2	Target diameter cutting with modified target diameter for Norway spruce
TDCS	Target diameter cutting with soil scarification

1. Introduction

Forest ecosystems worldwide are increasingly affected by climate change and anthropogenic pressures, including large-scale deforestation, forest degradation, and profound alterations of historically prevailing disturbance regimes. The expansion of production forests and forest plantations has contributed to substantial losses of forest biodiversity, while simultaneously increasing the reliance on remaining, more structurally diverse forest ecosystems to buffer biodiversity decline. Globally, forests cover more than four billion hectares of land, of which temperate forests account for approximately 17 percent (FAO, 2025). In Europe, forests cover about 35 percent of the land surface, with Sweden exhibiting one of the highest forest cover proportions at approximately 69 percent (Forest Europe, 2020).

Climate change has been shown to exert strong impacts on forest ecosystems, primarily through an increasing frequency and intensity of drought events, heat waves, and extreme precipitation (Seidl et al., 2017; Spioni et al., 2018, Hari et al., 2020). These abiotic stressors are often compounded by biotic disturbances, including insect outbreaks, fungal pathogens, and secondary pest infestations, which can further increase forest vulnerability (Meyer et al., 2015). Increasing evidence indicates that some foundational tree genera, including *Fraxinus* spp., *Ulmus* spp., and *Quercus* spp., have already experienced substantial declines under interacting abiotic and biotic stressors, with documented negative consequences for associated biodiversity that may, in turn, compromise the long-term resilience of forest ecosystems (Martín et al., 2010; Mitchell et al., 2019; Hultberg et al., 2020; Mitchell et al., 2022). In response, forest management strategies increasingly emphasize enhancing forest resilience and adaptive capacity to maintain ecosystem functioning under changing environmental conditions, a priority that is explicitly highlighted at the European level in the EU Biodiversity Strategy for 2030 through the promotion of biodiversity-oriented sustainable forest management practices (European Commission, 2021; Felton et al., 2024).

Within this context, oak forests represent multifunctional ecosystems that deliver a wide range of ecosystem services, including timber production, watershed protection, recreational opportunities, and a disproportionate contribution to forest biodiversity (Norman et al., 2010; Stavi et al., 2022). Oak-dominated systems are often characterized by high structural complexity, a feature that has been associated with increased resilience to climatic variability and disturbances (Felton et al., 2024). Despite these attributes, the long-term persistence of oak forests is increasingly threatened by insufficient regeneration and recruitment, which limits the development of future canopy trees and compromises the capacity of these ecosystems to maintain their ecological functions over time.

1.1 Oaks

The genus *Quercus* (hereafter referred to as oak) comprises approximately 435 species, with some estimates suggesting up to 600 species, divided into the two subgenera *Quercus* and *Cerris*, which include five and three sections, respectively (Denk et al., 2017). As a result, oak is among the most species-rich genera of temperate trees in the Northern Hemisphere (Gíl-Pelegrín et al., 2017), with Mexico alone harbouring 65 percent of the world's oak species (Hipp et al., 2017). Oaks are currently distributed from equatorial regions to approximately 60°N latitude in Europe and occur across a wide elevational range, from sea level to approximately 4000 m in China (Yang et al., 2020). Their habitats encompass a wide ecological range, extending from dense bottomland forests to open grasslands and savannas, and from alkaline to acidic soils (Abrams, 1992), where they occur either as large canopy trees or as small shrubs (Nixon, 2006).

In Europe, the sections *Quercus*, *Ilex*, and *Cerris* are represented, with *Quercus* being widely distributed across the continent and *Ilex* and *Cerris* occurring predominantly in southern Europe. Together, these sections comprise between 22 (Median et al., 2024) and 30 (Lyubenova et al., 2024) oak species, of which pedunculate oak (*Q. robur* L.) and sessile oak (*Q. petraea* (Matt.) Liebl.) are the most widespread (Nicolescu et al., 2025). These two species are ecologically and morphologically similar and are known to hybridize (Truffaut et al., 2017). Both are long-lived trees, with documented lifespan exceeding 1000 years, and can attain heights of up to 40 m and stem diameters ranging up to four meters. Pedunculate oak has a slightly broader geographic distribution, whereas sessile oak extends to higher elevations, exceeding 2000 m in some regions (Eaton et al., 2016).

Although both species occupy a wide range of habitats, pedunculate oak typically favours wetter and heavier soils, while sessile oak exhibits greater drought tolerance and is more commonly found on lighter, well-drained soils (Eaton et al., 2016). Both species are predicted to retain substantial portions of their current distribution ranges under future climate change scenarios, with potential expansion at their northern limits (Dyderski et al., 2025).

1.2 Multifunctional importance of oak forests

Oak forests have played a central role throughout human history and have been culturally and economically associated with societies for millennia. Acorns have been used as a food source since the Palaeolithic period (Chassé, 2016) and have even been referred to as the "bread of life" (Anderson, 2007). In North America, California black oak (*Q. kelloggii* Newb.) has been described as a "cultural keystone" species for indigenous communities in California and Oregon (Long et al., 2016), while in the Central Himalaya, banj oak (*Q. leucotrichophora* A.Camus) has been characterized as the "people's species" due to its importance for local livelihood (Singh and Singh, 1986). In these regions, oak woodlands provide multiple ecosystem services, including forage for livestock, firewood, timber, erosion control, and watershed protection. Similarly, on the Iberian Peninsula, holm oak (*Q. rotundifolia* Lam.) and cork oak (*Q. suber* L.) form characteristic woodlands known as "montado" in Portugal and "dehesa" in Spain, which are primarily managed for pig grazing and cork production (Lopes-Fernandes et al., 2024).

Historically, oak has been extensively used as a source of firewood and timber (Ruiz-Alonso et al., 2017). Coppicing was a widespread management practice, particularly in southern Europe, taking advantage of the strong resprouting capacity of oaks following cutting (Giovannini et al., 1992). With the decline in demand for firewood and charcoal, this traditional practice has largely been abandoned, resulting in many overaged coppice stands currently undergoing conversion to high forest systems. Oak timber has also played a crucial role in naval construction in many countries (Reboredo and Pais, 2014; Wing, 2012; Lindbladh and Foster, 2010). Another important use of oak wood is cooperage for wine and whiskey production, with white oak (*Q. alba* L.), pedunculate oak, sessile oak, and

Pyrenean oak (*Q. pyrenaica* Willd.) being among the most commonly used species. In addition, oak timber has long been valued for construction, veneer, and furniture due to its hardness and resistance to decay (Riesco Muñoz et al., 2014).

Currently in Europe, pedunculate and sessile oak rank among the most economically valuable and ecologically important deciduous tree species (Eaton et al., 2016). They provide a wide range of ecosystem services, including high quality timber, recreational opportunities, watershed protection, and potentially climate-resilient options for future forest management (Stavi et al., 2022). Oaks also function as keystone and foundation species in temperate forest ecosystems (Lindbladh and Foster, 2010; Franzén et al., 2024), exerting a disproportionate influence on biodiversity and ecosystem functioning (Ellison et al., 2019). Their long lifespan allows the development of stable habitats that can persist for centuries, including in the form of standing and downed dead wood (Paltto et al., 2008). Consequently, oaks support numerous threatened organisms, including invertebrates, lichens, bryophytes, fungi, and birds (Mölder et al. 2019). Although oak forests occupy a small proportion of Sweden's forest area and standing volume, they play, as mentioned, a very important role in biodiversity conservation and recreation. For example, 561 red-listed species are associated with oak in Sweden, of which 326 depend on oak as a key host (SLU Artdatabanken). Because most Swedish forest land is intensively managed for timber production, forests with high conservation value, i.e., many oak-dominated forests, are often set aside, creating ongoing challenges in reconciling biodiversity conservation with the production of high-value timber (Götmark, 2009).

In Sweden, oak forests are largely restricted to the southern temperate region (Figure 1), where they currently account for only 2.4 percent of the total standing volume (Skogsdata, 2025) and are far less abundant than during the previous two millennia (Lindbladh and Foster, 2010). Historical expansion of conifer plantations and intensive agricultural land use has substantially reduced oak-dominated forests (Lindbladh et al., 2014; Bobiec et al., 2018). Consequently, southern Swedish forests are dominated by Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.), which comprise 42 percent and 36 percent of the standing volume, respectively, while birch

(*Betula* spp.) is the most abundant broadleaved genus at 11 percent (Skogsdata, 2025). Oaks are particularly underrepresented in recruitment size classes, accounting for only one percent of the standing volume in the 10 –19 cm diameter class, whereas most oak biomass is concentrated in large trees exceeding 45 cm in diameter (Skogsdata, 2025). Petersson et al. (2019) reported that, although the density of large oak trees increased over time, smaller trees, particularly saplings, did not exhibit a corresponding increase.

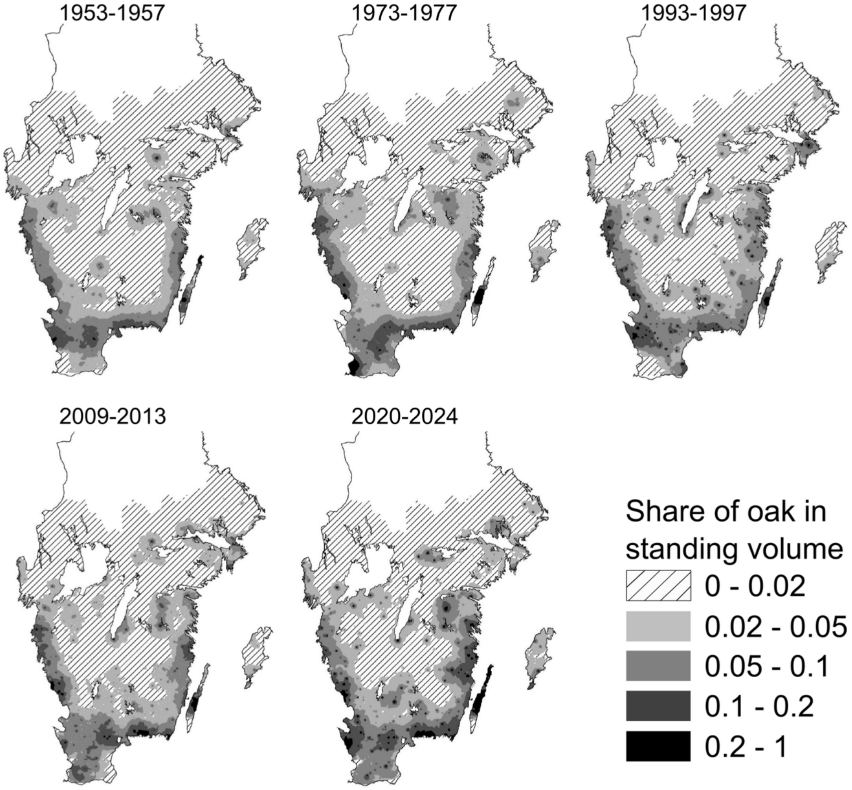


Figure 1. The share of oak (%) in total forest standing volume for 1953–1957, 1973–1977, 1993–1997, 2009–2013, and 2020–2024 in the study area of southern Sweden (National Forest Inventory, 2026).

1.3 Oak forest management

Oak forests represent multifunctional ecosystems that provide ecological, economic, and social values, necessitating management strategies tailored to specific objectives. Historically, high demand for wood and timber was met through coppice and coppice with standards systems (Nicolescu et al., 2025). Coppice-with-standards is a two-layer system characterized by an even-aged coppice understorey and an uneven-aged overstorey managed through single tree selection. Where the primary objective is the production of high-quality timber, shelterwood systems have commonly been applied, for example in France, Germany and Scandinavia (Carbonnier, 1975). These systems typically involve pre-commercial thinning to remove undesired trees, the selection of future crop trees, and repeated thinning to promote their development (Attocchi, 2015). Progressive canopy opening under shelterwood management creates light conditions that facilitate gradual natural regeneration beneath the remaining overstorey, with rotation periods generally ranging from 120 to 200 years depending on species and site quality (von Lüpke, 1998; Attocchi, 2015).

In Europe, semi-open woodlands were also used for centuries as grazing areas for livestock and for production of timber and non-timber forest products (Kirby and Watkins, 2015). As mentioned, these old management systems have declined markedly over the past centuries, and many former coppice areas and wood pastures are now in many cases unmanaged (Gil-Pelegrín et al., 2017). Many oak stands are currently designated as set aside areas for biodiversity conservation, managed with minimal human interventions. However, increasing competition and excessive shading have been shown to negatively affect oak crowns, even for large, mature trees (Spector and Putz, 2006). The widespread suppression of grazing, selective cutting, and low-intensity fires has favoured shade-tolerant and pioneer tree species that compete with and progressively replace oak in the understorey and midstorey, a process described as mesophication (Alexander et al., 2021). Consequently, historical shifts in land tenure and forest management have fundamentally altered the environments that led to oak development. Oak-dominated forests that were formerly maintained as semi-open systems through recurring disturbances such as grazing, selective cutting, and low-intensity fires have increasingly transitioned into dense, closed-canopy forests. In these conditions, oak is frequently underrepresented or entirely absent from younger size classes. These changes raise concerns regarding the long-term persistence of oak populations and the ecosystem functions they support. As a result, minimal intervention strategies have been increasingly debated over the last decade (Mölder et al., 2019). Several studies indicate that active management can help maintain structural diversity and biodiversity in these high values forests (Rohner et al., 2012), while reducing crown shading and thereby improving oak vitality and longevity (Spector and Putz, 2006; Götmark, 2009).

1.3.1 Continuous cover forestry

One approach to reconciling the multifunctionality of oak forests is continuous cover forestry (CCF). CCF is referred by several related terms, including close-to-nature forestry (Mason et al., 1999; Larsen et al. 2022), ecological silviculture (Benecke, 1996; Lähde et al., 1999; Palik et al., 2021), and nature-based forestry (Diaci, 2006), each with its own specific definition. Despite some differences, the concepts share several core principles. These include continuity of forest cover, reliance on natural processes such as natural regeneration, and the promotion of vertical and horizontal structural diversity while accounting for site limitations and maintaining species, size, and genetic diversity. In addition, they emphasize selective individual-tree silviculture, the conservation of old trees and deadwood, protection of endangered species, the promotion of native tree species and provenances, environmentally sensitive harvesting and wildlife management, and the establishment of forest margins (Pommerening, 2023).

In Europe, approximately 22 to 30 percent of forests are managed under some form of CCF (Mason et al., 2022). In Sweden, even-aged clear-cut forestry dominated by Norway spruce and Scots pine remains the prevailing management system, and CCF is still a niche practice (Hertog et al., 2022). Public interest in alternative forestry strategies is nonetheless increasing, driven by the need to balance ecological, economic, and social goals under changing environmental conditions. In Sweden, the Swedish Forest Agency refers to CCF as “clear-cut-free forestry” (*hyggesfritt skogsbruk*), which is currently applied on less than five percent of forest land (Skogsstyrelsen, 2023). In contrast, the Forest Stewardship Council (FSC) Sweden defines CCF (*kontinuitetsskogsbruk*) as management aimed at maintaining or developing forest stratification (FSC Sweden, 2020). Hertog et al. (2022)

identified several barriers to wider implementation of CCF in Sweden, including the dominance of traditional forestry regimes in timber markets, legislation, education, sectoral culture, and research priorities, as well as limited economic incentives.

In essence, CCF aims to maintain a continuous, structurally heterogeneous forests ecosystem that relies on natural regeneration, self-thinning, and the co-existence of multiple native or site-adapted tree species across all size classes, while minimizing silvicultural interventions and conserving associated biodiversity. Although CCF is not a new silvicultural approach but has been practiced for centuries, it has gained renewed interest as a potential strategy to enhance climate resilience, maintain biodiversity, and ensure economic viability (Pommerening, 2023). One key intervention within CCF is selective cutting, in which individual trees are harvested based on species, size, or quality, rendering the traditional concept of a fixed rotation period largely obsolete and enabling more targeted, site-adapted management aligned with specific objectives (Pommerening, 2023).

Many oak-dominated forests are characterized by high structural complexity, a strong association with biodiversity conservation values. Sustaining the continuity of these systems therefore often depends on targeted silvicultural interventions that maintain ecosystem functioning while supporting long-term stand development. Continuous cover forestry therefore represents a potential management framework for reconciling economic objectives, such as the production of high-quality timber, with biodiversity conservation in structurally complex oak forests. However, this approach requires a careful balance between maintaining low intervention intensity, which may inadvertently favour shade-tolerant competitors, and applying sufficient interventions to create the light conditions necessary to promote oak recruitment.

1.4 Oak recruitment challenges

Despite the broad ecological amplitude, functional diversity, and adaptive capacity of oaks, their regeneration and recruitment into the canopy have declined across much of their natural range (for example Watt, 1919; Götmark et al., 2005; Dey, 2014). Historical and ongoing changes in forest management have promoted denser, closed-canopy forest conditions increasingly dominated by shade-tolerant tree species (Lindbladh et al., 2014; Bobiec et al., 2018). Under such conditions, oaks often persist as dominant or co-dominant components of the overstorey, while being largely absent from the understorey and midstorey, indicating a pronounced bottleneck in regeneration and recruitment. This pattern has been documented across temperate regions, where species such as European beech (*Fagus sylvatica* L.), Norway spruce, red maple (*Acer rubrum* L.), and yellow-poplar (*Liriodendron tulipifera* L.) frequently outcompete oak during early developmental stages (Rohner et al., 2012; Dey, 2014).

Oak regeneration and recruitment represent two closely linked stages in the progression from seedling establishment to the development of mature canopy trees and are governed by a complex interplay of abiotic and biotic factors, including light availability, stand structure, site conditions, soil properties, competing vegetation, herbivory, and pathogen pressure (Kohler et al., 2020). While natural regeneration ensures the establishment of oak seedlings and saplings, recruitment refers to the subsequent transition of established individuals into pole-sized trees and intermediate or codominant positions in the overstory. Therefore, recruitment is an essential process for sustaining the oak component in a stand. Although oak seedlings may establish under a broad range of environmental conditions, successful oak recruitment into larger size classes is highly contingent on sufficient light availability and release from competition. In many current forest systems, particularly those managed without clear-cutting, understorey light levels remain below the threshold required for sustained oak growth. Oak seedlings typically require at least 20 percent of full light to maintain positive height and diameter growth (von Lüpke, 1998; Löf et al., 2007). However, light requirements increase with tree size and age, suggesting that oak recruits may benefit from substantially higher light availability than seedlings (von Lüpke and Hauskeller-Bullerjahn, 1999). Even at these levels, shrubs and more shade-tolerant tree species can suppress oak regeneration through competitive exclusion (Leonardsson et al., 2015; Kohler et al., 2020). As a result, although oak regeneration may be present, recruitment into the canopy often remains limited or fails entirely (Petersson et al., 2019).

These challenges are further compounded under continuous cover forestry (CCF), which aims to maintain permanent forest cover, promote structural diversity, and rely on natural regeneration through selective cutting. While CCF aligns well with biodiversity conservation and climate adaptation objectives, its emphasis on minimal intervention and closed-canopy conditions may inadvertently favour shade-tolerant competitors at the expense of light-demanding species such as oak. Consequently, it remains uncertain whether oak can successfully regenerate and recruit under typical CCF regimes without targeted interventions. For oak-containing stands managed under CCF, successful recruitment likely depends on achieving a delicate balance between maintaining low-intensity management that preserves structural continuity and biodiversity, and applying sufficiently frequent or intensive interventions to create and sustain light conditions conducive to oak development.

Several studies suggest that management approaches combining oak regeneration with selective cutting, gap creation, or disturbance-based interventions can enhance oak regeneration and thus benefit recruitment (for example Stahl-Streit, 2004; Király and Ódor, 2010; Leonardsson et al., 2015; Petersson et al., 2020). However, the effectiveness of such measures is highly context dependent and influenced by site fertility, stand density, competing vegetation, and browsing pressure. Moreover, increasing climate variability may further interact with stand structure to influence oak recruitment dynamics, potentially exacerbating drought stress in shaded understorey conditions or increasing mortality following release. Together, these factors highlight that oak recruitment represents a critical and poorly resolved bottleneck in sustaining oak-dominated and oak-rich forests, particularly in landscapes transitioning toward continuous cover forestry and multifunctional forest management.

1.5 Thesis aims and research questions

The overall objective of this thesis was to advance the understanding of oak recruitment dynamics in temperate forests managed under continuous cover forestry. By integrating long-term observational data with multiple field experiments conducted across the distribution range of oaks in Sweden, the thesis addresses a critical bottleneck affecting the long-term persistence of oak-dominated and oak-rich mixed temperate forests. Specifically, the thesis examines how management interventions, stand structure, and long-term growth patterns influence oak recruitment and associated biodiversity. The thesis addresses the following research questions:

I. How does selective cutting affect oak recruitment under continuous cover forestry?
(addressed in Chapter **I** and **II**)
II. How do stand structural attributes influence oak recruitment density and growth?
(addressed in Chapter **I** and **II**)
III. How does selective cutting affect oak-associated epiphytic diversity?
(addressed in Chapter **III**)
IV. How has oak recruitment growth changed over the last four decades in Sweden?
(addressed in Chapter **IV**)

2. Material and methods

This section provides an overview of the methodologies applied in each chapter of the thesis. In Chapters **I**, **II**, and **IV**, no distinction was made between the two native oak species, pedunculate and sessile oak, as these species largely overlap ecologically and the primary objective was to promote oak recruitment regardless of species identity. Similarly, in Chapter **III**, we did not differentiate because they both host comparable epiphytic communities, are difficult to distinguish based on trunk appearance, and frequently hybridize (Barkman, 1958; Jensen et al., 2009). Additional methodological details are provided in the respective chapters.
In Chapters **I**, **II**, and **IV**, an oak recruit was defined as:

- an oak tree with a dbh ≥ 5.0 cm and ≤ 19.9 cm (Chapter **I**)
- an oak tree with a dbh ≥ 5.0 cm and ≤ 20.0 cm (Chapter **II**)
- an oak tree with a dbh ≥ 10.0 cm and ≤ 20.0 cm (Chapter **IV**)

2.1 Field sites

Chapters **I**, **III**, and **IV** comprise multiple field sites across a wide range of oak distribution in southern Sweden, whereas Chapter **II** is located at one experimental field site in southern Sweden (Tönnersjöheden). Chapter **I** includes 12 experimental sites established in 2016 in approximately 40 to 80-year-old mixed broadleaved forest stands (Figure 2A). These stands exhibited limited evidence of management for timber production or grazing and had regenerated naturally following the abandonment of pastures and hay meadows (Nordén et al., 2019). Most sites were dominated by oak. The field experiment described in Chapter **II** was established in 2006 in a forest stand dominated by Scots pine and Norway spruce (Figure 2A). The original stand was established in 1912 through seeding of Scots pine on *Calluna* spp. heathland. Over time, numerous species have naturally colonized the site, and broadleaved tree species such as oak, silver birch (*Betula pendula* Roth), European beech, and European aspen (*Populus tremula* L.) occur in the under- and mid-stories. Prior to the establishment of the current experiment, the stand had been subjected to several thinning operations. Chapter **III** comprises 24 experimental sites established in 2000 in mixed broadleaved forest stands containing numerous oak trees aged 80 to 200 years, with the oldest oaks reaching up to 250 years (Figure 2B). Oak was the dominant tree species, occurring in mixtures with small-leaved lime (*Tilia cordata* Mill.), Norway spruce, European aspen, and birch (*B. pendula* Roth and *B. pubescens* Ehrh.) in the overstory, and European hazel (*Corylus avellana* L.) and hawthorn (*Crataegus* spp.*)* in the shrub layer. The stands were located on land formerly used as woodland pastures and meadows, which appear to have been abandoned between 1930 and 1950. Following spontaneous tree re-colonization of previously open areas, the stands are now designated as areas important for conservation, primarily woodland key habitats and nature reserves. Chapter **IV** is based on permanent plots from the Swedish National Forest Inventory established between 1983 and 1987 (Figure 2C). Over time, these stands have been dominated by Norway spruce and Scots pine, with oak representing the most common broadleaved species in terms of basal area.

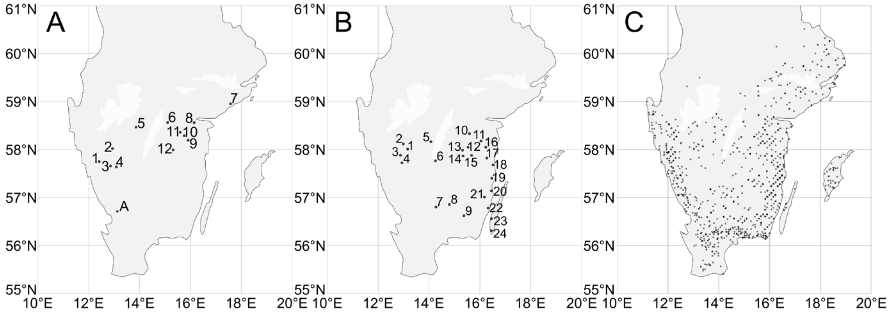


Figure 2. Overview of field sites in Chapter **I** and **II** (A), Chapter **III** (B), and Chapter **IV** (C). The sites of Chapter **I** are labelled 1–12, and the single site of Chapter **II** is labelled as A. The sites of Chapter **III** are labelled 1–24. The sites of Chapter **IV** are plotted based on disturbed coordinates provided by the National Forest Inventory.

2.2 Chapter I – Six years of oak recruitment in a field experiment across southern Sweden

This chapter is based on a field experiment conducted at multiple sites across southern Sweden (see Section 2.1). At each site, we established two, 1-ha treatment plots (100 x 100 m) separated by 25–125 m. We randomly assigned plots one of two treatment levels, either a control (C), which received no cutting, or selective cutting (S), which was applied across the entire 1-ha plot during the winter 2016/2017. Selective cutting primarily targeted strong competitors of oak (e.g. Norway spruce, birch, dense patches of hazel). In some stands, we removed a limited number of oaks, however, we consistently retained most temperate broadleaved tree species as well as trees with high biodiversity value (including trees with cavities, injuries and dead wood). Harvesting was conducted using a combination of harvester, forwarder, chain saw, and a tractor (Nordén et al., 2019). On average, selective cutting removed approximately 25–30 percent of the basal area in the S treatment level. Within each treatment level, we established two parallel transects located 30 m (T30) and 70 m (T70) from the south-west corner (Chapter **I** – Figure 1). Each transect was 100 m long and was divided into four 25 m sections. We delineated circular sub-plots with a 10 m radius at the centre of section 1 and 3 along T30 and section 2 along T70, resulting in three sub-plots per treatment plot for tree measurements. These sub-plots were semi-permanent, as we did not monument their centres but instead relocated them by measuring distance along the transects.

We collected data during summer 2016 (pre-treatment) and again after six growing seasons in summer 2022 (post-treatment) in all sub-plots. In each sub-plot, we recorded species identity and diameter at breast height (dbh, cm) for all living trees with dbh ≥ 5 cm. We assessed canopy openness as a proxy for light availability using hemispherical photography. Images were collected at the centre of the first and third sections of both transects per treatment plot, using a camera mounted on a tripod at 1.3 m above the forest floor. This sampling was conducted early in the morning to avoid direct sunlight. The images were analysed using the *Hemiphot.R* package (ter Steege, 2018) to calculate percentage of canopy openness.

To assess oak recruitment, we calculated oak recruit density (stems ha^{-1}) for oak individuals with dbh between 5.0 and 19.9 cm. For the analyses, we assigned oak recruits to two diameter classes: 5.0–9.9 cm (class 'A') in the lower canopy and 10.0–19.9 cm (class 'B') in the middle canopy. To evaluate the influence of overstory trees and the shrub layer on oak recruitment, we classified oak trees with dbh ≥ 20 cm and all other tree species, regardless of size, as overstory trees, while we considered European hazel as the shrub layer. Using data collected in 2022, we calculated stand density (stems ha^{-1}) and stand basal area (m^2 ha^{-1}) separately for the overstory and shrub layer. To estimate species-specific effects on light availability, we calculated a shade-casting ability index (SCA index, see Verheyen et al., 2021; De Lombaerde et al., 2019; Depauw et al., 2020) for each sub-plot. Oak recruits were excluded from the SCA index calculations.

2.3 Chapter II – Sixteen years of oak recruitment in a field experiment in southern Sweden

This chapter is based on a field experiment conducted in a single forest stand at the Tönnersjöheden Experimental Forest in southern Sweden (see Section 2.1). The experimental stand consists of three blocks, each containing four 1-ha treatment plots that were randomly assigned to one of the following treatment levels: control, no target diameter cutting (C); target diameter cutting (TDC); target diameter cutting with soil scarification (TDCS); and target diameter cutting with modified target diameters compared to the other treatment levels (TDC2) (Drössler et al., 2012). Table 1 lists the species-specific dbh thresholds applied in each treatment level. The dbh thresholds in TDC and TDCS were selected based on economic criteria related to timber quality and prices prevailing in 2006 (Drössler et al., 2017). In TDC2, the thresholds were slightly modified to increase removal of Norway spruce by lowering its target diameter, thereby promoting broadleaved tree development. In all cutting levels, trees were harvested once their dbh equalled or exceeded the specific threshold, while retaining selected trees to enhance the ecological value of the stand. Twenty retention trees per ha were retained in the TDC2 treatment level and ten retention trees per ha in the TDC and TDCS treatment levels. None of the retention trees occurred within the sample plots. Cutting operations were carried out in spring 2008/2009, and soil scarification in the TDCS treatment level was implemented in autumn 2010. Chapter **II** – Table S1 provides details on the number and basal area of trees removed and the cutting intensity (%) for each treatment level and block.

Table 1. Target diameter (dbh in cm) thresholds for each species and treatment level during the target diameter cutting in spring 2008/2009. TDC represents target diameter cutting, TDCS target diameter cutting with soil scarification, TDC2 target diameter cutting with increased removal of Norway spruce. Stem quality is represented by Class 1 and 2; Class 1 are trees with branches < 6 cm in, and Class 2 including trees with low timber quality with branches > 6 cm, spike-knots or forks.

Tree species	**TDC/TDCS**		**TDC2**
	Class 1	**Class 2**	
Scots pine	40	30	40
Norway spruce	36	26	26
Birch	30	20	30
Oak	60	30	60
European beech	50	30	50

Within each treatment in each block, four systematically distributed circular sample plots with a 10 m radius were permanently established (total = 48 sample plots (Chapter **II** – Figure 1). All individual trees were numbered and measured in 2006 (pre-treatment), 2016, and 2021 (both post-treatment). In each sample plot, we recorded species identity and dbh (mm) for all living trees with dbh ≥ 50 mm. At each measurement occasion, we measured tree height for a sub-sample using a Vertex hypsometer and transponder (Haglöf, Sweden AB). The sub-sample consisted of the five largest trees by dbh in each sample plot and several randomly chosen individuals of each species across all diameter classes. We used observed height-diameter pairs to estimate heights of trees without direct height measurements using the height-diameter function by Näslund (1936):

$$H = 1.3 + \frac{DBH^{\gamma}}{(\alpha + \beta \times DBH)^{\gamma}}$$

where H is tree height (m), DBH is diameter at breast height (cm), α and β are estimated parameters, and γ equals 3 for Norway spruce and 2 for Scots pine, birch, European beech and oak (Holmström et al., 2018; Ogana et al., 2023). We estimated model coefficients separately for each species, treatment, and measurement occasion. Due to limited sample size, the oak diameter-height equation was applied to birch and European beech. Predicted heights were assigned to all trees lacking direct height measurements.

To classify tree social position (tree size relative to its neighbours), the tallest and largest tree within each sample plot, regardless of species, was identified as the reference individual. At each measurement occasion, all trees were assigned to one of four crown classes based on their relative social position (Drössler et al., 2012; Figure 3). Since only 18 oak recruits were classified as co-dominant, they were merged with the intermediate canopy class for the analysis. We defined oak recruits as oak individuals with a dbh ≥ 5.0 cm and ≤ 20.0 cm. Individual diameter growth (cm year^{-1}) and height growth (m year^{-1}) were calculated for each oak recruit. Annual growth rates were derived for the periods 2006–2016 and 2016–2021 by dividing periodic growth with the number of years between measurements. For stand structural variables, we calculated stand density (stems ha^{-1}), stand basal area (m^2 ha^{-1}), coefficient of deviation of dbh (CVd), and coefficient of deviation of height (CVh) for each sample plot, treatment level, and measurement occasion. Stand density and basal area were calculated separately for conifers (Norway spruce and Scots pine) and broadleaved species (birch, European beech, and oak). Additionally, we calculated the basal area of larger trees (BAL) neighbouring each oak recruit (Wykoff, 1990; Schröder, 1999). For the smallest oak recruit, BAL approximates total stand basal area. We also calculated the total number of trees (stems ha^{-1}) and total basal area (m^2 ha^{-1}) removed during target diameter cutting.

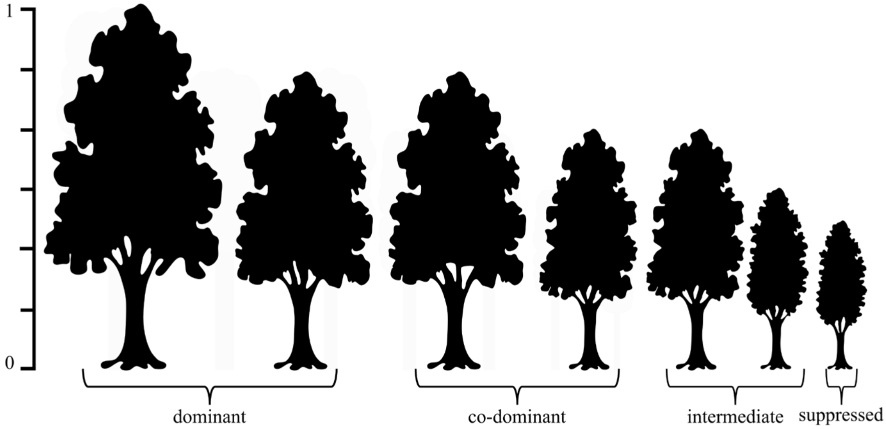


Figure 3. Schematic overview of tree social positions. Dominant trees form the top canopy layer and included trees attaining at least five-sixth of the tallest tree height. Co-dominant trees are slightly lower and reach between four-sixth and five-sixth of the tallest

tree height. Intermediate trees reach between three-sixth to four-sixth of the tallest tree height, while suppressed trees attained less than three-sixth of the tallest tree height.

2.4 Chapter III – Twenty-two years of epiphyte diversity in a field experiment across southern Sweden

This chapter is based on a field experiment conducted at multiple sites across southern Sweden (see Section 2.1). At each site, we established two 1-ha plots (100 x 100 m at most sites) separated by 30–200 m. We randomly assigned plots to either a control (C) treatment level that received no cutting or a selective cutting (S) treatment level, which was applied during winter 2002/2003 (Götmark, 2013). On average, selective cutting removed about 25 percent of the basal area per treated plot. Cutting primarily focused on Norway spruce, non-oak broadleaved trees of intermediate size in the lower canopy, and, where abundant, oaks of intermediate size. We retained larger broadleaved trees and approximately 50 percent of all European hazel. The cutting was conducted manually using chainsaws, except on three sites where a harvester was used.

Within each treatment plot, we randomly selected five host oak trees from among the largest individuals prior to selective cutting in 2002, maintaining a minimum distance of 10 m between selected trees. Selected oaks had a dbh ≥ 40 cm when possible, otherwise, we accepted individuals with dbh ≥ 30 cm. On each host oak, we surveyed epiphytic lichens and bryophytes using a flexible 40 x 40 cm plastic grid placed at breast height on both the north- and south-facing aspects of the trunk. The grid consisted of 100 squares (4x4 cm). During sampling, it was placed on the trunk of selected oaks in alignment with nails used to mark the initial position of the grid corners. This ensured consistent positioning across surveys.

We collected epiphyte data in 2001 (pre-treatment), 2009, and 2023. Twenty-four sites were sampled in 2001 and 2009 and 20 sites in 2023 (sites 1, 2, 3, and 5 were excluded at the request of forest managers) (Figure 2). For each grid cell, we recorded the presence of all lichen and bryophyte species, resulting in a frequency value ranging from 1 to 100 per species and trunk aspect. We identified all foliose and fruticose lichens and all bryophytes in the field, while we collected some crustose lichens for lab identification. Whenever possible, we collected specimens outside the sampling grid to minimize disturbance. We followed Santesson et al. (2004) for lichen nomenclature and Hallingbäck et al. (2006) for bryophytes, and we classified red-listed species according to SLU Artdatabanken (2020). We analysed *Trentepohlia umbrina* ((Kütz.) Bornet), a green alga that is often dominant on tree trunks and may occur independently or in association with lichens, together with epiphytic lichens. We further classified lichens and bryophytes into life forms following Wirth (1995): algae (*T. umbrina*), crustose, foliose, and fruticose lichens, and liverworts and mosses for bryophytes.

We measured oak host tree variables in summer 2002 and 2023. In all survey years, we measured dbh (cm) of host oaks to the nearest millimetre using a measuring tape and used these data to calculate diameter and basal area increment for the period 2002–2023. In 2023, we additionally estimated the percentage of openness around the crown and percentage of large dead branches in the crown, recording values in 5 % intervals. We also measured dbh ($\geq$ 1 cm) and recorded species identity of all living trees and shrubs within a 10 m radius circular sub-plot around each host oak. Shrubs were defined as individuals with dbh between 1.0 and 4.99 cm and trees as individuals with dbh $\geq$ 5 cm, regardless of species. From these data, we calculated shrub density (stems per 10 m plot), tree basal area (m^2 per 10 m plot), and percentage of broadleaved trees based on basal area.

2.5 Chapter IV – National Forest Inventory data across southern Sweden

This chapter is based on long-term data collected from permanent plots of the Swedish National Forest Inventory (NFI). The sampling design of the NFI is based on square clusters with circular sample plots (tracts, Chapter **IV** – Figure 1). Between 1983 and 1988, the NFI established permanent plots in tracts across Sweden with a re-measurement interval of five years (Fridman et al., 2014). Each tract holds four to eight circular sample plots arranged along the sides of squares with side lengths ranging from 300 to 1800 m, depending on geographic location. In southern Sweden, the tracts are smaller due to higher landscape variability which results in higher plot density compared to northern regions. Each circular sample plot covers an area of 314 m^2 (10 m radius). During the 1990s, financial constraints extended re-measurement intervals to 5–10 years and reduced the number of tracts by 50 percent. The sampling design for the 10 m radius plot with measurement trees with a dbh ≥ 100 mm remained consistent. Since 2003, the NFI has re-measured all permanent plots at five-year intervals using a stable sampling design.

Across all permanent plots, the NFI recorded a wide range of plot- and tree-level variables. Plot-level information includes unique plot identifiers, geographic coordinates, land use class, soil moisture class, and site productivity. Soil moisture class is divided into five categories (wet, moist, moist-mesic, mesic, dry) based on estimated groundwater depth during the growing season (SLU, 2025). Site productivity is expressed as a site index derived from site factors such as climate, vegetation type, and soil characteristics (Hägglund and Lundmark, 1977) and represent expected dominant height at age 100 years for either Norway spruce or Scots pine. Tree-level data include unique tree identifiers, species identity, and diameter at breast height (dbh). Within each 10 m radius plot, all living trees with dbh ≥ 100 mm were measured at 1.3 m above ground. Climate data were provided by the Swedish Meteorological and Hydrological Institute (SMHI), with annual temperature and precipitation interpolated to a 4 x 4 km grid using data from the nearest meteorological stations (SMHI, 2025).

From the full NFI dataset, we selected plots from tracts classified as productive forest land that contained oak trees at any time between 1983 and 2024 and that were continuously re-measured throughout this period. To address our questions on oak recruitment, we considered recruiting oaks to be trees with dbh ≥ 100 mm and ≤ 200 mm and included only those trees measured on more than one occasion. For each oak recruit, we calculated periodic basal area increment (PBAI, cm^2 $year^{-1}$) by dividing basal area growth within each measurement interval by the number of years between the measurements. For stand structure, we calculated stand basal area (m^2 ha^{-1}), stem density (stems ha^{-1}), and the proportion of shade-tolerant late successional species Norway spruce and European beech for the plot. To represent site productivity, we included the site index of spruce, as spruce is the dominant tree species in southern Sweden. We also merged the two soil moisture classes ‘moist’ and ‘mesic-moist’ since soil moisture class ‘moist’ had few observations (< 200). None of the plots had the moisture classification ‘wet’. As climate variables, we calculated the long-term mean annual temperature and precipitation (1983–2024) for each plot and the mean temperature and precipitation for each measurement interval and plot. Additionally, we calculated climatic deviations by subtracting the long-term plot-specific mean from the corresponding interval-specific mean (Figure 4).

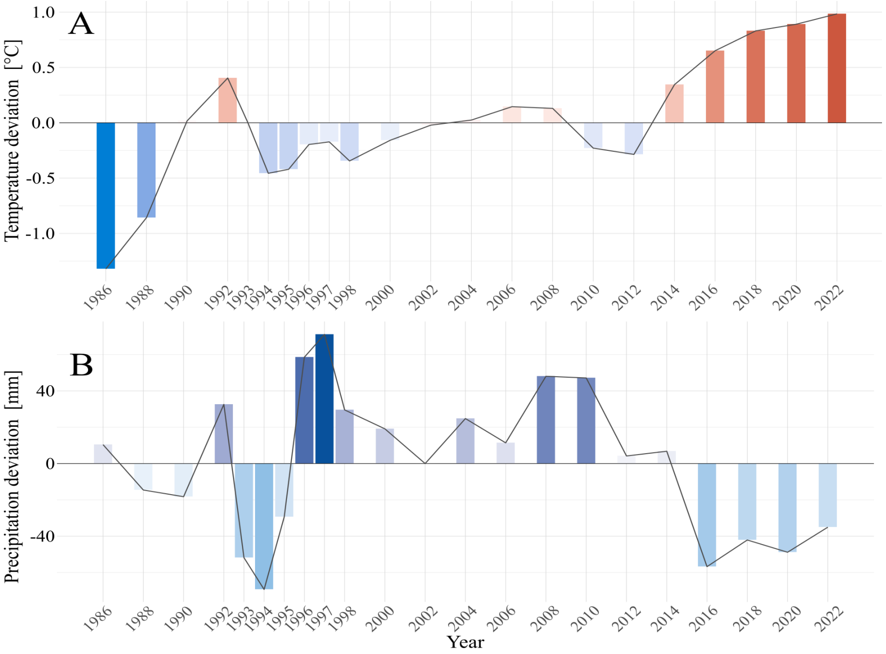


Figure 4. Temperature (A) and precipitation (B) deviation from the long-term mean (1983–2024) per interval period. No visible bars indicate no deviation from the mean.

2.6 Statistical analysis

All statistical analyses in this thesis were conducted in R (R Core Team, 2025) using a significance level of α = 0.05. We implemented all models using the glmmTMB function from the *glmmTMB* package (Brooks et al., 2017; McGillycuddy et al., 2025). Post-hoc comparisons were performed with the *emmeans* and *multcomp* packages (Lenth, 2025; Hothorn et al., 2008). Model performance was evaluated with Akaike Information Criterion (AIC) calculated with the AIC function in the *stats* package (R Core Team, 2025). We assessed model residuals using the *DHARMa* package (Hartig, 2024) and tested for multicollinearity with the check_collinearity function in the *performance* package (Lüdecke et al., 2021). For data visualization, we used the ggplot2 package (Wickham, 2016) and the *sjPlot* package (Lüdecke, 2024) to generate model predictions.

2.6.1 Chapter I

We used Generalized Linear Mixed-effects Models (GLMMs) to evaluate the effects of stand structural attributes on oak recruit density and to assess the impact of selective cutting on both stand structure and oak recruitment.

In the first part of the analysis, we analysed data at sub-plot level to capture the maximum variation in stand structural attributes among sub-plots. In the first model, we specified oak recruit density as the response variable and included diameter class ('A' and 'B'), oak recruit density in 2022, and their interaction as fixed effects. In the second model, we compared three candidate models (Chapter **I** – Table S2), all of which included oak recruit density as the response variable but differed in the interaction structures among diameter class, canopy openness and SCA index. All models included sub-plot nested within site as a random effect, assumed a negative binomial error distribution with a log link, and incorporated a zero-inflation component (ziformula) including the intercept and diameter class. To test for zero-inflation, we used the testZeroInflation function from the DHARMa package.

In the second, we analysed data at the plot level because the treatment was applied across the entire 1-ha plots, i.e., the 1-ha plot was the experimental unit. We tested the effect of selective cutting on each stand structural attribute separately, including stand basal area (m^2 ha^{-1}), stand density (stems ha^{-1}), number of tree or shrub species, and canopy openness (Chapter **I** – Table S3). In each model, we included the interaction between sampling year (two levels) and treatment (two levels) as fixed effects and site as a random effect. We used a Gaussian distribution with an identity link for models of stand basal area, a negative binomial distribution with log link for stand density and number of tree or shrub species, and a beta distribution with a logit link for canopy openness.

In the third part, we also analysed data at the plot level. We tested the effect of selective cutting on the proportion and density (stems ha^{-1}) of oak recruits measured in 2022 (Chapter **I** – Table S4). For the modelling the proportion of oak recruits, we included diameter class, treatment, and their interaction as fixed effects and specified the pre-treatment proportion of oak recruits as an offset (Buckley, 2015). We fit this model using a beta distribution with a logit link, included site as a random effect, and incorporated the same zero-inflation structure as described above. For the modelling oak recruit density, we included diameter class, treatment, their interaction, and pre-treatment oak recruit density as fixed effects, with site as a random effect. We fit this model using a negative binomial distribution with a log link and the same zero-inflation structure as in the previous models.

2.6.2 Chapter II

We used Generalized Linear Mixed-effects Models (GLMMs) to evaluate the effects of individual oak tree characteristics, stand structural attributes, target diameter cutting on oak recruit diameter and height growth, and to assess the impact of target diameter cutting on the probability that oak recruits transition into higher crown classes.

In the first part of the analysis, we modelled oak recruit diameter and height growth as response variables in separate models. As fixed effects, we included dbh, height, and crown class (initial tree characteristics) and conifer density (stems ha^{-1}), broadleaved density (stems ha^{-1}), conifer basal area (m^2 ha^{-1}), broadleaved basal area (m^2 ha^{-1}), BAL (m^2 ha^{-1}), CVd, and CVh (stand structural attributes). Additionally, we included the number (stems ha^{-1}) and basal area (m^2 ha^{-1}) of trees removed as fixed effects in the full GLMM (Chapter **II** – Table S3). We removed variables with high multicollinearity (variance inflation factor, VIF > 5) until all remaining fixed effects had VIF values below this threshold. We then used the *MuMIn* package (Bartoń, 2025) for model selection. For the diameter growth model, we fit a Gaussian error distribution with an identity link and square-root transformed diameter growth values to meet model assumptions. For the height growth model, we fit a Tweedie distribution to accommodate continuous growth data including zeros. In both models, we included tree nested within plot as a random effect.

In the second part, we compared oak recruit diameter and height growth rates among treatments using separate models (Chapter **II** – Table S3). Annual growth rates were used as response variables, and we included the interaction between treatment and measurement year as fixed effects. The applied random-effect structure and distribution families were the same as in the first part of the analysis.

In the third part, we examined the effect of target diameter cutting on the transition probability of oak recruits into higher crown classes. We assigned oak recruits that transitioned to a higher crown class as 1 and those that remained in the same class as 0. In the first model, we included the interaction between treatment and measurement year as a fixed effect and tree nested within plot as a random effect. In a second model, we included individual tree characteristics, stand structural attributes, and the number and basal area of cut trees as fixed effects, with plot as a random effect (Chapter **II** – Table S3). We fit all crown transition models using a binomial distribution with a logit link. Variable and model selection procedures were the same as described for the previous analysis.

2.6.3 Chapter III

Generalized Linear Mixed-effects Models (GLMMs) were used to evaluate the effects of selective cutting, stand structural attributes, and host tree characteristics on species richness of lichens and bryophytes and their associated life forms.

In the first part of the analysis, we modelled lichen and bryophyte species richness and evenness as response variables in separate models. For species evenness, we calculated Pielou's evenness index (Pielou, 1966) based on the Shannon diversity index divided by the natural logarithm of species richness, using the diversity function in the *vegan* package (Oksanen et al., 2025). In all models, we included treatment (two levels), sampling year (three levels), and their interaction as fixed effects, and host oak nested within site as a random effect. For species richness, we fit models with a Poisson error distribution and log link, and for species evenness we used a beta distribution with a logit link. Additionally, we included trunk aspect (two levels), treatment, sampling year, and all interactions as fixed effects. To account for underdispersion in species richness data, we fit models using a Conway-Maxwell-Poisson (compois) distribution with a log-link (Sellers et al., 2011), while retaining the same random-effect structure. All previous mentioned models included host oak nested in site as a random effect. To test the effect of stand structural attributes on lichen and bryophyte species richness, we selected data from the last sampling year as the response variable and included the following host tree characteristics and stand structural attributes: host oak diameter increment, openness around the host oak crown, percentage of dead branches in the crown, neighbouring shrub density, neighbouring tree basal area, and the proportion of neighbouring broadleaf trees. We used the same error distributions and link-functions described above and site as a random effect.

In the second part, we tested the effect of selective cutting on the probability of occurrence of different lichen and bryophyte life forms. We included treatment, sampling year, life form (four levels for lichens and two levels for bryophytes), and all two-way and three-way interactions as fixed effects, with host oak nested within site as a random effect. We further tested the effects of host tree characteristics and environmental variables on occurrence probability in the last sample year. We fitted a binomial distribution with a logit link and site as a random effect for these models.

In the third part, we conducted indicator species analysis to quantify the association between individual species and combinations of treatment and sampling year. We used the multipatt function with 999 permutations in the *indicspecies* package (De Cáceres and Legendre, 2009) to calculate indicator values for each species separately for each treatment and year combination. Additionally, specificity (relative abundance, A) and fidelity (relative frequency, B) were calculated for each species within each group.

2.6.4 Chapter IV

A Generalized Linear Mixed-effects Model (GLMMs) was used to evaluate long-term growth trends of oak recruits and assess the effects of stand structural attributes, plot characteristics, and climate variables on oak recruit growth.

In the analysis, periodic basal area increment (PBAI) of individual oak recruits was used as the response variable. The time between measurements (*time*) was included as a fixed effect. As stand structural attributes, we included the starting basal area of each oak recruit at each interval (*starting ba*), stand basal area (*stand ba*), stem density (*stem dens*), and the proportion of shade species (*shade*). As plot characteristics, we included site index of spruce (*site ind s*) and soil moisture class (*soil m*). Climate variables were included as the 41-year average temperature (*temp avg*) and precipitation (*precip avg*), and the temperature (*temp dev*) and precipitation (*precpi dev*) deviation of each interval from the mean. Further, the following interactions were included: starting basal area of each oak recruit with stand basal area (*starting ba*stand ba*) and stem density (*starting ba*stem dens*), stand basal area with proportion of shade species (*stand ba*shade*), soil moisture class with temperature (*soil m*temp dev*) and precipitation (*soil m*precip dev*) deviation of each interval from the mean. We included tree within plot as a random effect in the model and fit the model using a Tweedie distribution with a log link. We log-transformed and standardized stand basal area, stand density, and starting basal area prior to analysis. All remaining continuous fixed effects were standardized to facilitate comparison of effect sizes among model coefficients. To capture non-linear temporal trends, we used the poly function from the *stats* package to model both the linear and quadratic effects of time.

3. Results and discussion

3.1 Oak recruitment response six years after selective cutting across southern Sweden (Chapter **I**)

The findings from our study of twelve experimental sites in southern Sweden show that a single selective cutting intervention did not directly increase oak recruit density within six years but did modify stand structural conditions in ways that may favour oak recruitment over longer time frames. In total, 145 oak recruits were recorded in 2022, comprising 58 recruits in diameter class A (5.0–9.9 cm) and 87 recruits in diameter class B (10.0–19.9 cm). Mean recruit density did not differ between selectively cut and untreated plots, suggesting that a single intervention was insufficient to generate measurable increases in recruitment within the observed period.

Several factors may explain the absence of a direct treatment effect. At several sites, the pre-treatment regeneration pool of oak seedlings and saplings appeared limited, reducing the potential for ingrowth into recruitment size classes. This likely reflects the weak competitive ability of oak seedlings under dense canopies prior to treatment (Kanjevac et al., 2021), combined with high browsing pressure in southern Sweden (Wallgren et al., 2023). Although a substantial number of oak seedlings were observed across plots six years after treatment, particularly at western sites, this period may have been sufficient to improve regeneration availability but not long enough to result in detectable increases in recruit density. Moreover, pioneer species such as birch and aspen may have responded more rapidly to increased light availability, thereby intensifying competition with oak. These findings suggest that repeated silvicultural interventions may be necessary to prevent oak recruits from becoming overtopped and to promote their progression into favourable canopy positions (Zenner et al., 2012).

Despite the lack of a direct recruitment response, selective cutting significantly reduced overstory basal area and stem density and increased canopy openness six years after treatment. Shrub basal area and tree species richness were not affected. Analysis of stand structural effects revealed a strong negative relationship between stand density and oak recruit density, which was significant for diameter class A but not for diameter class B. For diameter class A, model predictions indicated a 42 percent decrease in recruit density, from 50 stems ha^{-1} at 1000 stems ha^{-1} to 29 stems ha^{-1} at 2000 stems ha^{-1} (Figure 5b). This pattern was consistent when overstory density and shrub layer density were analysed separately, highlighting the importance of managing stand density to facilitate oak recruitment.

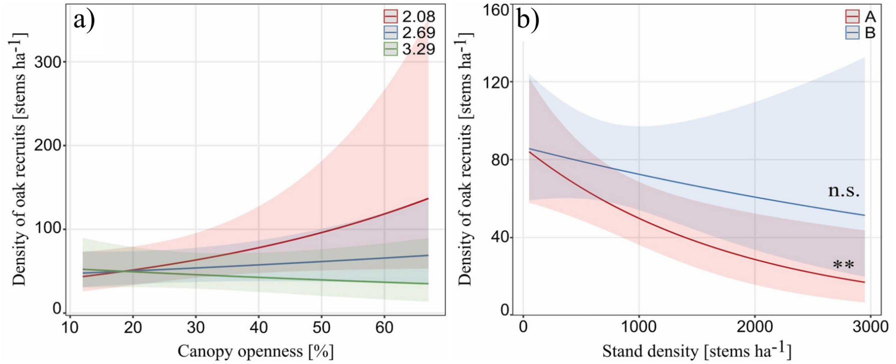


Figure 5. Combined effect of shade-casting index and canopy openness on density of oak recruits (a). Density of oak recruits in diameter class A and B as a function of stand density (b). The moderator in (a) is set to its mean (2.69) ± standard deviation (2.08, 3.29). Lines represent model predictions across the continuous variable range. 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. "**" $P \leq 0.01$ and "n.s" $P \geq 0.05$. Note that the interaction terms illustrated in (a) were non-significant ($P = 0.071$), see Chapter **I** – Table S3.

Reducing stand density may also enhance competitive conditions by increasing light availability alleviating belowground competition, potentially improving soil water availability and mitigating drought stress (Aussenac, 2000; Schmitt et al., 2020). Given projections of increased summer drought frequency in Europe (Bolte et al., 2009), lower stand density may enhance the resistance and resilience of oak recruits, particularly at sites where oaks are not adapted to dry conditions due to historically high precipitation (Trouvé et al., 2017).

In addition, the combined effects of canopy openness and species shade-casting attributes influenced oak recruitment. Model predictions indicate higher recruit densities under conditions of increased canopy openness and lower shade-casting index. For example, at a canopy openness of 65 percent, predicted recruit density was 104 stems ha^{-1} at a shade-casting index of 2.08, compared with 26 stems ha^{-1} at an index of 3.29 (Figure 5a). Lower shade-casting indices are characteristic of stands dominated by species with high light transmission through their crowns, such as pine and birch. Oak regeneration in association with pioneer species has been reported as successful in several contexts (Mosandl and Kleinert, 1998; von Lüpke, 1998, Forrester et al., 2017), although, the rapid growth and competitive strength of these species must be considered. In contrast, oak has been shown to regenerate successfully alongside pioneer species following large-scale disturbances (Brunet et al., 2014; Götmark and Kiffer, 2014). These findings emphasize the importance of species composition and crown architecture in mixed stands, as shade-tolerant tree species with deeper crowns, such as beech, maple, and spruce, cast deeper shade that can suppress oak regeneration.

Overall, this study highlights the recruitment stage as a critical and previously underexplored bottleneck for oak persistence. If sustaining the oak component is a management objective, targeted interventions should focus on recruitment size classes by maintaining stand densities below approximately 1000 stems ha^{-1}. Based on model predictions, a 50 percent increase in stand density resulted in a 42 percent decline in oak recruit density for smaller size classes. Furthermore, increasing canopy openness while promoting species with lower shade-casting ability was associated with up to a fourfold increase in predicted oak recruit density. Given the prevalence of strong shade-casting competitors such as beech, maple, and spruce in temperate forests, their management should be explicitly considered when the objective is to promote oak recruitment into the future canopy.

3.2 Oak recruitment response sixteen years after selective cutting in southern Sweden (Chapter **II**)

Our results from our one study site in southern Sweden demonstrate that all three target diameter cutting treatments primarily promoted the diameter growth of oak recruits, with effects persisting up to sixteen years after intervention. In total, 302 oak recruits were included in the analysis. Mean diameter growth rates over the period 2006–2021 were significantly higher in all treated plots compared to the control, with no differences among cutting treatments (Figure 6A). Eight years after cutting, increased diameter growth was evident only in the TDC (target diameter cutting) and TDC2 (smaller target diameter for Norway spruce to promote broadleaved species) treatment levels, whereas after sixteen years, all three treatment levels showed similarly enhanced growth (Figure 6B). Although annual diameter growth declined slightly over time regardless of treatment level, the positive effects of selective cutting persisted for at least sixteen years. This long-term response is consistent with previous studies reporting sustained but gradually diminishing thinning effects on oak growth (Cabon et al., 2018; Barbeito et al., 2024; Dodan et al., 2024). In contrast, target diameter cutting did not increase height growth of oak recruits. Overall height growth was lower in treated plots compared to controls, with treatment-specific differences varying over time (Figure 6C). Eight years after cutting, height growth of trees receiving the TDC treatment level was significantly lower than in control and TDC2 treatment level, while after sixteen years, height growth was lowest for trees that received the TDCS (target diameter cutting with soil scarification) treatment level (Figure 6D). These results indicate that target diameter cutting promotes diameter increment more so than height growth. This pattern is consistent with previous findings showing that oaks exhibit limited height responses under partial shade and primarily allocate growth to diameter following release (Miller, 2000; Johnson et al., 2019; Dodan et al., 2024). Similar responses have been reported across oak species and management systems, including coppice and high forest stands (Canellas et al., 2004; Fedorová et al., 2016).

Oak diameter growth was positively related to initial tree size and negatively influenced by competitive pressure, as indicated by the basal area of larger trees (BAL) than the individual oak recruit and the basal area of broadleaved competitors (birch, European beech, and oak). These results confirm that increasing dominance of larger trees constrains diameter growth of oak recruits, consistent with previous studies highlighting the role of asymmetric competition (Rohner et al., 2017; Schelhaas et al., 2018). Given Norway spruce and Scots pine accounted for more than 70 percent of stem density in the studied stands, their combined effects, together with those of broadleaved competitors, strongly limited oak growth. Height growth was positively associated with initial diameter but declined with increasing initial oak recruit height, broadleaved density, and height variation, suggesting that light limitation and asymmetric competition suppress vertical growth in structurally dense stands. Although height growth is generally expected to decline with increasing diameter, the positive diameter effect observed here likely reflects the focus on relatively small recruits, for which height increment still increases with size (Sumida et al., 1997; Trouvé et al., 2015). Structural heterogeneity played a nuanced role in oak growth responses in this study. While greater variation in height of surrounding trees reduced height growth of the oak recruits by intensifying asymmetric competition, higher diameter variation among other trees in the stand was associated with increased height growth of the oak recruits, likely reflecting more heterogeneous light conditions. This contrasts with studies on larger oaks, where vertical structural complexity more clearly has been linked to increased height growth (Stimm et al., 2021), highlighting the size-dependent nature of oak growth responses. Additionally, the number of trees removed showed a negative effect on height growth of oak recruits. This suggests that high-intensity selective cutting does not necessarily benefit height development, even when light availability increases, in line with earlier findings (Vallet and Perot, 2016).

Analysis of canopy transition of oak recruits revealed that target diameter facilitated oak recruitment by reshaping competitive hierarchies and enabling upward shifts in canopy position, rather than by directly enhancing height growth rates. Sixteen years after treatment, the TDC2 treatment level showed highest overall transition rate into higher canopy classes (Figure 6E), whereas differences were smaller or absent at earlier measurement points (Figure 6F). Transition probability was strongly dependent on initial tree size and stand structure. Larger recruits, in terms of dbh and height, were more likely to advance into higher canopy positions. Suppressed trees, in terms of social position, exhibited higher probabilities of upward transition than intermediate trees, likely due to shifts in social position following removal of dominant competitors. Intermediate trees may already occupy relatively stable canopy positions and therefore experience limited competitive release. These findings underscore the importance of release from competition during early recruitment stages, as suppressed oaks are otherwise unlikely to recover without intervention (Miller, 2000; Zenner et al., 2012). The higher transition rates observed in the TDC2 treatment level likely reflect its design, which favoured broadleaved species by removing a greater proportion of dominant conifers, particularly Norway spruce. This resulted in lower stand density and basal area, facilitating the advancement of suppressed oak recruits. Similar patterns have been reported for red oak (*Quercus rubra* L.) in North America, where canopy recruitment was rare without thinning (Ward, 2009). Although oak recruits can persist in suppressed positions for extended periods, their transition into the overstorey is typically contingent on timely silvicultural release (O’Hara, 1986; Dey, 2014).

Overall, our findings indicate that target diameter cutting of large trees across species can support oak recruitment by promoting diameter growth and facilitating upward canopy transitions, but it does not inherently increase height growth. Management strategies aiming to sustain oak recruitment should therefore focus on repeated, lower intensity interventions that reduce competition directly above oak recruits while maintaining structural heterogeneity. Retaining mixed size classes may help balance light availability, stand productivity, genetic diversity and long-term forest resilience.

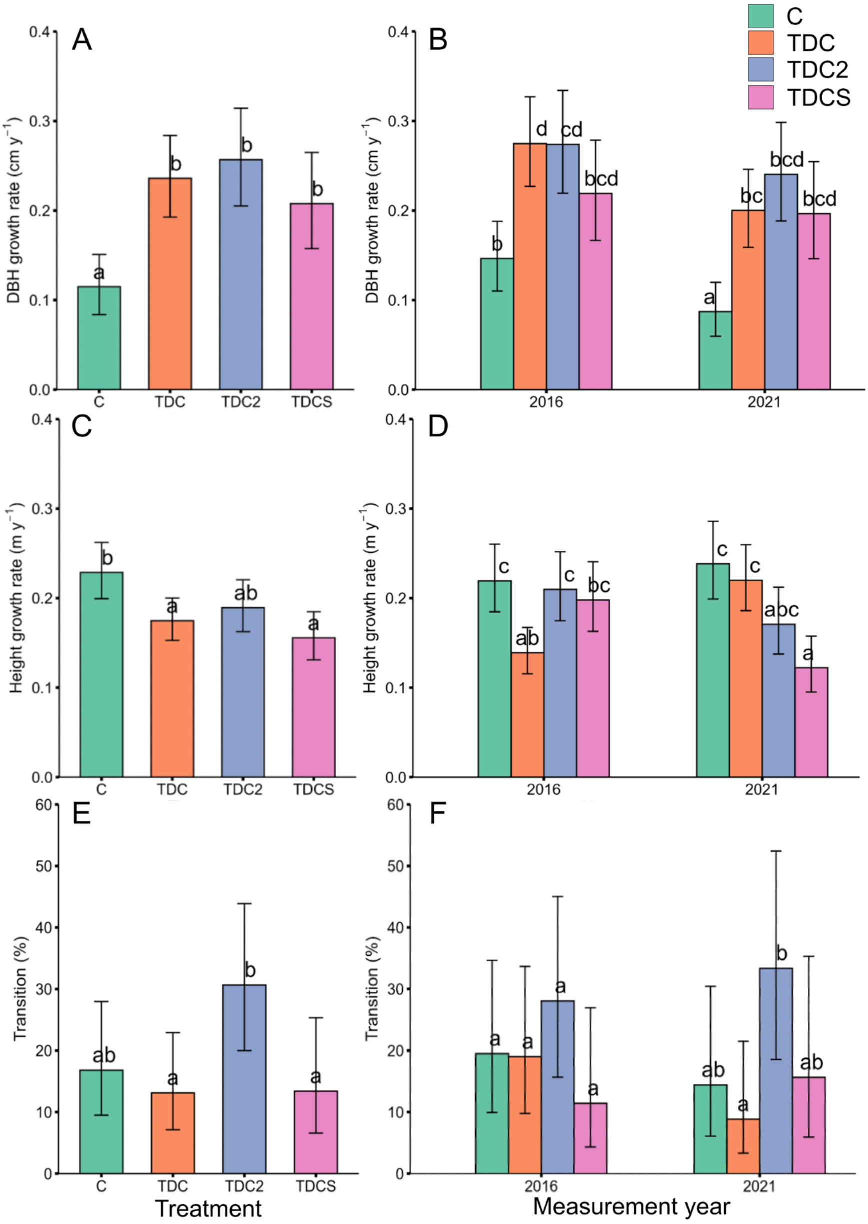


Figure 6. Diameter (A, B) and height (C, D) growth rates, and the observed transition probability into higher canopy classes (E, F) of oak recruits in different treatment levels from 2006–2021 (A, C, E) and in different measurements years (B, D, F). Measurement year 2016 in (B, D, F) represents the period 2006 to 2016, and 2021 represents the period 2016 to 2021. C represents control, TDC target diameter cutting, TDC2 target diameter

cutting with focus on Norway spruce removal, TDCS target diameter cutting with soil scarification. Error bars indicate ± standard error for growth rates and the mean probability of canopy class transition. Letters in common denote no significant differences.

3.3 Epiphyte diversity response twenty-two years after selective cutting across southern Sweden (Chapter III)

In this study, we evaluate epiphytic diversity response on mature host oak trees in twenty-four sites across southern Sweden. In total 150 epiphytic taxa were recorded across the three inventory years, including 136 identified to species level and 14 to genus level. The total number of species recorded was 110 species (68 genera) in 2001, 116 species (74 genera) in 2009, and 110 species (72 genera) in 2023. The most frequent lichens were *Lepraria incana* (L. Ach.), *Pertusaria amara* (Ach. Nyl.), and *Phlyctis argena* (Spreng. Flot), while common bryophytes included *Hypnum cupressiforme* (Hedw.), *Dicranum montanum* (Hedw.), and *Pseudoleskeella nervosa* (Brid. Nyholm). Among the lichens, 11 species (13.6 %, 8 near threatened [NT], 2 vulnerable [VU], 1 endangered [EN]) were on the Swedish Red List (SLU Artdatabanken, 2020) all of which were crustose lichens, whereas no bryophytes were red listed. Selectively cut plots were characterized by larger host oak growth, greater openness around the crown, and a higher proportion of broadleaved trees, while control plots exhibited higher shrub density and a greater neighbouring tree basal area.

Selective cutting had clear and persistent effects on oak-associated epiphytic lichens, whereas responses of bryophytes were weak and inconsistent. Lichen species richness remained stable on host oaks in selectively cut stands but declined in unmanaged control stands over the 22-year period, indicating that selective cutting buffered against long-term species loss. This pattern is consistent with earlier studies showing that heterogeneous and intermediate light conditions promote epiphytic lichen diversity (Moning et al., 2009; Király et al., 2013; Nascimbene et al., 2013). In contrast, continued canopy closure under unmanaged conditions likely reduced light availability around oak crowns, contributing to declining lichen richness through secondary succession (Leppik et al., 2011). Lichen species evenness showed a more gradual and delayed response. Evenness remained stable in selectively cut plots but declined in control stands, with treatment differences becoming apparent only after more than two decades. This pronounced time lag suggests that evenness responds more slowly than species richness and reflects gradual shifts in relative abundances rather than rapid species turnover. As such, evenness provides complementary information on longer-term community reorganization following management interventions (Nascimbene et al., 2013).

Tree- and stand-level variables further shaped lichen diversity patterns. Higher host oak growth, greater openness around the crown, and a higher proportion of neighbouring broadleaved trees were positively associated with lichen richness and evenness, likely reflecting improved light conditions and dispersal opportunities (Paltto et al., 2010; Nascimbene et al., 2009b; Wierzcholska et al., 2024). In contrast, higher shrub density and stand basal area consistently reduced lichen diversity, suggesting that excessive shading outweighed potential benefits of moisture retention (Nascimbene et al., 2012; Király et al., 2013).

Responses differed among lichen life forms. Crustose lichens dominated the epiphytic community and were the only life form containing red-listed species. Their stable occurrence under selective cutting is therefore of conservation relevance. In contrast, foliose lichen occurrence showed a stronger decline, particularly in unmanaged stands, indicating a higher sensitivity to the denser and more structurally homogeneous canopy conditions that develop in the absence of intervention (Barkman, 1958). Fruticose lichens showed a different but related pattern, with occurrence declining in the control treatment but remaining stable under selective cutting, suggesting that their dynamics may be influenced by additional drivers not fully captured by treatment effects alone. Together, these contrasting responses among lichen life forms indicate that selective cutting alters epiphytic lichen communities in life-form-specific ways rather than producing uniform responses.

Host tree characteristics and stand structure further shaped life-form responses (Figure 7). Higher percentage of crown dead branches and openness around the host oak crown were positively associated with crustose lichen (Figure 7A) and algae (Figure 7B) occurrence, respectively. In contrast, a higher shrub density (Figure 7C) and tree basal area (Figure 7D) were negatively associated with algae, crustose and foliose lichen occurrence. No explanatory variables were significantly associated with the occurrence probability of fruticose lichen, mosses, and liverworts.

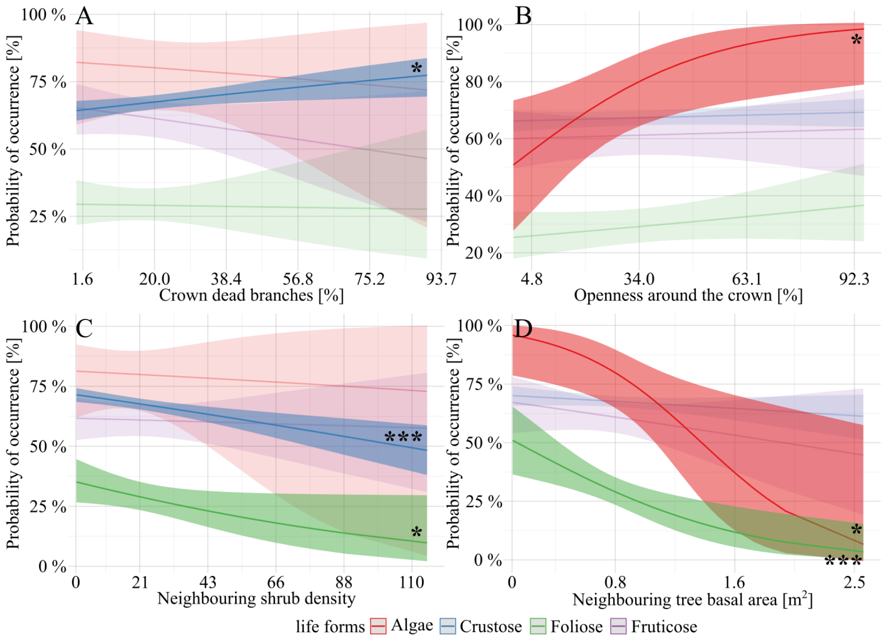


Figure 7. Probability of occurrence of algae (red) and the three lichen life forms: crustose (blue), foliose (green), and fruticose (purple) as a function of percentage of crown dead branches (A), percentage of openness around the host crown (B), neighbouring shrub density (C), neighbouring tree basal area (D). Lines represent model predictions from GLMMs. Shaded areas around the lines represent the 95 percent confidence intervals of the predictions. Darker shaded areas, lines, and asterisks represent the life forms with a significant effect of the tested variable. “***” $P \leq 0.001$, “*” $P \leq 0.05$

Indicator species analysis further supported the importance of canopy structure. Species associated with selectively cut stands in 2023 were predominantly light-demanding taxa, including *Lecanora argentata* (Ach. Röhl.) and *L. expallens* (Ach.), whereas shade-tolerant species such as *Lepraria incana* (L. Ach) and *Micarea prasina* (Fr.) were linked to control plots, consistent with Ellenberg light values (Ellenberg and Leuschner, 2010). The strong association of the green-alga *Trentepohlia umbrina* (Kütz. Bornet) with selective cutting is noteworthy, given evidence that this photobiont can benefit from relatively open conditions (Rindi and Guiry, 2002; Ellwood et al., 2021).

Bryophytes showed no consistent responses to selective cutting or environmental variables. Overall richness was low, averaging only a few species per tree, and bryophytes played a minor role in shaping treatment-level diversity patterns. This likely reflects their greater tolerance of low light and reliance on stable humidity conditions (Barkman, 1958; Vanderpoorten and Goffinet, 2009).

Together, these results demonstrate that selective cutting can buffer long-term biodiversity loss on mature oaks by maintaining lichen species richness and evenness, while unmanaged stands showed clear declines. While crustose lichens, including all red-listed species, benefited most clearly, the decline of macrolichens could not be fully explained by the measured structural or environmental variables. This suggests a potentially underrecognized signal of environmental change that merits further investigation, particularly in the context of ongoing climate warming and increasing evaporative stress (Pisani et al., 2007; SMHI, 2025). Overall, these findings indicate that moderate canopy opening through selective cutting can sustain key components of oak-associated epiphytic diversity, while also highlighting taxon- and life-form-specific sensitivities that warrant further investigation.

3.4 Long-term trend of oak recruitment across southern Sweden (Chapter **IV**)

Analysis of the permanent plots of the Swedish National Forest Inventory showed that growth of oak recruits has declined markedly over the past four decades in southern Sweden (Figure 8A), and that this decline persisted even after accounting for stand structural attributes and plot-specific climatic conditions. This indicates that while stand structure and climate are important drivers of growth of oak recruits, they do not fully explain the long-term downward trend, pointing to the influence of additional site-specific constraints, legacy effects, and management history.

A higher proportion of shade-tolerant species (European beech and Norway spruce) was associated with reduced growth (Figure 8B), reflecting their strong competitive advantage through deep shading and rapid canopy closure (Hein and Dhôte, 2005; Leonardsson et al., 2015; Vanhellemont et al., 2018; Kohler et al., 2020). In addition, increasing stand basal area and stem density further constrained oak recruit growth by intensifying competition for light, water, and nutrients. Stand basal area exerted a particularly strong suppressive effect on smaller recruits (Figure 8D), while stem density reduced growth across size classes (Figure 8E). Dense canopies limit light availability for light-demanding oaks and reduce throughfall to the forest floor (von Lüpke, 1998; von Lüpke and Hauskeller-Bullerjahn, 1999; Sadeghi et al., 2020), while dense under- and midstory layers exacerbate above- and belowground competition (Aussenac, 2000; Schmitt et al., 2020).

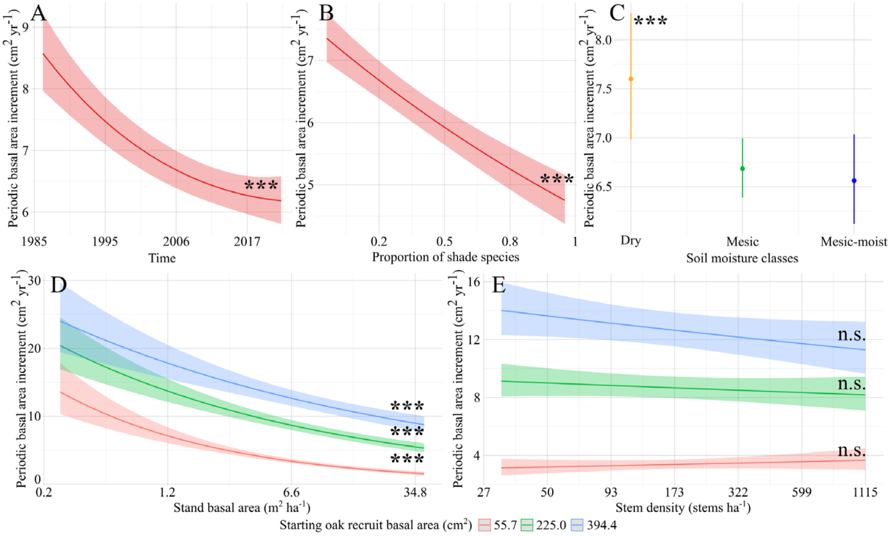


Figure 8. Periodic basal area increment in relation to time (A), proportion of shade-tolerant species (B), and soil moisture class (C), as well as the combined effects of starting oak recruit basal area and stand basal area (D) and stem density (E). Lines indicate model-based predictions across the observed range of the continuous variable, while other continuous predictors were held at their mean values. In interactions panels (D, E), initial oak recruit basal area was fixed at its mean (225.0) and ± standard deviation (55.7, 394.4). Shaded areas indicate 95 percent confidence intervals around the predicted values. "***" $P \leq 0.001$, "n.s." $P > 0.05$.

Soil moisture conditions strongly shaped growth responses to climatic variability. Oak recruits on dry sites showed higher overall growth (Figure 8C) and responded positively to increasing above-average precipitation (Figure 9A), likely reflecting a competitive advantage associated with deep rooting and relatively high drought tolerance, particularly for sessile oak (Nicolescu et al., 2025). In contrast, recruits on mesic sites exhibited reduced growth during warmer-than-average periods (Figure 9B), suggesting increased sensitivity to water limitation under warming conditions, especially in populations less acclimated to drought (Kunz et al., 2018; Schmitt et al., 2020). Importantly, these climate–growth relationships were detected despite climatic variables being averaged across inventory intervals, indicating that climatic influences on recruit growth are sufficiently strong and persistent to be captured even at coarse temporal resolution.

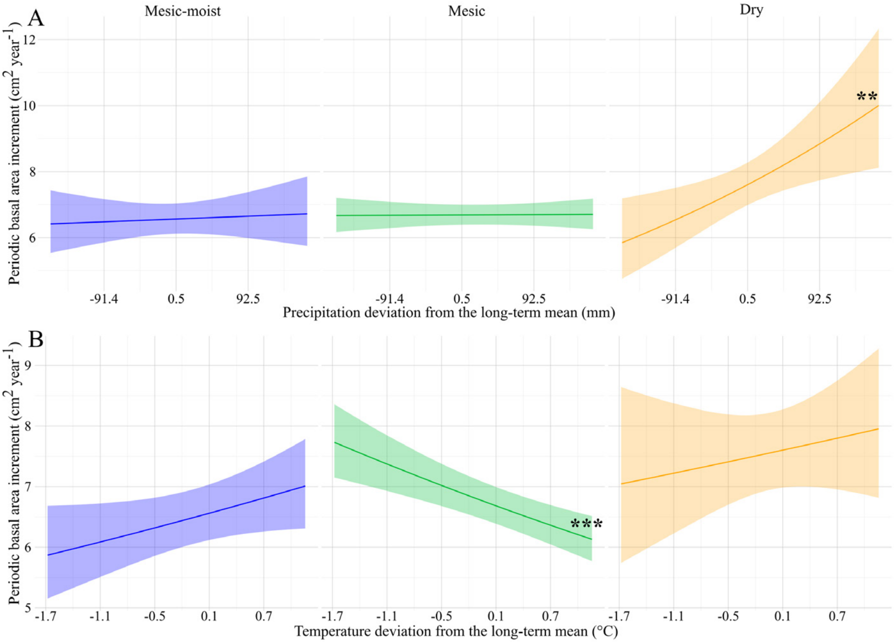


Figure 9. Periodic basal area increment as a function of interactions between soil moisture class (mesic-moist, mesic, dry) and deviations in precipitation (A) and temperature (B) from the long-term mean (1983-2024). Lines represent model predictions, with shaded area indicating 95 percent confidence intervals. "***" $P \leq 0.001$, "**" $P \leq 0.01$.

The long-term decline in oak recruit growth observed in this study differs from the growth increases reported for several regions in Central Europe, including France, Belgium, the Czech Republic, and parts of Germany (Becker et al., 1994; Bergès et al., 2000; Kint et al., 2012; Kašpar et al., 2024), yet is consistent with decreasing trends documented in northern Germany (Bauwe et al., 2015). Such regional discrepancies likely arise from interacting differences in species composition, soil conditions, and climatic regimes. In Sweden, oak populations occur near the northern limit of their distribution and may therefore be adapted to comparatively cool growing conditions. Recent years, however, have been characterized by higher temperatures and reduced precipitation (Figure 4), which may increasingly constrain soil water availability during warm periods and may lead to persistent growth reductions through legacy effects. Future climate projections indicating a temperature increase of 2–6 °C by the end of the century (SMHI, 2025), together with a potential northward shift in oak distribution (Dyderski et al., 2025), further increase uncertainty surrounding future growth trajectories (Friedrichs et al., 2009b).

Overall, our results highlight the recruitment phase as a critical bottleneck for oak persistence in temperate forests at the northern distribution margin. Sustaining oak populations under continued climate change will likely depend on active management of species composition, stem density, and basal area, as well as improved integration of higher resolution climate data, additional site characteristics and historical legacies. Integrating these approaches will enhance our ability to project oak recruitment under changing climatic conditions and to design management strategies that support long-term oak persistence and biodiversity in temperate forest ecosystems.

3.5 General limitations

While the studies in this thesis provide new insights into oak recruitment challenges and biodiversity implications of oak-dominated forests under continuous cover forestry, several limitations should be acknowledged. Across chapters, site- and plot-specific factors such as detailed soil properties, microclimatic conditions, and light availability (except Chapter **I**) were not explicitly measured. Incorporating such variables could have improved the explanatory power of the analyses, particularly disentangling structural effects from direct environmental drivers. In addition, landscape context and management history were not consistently available, which may have contributed to unexplained variability among plots.

Several limitations are specific to individual chapters. In Chapter **I**, the study design did not allow individual oak recruits to be tracked over time, which limits inference on short-term growth responses and may have contributed to the absence of treatment effects on recruit density. Permanent marking of recruits, combined with information about the size of the regeneration pool would have enabled a clearer assessment of ingrowth processes and treatment effects. In Chapter **II**, the experimental site was located on a highly productive site, whereas oak forests in Sweden more commonly occur on sites with lower productivity, which constrains the generalizability of the findings. In Chapter **III**, direct measurements of light, temperature, and moisture conditions on tree trunks were not collected. Although crown openness served as a proxy for light conditions, it does not fully capture microhabitat conditions experienced by epiphytes, and the exclusion of upper trunk and canopy sections likely led to an underestimation of total epiphytic diversity. In Chapter **IV**, the absence of detailed soil data, direct light measurements, and oak recruit age limited the ability to separate ontogenetic, structural, and environmental effects. Moreover, climatic variables were averaged across inventory intervals, reducing sensitivity to short-term extreme events.

Taken together, these limitations highlight the importance of long-term monitoring approaches that integrate repeated silvicultural interventions with detailed measurements of site conditions, stand history, and microclimate. Future research combining permanent plot designs and higher-resolution environmental data will be essential to refine understanding of oak recruitment processes and to support adaptive management under changing climatic conditions.

4. Forest management implications

4.1 Recruitment of oaks and associated biodiversity under continuous cover forestry

Continuous cover forestry (CCF) is increasingly promoted as a management approach capable of reconciling timber production, biodiversity conservation, and climate adaptation in temperate forests. Its emphasis on permanent forest cover, structural heterogeneity, and natural regeneration aligns well with the ecological characteristics of oak-dominated forests, which are often structurally complex and support a high diversity of associated organisms. However, the synthesis of results across this thesis demonstrates that oak recruitment represents a critical and unresolved bottleneck under CCF, with important consequences for both long-term stand continuity and biodiversity conservation.

Across chapters, oak recruitment was consistently constrained by stand conditions that favoured competitors, particularly a high proportion of shade-tolerant species, elevated stand basal area, and high stem density. In Chapter **I**, a single selective cutting intervention altered stand structure by reducing basal area and increasing canopy openness but did not result in higher oak recruit density within six years. This suggests that short-term structural changes alone may be insufficient to overcome recruitment limitations, especially where regeneration pools are limited or competition remains strong. In Chapter **II**, target diameter cutting clearly enhanced diameter growth of oak recruits but did not increase height growth, indicating that partial release primarily promotes lateral growth and that additional or repeated interventions may be required to facilitate vertical progression into the canopy. Together, these experimental results show that under CCF, oak may persist in the regeneration layer, but it struggles to advance into larger size classes. Targeted management interventions may therefore need to be applied repeatedly or with greater intensity to support the transition of oak recruits into the canopy.

The long-term analysis in Chapter **IV** reinforces this interpretation by documenting a pronounced decline in oak recruit growth over the past four decades, even after accounting for stand structure, site conditions, and climatic variability. Increasing proportions of shade-tolerant species, higher stand basal area, and greater stem density were consistently associated with reduced growth of oak, underscoring the cumulative effects of competition in increasingly closed-canopy systems. Climate–growth relationships were strongly mediated by soil moisture conditions. Oak recruits on dry sites showed higher overall growth and responded positively to above-average precipitation, whereas recruits on mesic sites exhibited strongly reduced growth during warmer-than-average periods. This pattern is particularly relevant in Sweden, where oak occurs near its northern distribution limit and may be historically adapted to relatively cool climatic conditions. Recent warming trends, interacting with site moisture and competitive stand structure, therefore, appear to exacerbate recruitment constraints rather than compensate for them. Importantly, these climate signals were detectable despite climatic variables being averaged across inventory intervals, suggesting that climatic influences on oak recruit growth are strong and persistent.

At the same time, the results from Chapter **III** demonstrate that selective cutting under continuous cover forestry can provide clear and long-lasting benefits for oak-associated biodiversity. Lichen species richness and evenness were maintained in selectively cut stands, whereas declines occurred in unmanaged controls. These patterns were driven primarily by crustose lichens, which dominated the epiphytic community and represented the only life form containing red-listed species. The stability of crustose lichens under selective cutting is therefore of particular conservation significance, indicating that moderate canopy opening can buffer biodiversity loss without compromising forest continuity. In contrast, bryophytes were comparatively rare across treatments, limiting inference about their responses. Moreover, some declines could not be fully explained by the measured stand or host-tree variables, including the pronounced decline of foliose lichens in both treatments and the decline of fruticose lichens in the control treatment. These unresolved patterns likely reflect the influence of unmeasured factors such as microclimatic variability, air humidity, or broader environmental pressures, underscoring that biodiversity responses to CCF are taxon-specific and closely linked to fine-scale habitat conditions shaped by stand structure.

Taken together, the findings indicate that CCF can support oak-associated biodiversity while maintaining forest cover, but successful oak recruitment requires more deliberate structural management than is often assumed under low-intervention regimes. While CCF provides a suitable framework for maintaining structural complexity and oak-associated biodiversity, it does not inherently ensure successful oak recruitment. Without targeted reduction of stand density and shade-tolerant competitors, CCF may inadvertently favour species such as beech and spruce at the expense of oak, leading to long-term recruitment failure despite the persistence of mature oaks. A key management insight emerging from this thesis is that oak recruitment responds to broadly similar stand structural conditions as oak regeneration, according to the literature. Both stages benefit from reduced competition, lower proportions of shade-tolerant species, and increased light availability. This coherence is encouraging from a silvicultural perspective, as it suggests that management interventions aimed at promoting oak regeneration can simultaneously support recruitment into larger size classes. Rather than treating regeneration and recruitment as separate challenges, CCF management can be designed to address the entire oak regeneration-recruitment continuum, potentially simplifying long-term planning and increasing the effectiveness of adaptive strategies.

Therefore, effective oak recruitment under CCF requires a deliberate balance between maintaining continuous cover and applying sufficiently intensive or repeated interventions to sustain light availability and reduce competitive pressure, particularly as light requirements of oak increase with size. Failure to address this balance risks decoupling biodiversity conservation from long-term stand continuity, with mature oak-dominated systems gradually losing their regenerative capacity. Adaptive CCF strategies that explicitly integrate oak recruitment objectives alongside biodiversity goals are therefore essential to sustain oak-dominated and oak-rich forests under ongoing climate change.

4.2 Outlook and research needs

Species-specific recruitment dynamics In our studies, we did not distinguish between pedunculate and sessile oak, as the primary objective was to promote oak recruitment irrespective of species. Future studies should explicitly differentiate between the two species to assess species-specific recruitment patterns, particularly in relation to climatic conditions, soil properties, and moisture availability.

More long-term field studies Our experimental studies (Chapter I and II) spanned periods of six to sixteen years which might have been too short to fully capture growth responses in diameter and height growth, given the relatively slow growth rates of oak. More extended long-term field experiments are therefore essential to robustly evaluate oak growth responses to selective cutting and other management interventions.

Multi-site selection system studies The selection system that we examined in Chapter II was implemented at a single, highly productive site. To improve the applicability of our results, more studies are necessary that apply similar management approaches across multiple sites spanning a gradient of site productivity. This would allow evaluating whether target diameter cutting could consistently promote oak recruitment under varying site conditions.

Repeated silvicultural intervention studies Our experimental studies assessed oak recruit responses to a single silvicultural intervention. Although selective cutting increased canopy openness and light availability, faster-growing species may respond more rapidly to these changes and potentially outcompete oak over time. Studies incorporating repeated silvicultural interventions over longer periods are therefore needed to assess whether oak recruitment can be sustained under dynamic stand structural conditions.

Landscape-level biodiversity responses Our study in Chapter III included multiple experimental sites across southern Sweden. However, we could not revisit the experiment on several sites due to discontinuation of the experiment which limited our ability to conduct landscape-level analyses along climatic gradients. Future research should prioritize long-term biodiversity monitoring across well-distributed sites to evaluate how climatic context influences taxon-specific responses to selective cutting and stand structure.

Recruitment and environmental stressors Future studies are necessary to assess how single or repeated silvicultural measures influence oak recruitment under increasing environmental stress, including the combined effect of recurrent drought events and pathogen pressure. It would further our understanding how stand structure mediates oak responses to such stressors which will be critical under projected climate change.

Latitudinal gradient studies Our analysis of Swedish National Forest Inventory data revealed growth trends that contrast with patterns reported from parts of Central Europe. Comparative studies across a latitudinal gradient covering the European distribution of oak are needed to determine whether declining recruitment-stage growth is specific to northern range limits or reflects broader regional patterns.

Establishment of consistent terminology The diversity of terms used to describe continuous cover forestry and related approaches has been highlighted as a practical barrier to wider implementation of CCF in Sweden. From our perspective, future research that aims to inform policy and management would benefit from using clearer and more consistent terminology when referring to continuous cover forestry. Greater conceptual clarity would not only facilitate communication among researcher, practitioners, and policymakers, but also improve the comparability and applicability of research outcomes, which is essential if the ambition is to promote more sustainably managed forests.

Together, these research needs highlight that advancing sustainable management of oak-dominated forests requires a stronger focus on the recruitment phase, longer-term and spatially explicit studies, and a clearer integration of stand structure, species-specific responses, and environmental stressors. Addressing these gaps will improve our ability to predict oak recruitment dynamics across environmental gradients and management regimes, thereby supporting the development of adaptive continuous cover forestry strategies that sustain both oak populations and their associated biodiversity under ongoing climate change.

References

Abrams, M.D. (1992). Fire and the development of oak forests: in eastern North America, oak distribution reflects a variety of ecological paths and disturbance conditions. *BioScience*, 42(5), 346–353.

Alexander, H.D., Siegert, C., Brewer, J.S., Kreye, J., Lashley, M.A., McDaniel, J.K., Paulson, A.K., Renninger, H.J. and Varner, J.M. (2021). Mesophication of oak landscapes: Evidence, knowledge gaps, and future research. *BioScience*, 71(5), 531–542.

Anderson, M.K. (2007). Indigenous uses, management, and restoration of oaks of the far western United States. Technical Note No. 2. NRCS, National Plant Data Center, Washington, DC.

Attocchi, G. (2015). Silviculture of oak for high-quality wood production. *Acta Universitatis Agriculturae Sueciae*, 2015:39.

Aussenac, G. (2000). Interactions between forest stands and microclimate: ecophysiological aspects and consequences for silviculture. *Annals of Forest Science*, 57(3), 287–301.

Barkman, J.J. (1958). *Phytosociology and ecology of cryptogamic epiphytes*. Assen: Van Gorcum.

Bartoń, K. (2025). *MuMIn: Multi-Model Inference*. R package version 1.48.11. Available at: https://CRAN.R-project.org/package=MuMIn

Bauwe, A., Jurasinski, G., Scharnweber, T., Schröder, C. and Lennartz, B. (2015). Impact of climate change on tree-ring growth of Scots pine, common beech and pedunculate oak in northeastern Germany. *iForest*, 9, 1–11.

Benecke, U. (1996). Ecological silviculture: the application of age-old methods. *New Zealand Journal of Forestry*, 41, 27–33.

Bobiec, A., Reif, A. and Öllerer, K. (2018). Seeing the oakscape beyond the forest: a landscape approach to the oak regeneration in Europe. *Landscape Ecology*, 33, 513–528.

Bolte, A., Ammer, C., Löf, M., Madsen, P., Nabuurs, G.-J., Schall, P., Spathelf, P. and Rock, J. (2009). Adaptive forest management in central Europe: climate change impacts, strategies and integrative concept. *Scandinavian Journal of Forest Research*, 24, 473–482.

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Mächler, M. and Bolker, B.M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, 9(2), 378–400.

Brunet, J., Bukina, Y., Hedwall, P.-O., Holmström, E. and von Oheimb, G. (2014). Pathogen induced disturbance in temperate forests: Evidence from a 100-year data set in southern Sweden. *Basic and Applied Ecology*, 15, 114–121.

Buckley, Y.M. (2014). Generalised linear models. In: Zuur, A.F., Ieno, E.N. and Smith, G.M. (eds.) *Ecological statistics: contemporary theory and application*. Oxford: Oxford University Press, pp. 131–148.

Cabon, A., Mouillot, F., Lempereur, M., Ourcival, J.-M., Simioni, G. and Limousin, J.-M. (2018). Thinning increases tree growth by delaying drought-induced growth cessation in a Mediterranean evergreen oak coppice. *Forest Ecology and Management*, 409, 333–342.

Cañellas, I., del Río, M., Roig, S. and Montero, G. (2004). Growth response to thinning in *Quercus pyrenaica* Willd. coppice stands in Spanish central mountain. *Annals of Forest Science*, 61(3), 243–250.

Carbonnier, C. (1975). Produktionen av kulturbestånd av ek i södra Sverige. *Studia Forestalia Suecica*, 125.

Chassé, B. (2016). Eating acorns: what story do the distant, far and near past tell us, and why. *International Oaks*, 27, 107–135.

De Cáceres, M. and Legendre, P. (2009). Associations between species and groups of sites: indices and statistical inference. *Ecology*, 90, 3566–3574.

De Lombaerde, E., Verheyen, K. and Van Calster, H. (2019). Tree regeneration responds more to shade casting by the overstorey and competition in the understorey than to abundance per se. *Forest Ecology and Management*, 450, 117492.

Denk, T., Grimm, G.W., Manos, P.S., Deng, M. and Hipp, A.L. (2017). An updated infrageneric classification of the oaks: Review of previous taxonomic schemes and synthesis of evolutionary patterns. In: Gil-Pelegrín, E., Peguero-Pina, J. and Sancho-Knapik, D. (eds.) *Oaks physiological ecology: Exploring the functional diversity of genus Quercus L.* Tree Physiology, Vol. 7. Cham: Springer, pp. 13–38.

Depauw, L., Perring, M.P., Landuyt, D., Maes, S.L., Blondeel, H., De Lombaerde, E., Brūmelis, G., Brunet, J., Closset-Kopp, D., Decocq, G., den Ouden, J., Härdtle, W., Hédl, R., Heinken, T., Heinrichs, S., Jaroszewicz, B., Kopecký, M., Liepiņa, I., Macek, M., Máliš, F., Schmidt, W., Smart, S.M., Ujházy, K., Wulf, M. and Verheyen, K.(2021). Evaluating structural and compositional canopy characteristics to predict the light-demand signature of the forest understorey in mixed, semi-natural temperate forests. *Applied Vegetation Science*, 24(1), e12532.

Dey, D.C. (2014). Sustaining oak forests in eastern North America: regeneration and recruitment, the pillars of sustainability. *Forest Science*, 60(5), 926–942.

Diaci, J. (2006). Nature-based forestry in Central Europe: alternatives to industrial forestry and strict preservation. *Studia Forestalia Slovenica*, 126.

Drössler, L., Fahlvik, N. and Ekö, P.M. (2012). Stand structure and future development of a managed multi-layered forest in southern Sweden: Eriksköp – a case study. *Sveriges lantbruksuniversitet*, Institutionen för sydsvensk skogsvetenskap.

Drössler, L., Fahlvik, N., Wysocka, N.K., Hjelm, K. and Kuehne, C. (2017). Natural regeneration in a multi-layered *Pinus sylvestris–Picea abies* forest after target diameter harvest and soil scarification. *Forests*, 8(2), 35.

Dyderski, M.K., Paź-Dyderska, S., Jagodziński, A.M. and Puchałka, R. (2025). Shifts in native tree species distributions in Europe under climate change. *Journal of Environmental Management*, 373, 123504.

Eaton, E., Caudullo, G., Oliveira, S. and de Rigo, D. (2016). *Quercus robur* and *Quercus petraea* in Europe: distribution, habitat, usage and threats. In: San-Miguel-Ayanz, J., de Rigo, D., Caudullo, G., Houston Durrant, T. and Mauri, A. (eds.) *European Atlas of Forest Tree Species*. Luxembourg: Publications Office of the European Union, pp. e01c6df.

Ellenberg, H. and Leuschner, C. (2010). Vegetation Mitteleuropas mit den Alpen: in ökologischer, dynamischer und historischer Sicht. Stuttgart: UTB.

Ellison, A.M. (2019). Foundation species, non-trophic interactions, and the value of being common. *iScience*, 13, 254–268.

Ellwood, N.T.W., Bruno, L. and Caneva, G. (2021). Photosynthetic response to different light exposures and associated environmental conditions of the subaerial, epilithic green alga *Trentepohlia umbrina*. *Phycologia*, 60(5), 449–461.

European Commission: Directorate-General for Environment. (2021). EU biodiversity strategy for 2030: Bringing nature back into our lives. Luxembourg: Publications Office of the European Union.

FAO. (2025). *Global Forest Resources Assessment 2025*. Rome: FAO.

Forest Europe. (2020). *State of Europe's forests 2020*.

Franzén, M., Hall, M., Sunde, J. and Forsman, A. (2024). Regeneration patterns of native and introduced oak species in Sweden: Investigating the roles of latitude, age, and environmental gradients. *Forest Ecology and Management*, 561, 121871.

Friedrichs, D.A., Trouet, V., Büntgen, U., Frank, D.C., Esper, J., Neuwirth, B. and Löffler, J. (2009). Species-specific climate sensitivity of tree growth in Central-West Germany. *Trees*, 23(4), 729–739.

Fridman, J., Holm, S., Nilsson, M., Nilsson, P., Ringvall, A.H. and Ståhl, G. (2014). Adapting National Forest Inventories to changing requirements: the case of the Swedish National Forest Inventory at the turn of the 20th century. *Silva Fennica*, 48(3).

FSC Sweden. (2020). *FSC-standard för skogsbruk i Sverige*.

Giovannini, G., Perulli, D., Piussi, P. and Salbitano, F. (1992). Ecology of vegetative regeneration after coppicing in macchia stand in central Italy. *Vegetatio*, 99–100, 331–343.

Gil-Pelegrín, E., Peguero-Pina, J.J. and Sancho-Knapik, D. (2017). Oaks and people: a long journey together. In: Gil-Pelegrín, E., Peguero-Pina, J. and Sancho-Knapik, D. (eds.) *Oaks physiological ecology: Exploring the functional* *diversity of genus Quercus L.* Tree Physiology, Vol. 7. Cham: Springer, pp. 1–11.

Götmark, F. (2005). Browsing damage on broadleaved trees in semi-natural temperate forest in Sweden with a focus on oak regeneration. *Scandinavian Journal of Forest Research*, 20, 223–234.

Götmark, F. (2009). Experiments for alternative management of forest reserves: effects of partial cutting on stem growth and mortality of large oaks. *Canadian Journal of Forest Research*, 39, 1322–1330.

Götmark, F. (2013). Habitat management alternatives for conservation forests in the temperate zone: review, synthesis, and implications. *Forest Ecology and Management*, 306, 292–307.

Götmark, F. and Kiffer, C. (2014). Regeneration of oaks (*Quercus robur/Q. petraea*) and three other tree species during long-term succession after catastrophic disturbance (windthrow). *Plant Ecology*, 215, 1067–1080.

Hallingbäck, T., Hedenäs, L. and Weibull, H. (2006). Ny checklista för Sveriges mossor [New checklist of Swedish bryophytes]. *Svensk Botanisk Tidskrift*, 100, 96–148.

Hari, V., Rakovec, O., Markonis, Y., Hanel, M. and Kumar, R. (2020). Increased future occurrences of the exceptional 2018–2019 Central European drought under global warming. *Scientific Reports*, 10, 12207.

Hartig, F. (2022). *DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression models*. R package version 0.4.6. Available at: https://CRAN.R-project.org/package=DHARMa

Hein, S. and Dhôte, J.-F. (2006). Effect of species composition, stand density and site index on the basal area increment of oak trees (*Quercus* sp.) in mixed stands with beech (*Fagus sylvatica* L.) in northern France. *Annals of Forest Science*, 63(5), 457–467.

Hertog, I.M., Brogaard, S. and Krause, T. (2022). Barriers to expanding continuous cover forestry in Sweden for delivering multiple ecosystem services. *Ecosystem Services*, 53, 101392.

Holmström, E., Goude, M., Nilsson, O., Nordin, A., Lundmark, T. and Nilsson, U. (2018). Productivity of Scots pine and Norway spruce in central Sweden and competitive release in mixtures of the two species. *Forest Ecology and Management*, 429, 287–293.

Hothorn, T., Bretz, F. and Westfall, P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal*, 50, 346–363.

Hultberg, T., Sandström, J., Felton, A., Öhman, K., Rönnberg, J., Witzell, J. and Cleary, M. (2020). Ash dieback risks an extinction cascade. *Biological Conservation*, 244, 108516.

Hägglund, B. and Lundmark, J.E. (1977). Site index estimation by means of site properties: Scots pine and Norway spruce in Sweden. *Studia Forestalia Suecica*, 138, 38.

Hipp, A.L., Manos, P.S., González-Rodríguez, A., Hahn, M., Kaproth, M., McVay, J.D., Avalos, S.V. and Cavender-Bares, J. (2018). Sympatric parallel diversification of major oak clades in the Americas and the origins of Mexican species diversity. *New Phytologist*, 217(1), 439–452.

Jensen, J., Larsen, A., Nielsen, L.R. and Cottrell, J. (2009). Hybridization between *Quercus robur* and *Q. petraea* in a mixed oak stand in Denmark. *Annals of Forest Science*, 66, 706.

Johnson, P.S., Shifley, S.R. and Rogers, R. (2019). *The ecology and silviculture of oaks*. 3rd edn. Wallingford: CABI.

Kanjevac, B., Krstić, M., Babić, V. and Govedar, Z. (2021). Regeneration dynamics and development of seedlings in sessile oak forests in relation to light availability and competing vegetation. *Forests*, 12(4), 384.

Kašpar, J., Tumajer, J., Altman, J., Altmanova, N., Čada, V., Čihák, T., Doležal, J., Fibich, P., Janda, P., Kaczka, R. and Kolář, T. (2024). Major tree species of Central European forests differ in their proportion of positive, negative, and nonstationary growth trends. *Global Change Biology*, 30(1), e17146.

Keersmaeker, L., Vandekerkhove, K. and Verheyen, K. (2018). Species and structural diversity affect growth of oak, but not pine, in uneven-aged mature forests. *Basic and Applied Ecology*, 27, 41–50.

Kint, V., Aertsen, W., Campioli, M., Vansteenkiste, D., Delcloo, A. and Muys, B. (2012). Radial growth change of temperate tree species in response to altered regional climate and air quality in the period 1901–2008. *Climatic Change*, 115(2), 343–363.

Király, I. and Ódor, P. (2010). The effect of stand structure and tree species composition on epiphytic bryophytes in mixed deciduous–coniferous forests of western Hungary. *Biological Conservation*, 143, 2063–2069.

Király, I., Nascimbene, J., Tinya, F. and Ódor, P. (2012). Factors influencing epiphytic bryophyte and lichen species richness at different spatial scales in managed temperate forests. *Biodiversity and Conservation*, 22, 209–223.

Kirby, K. and Watkins, C. (eds.) (2015). *Europe's changing woods and forests: From wildwood to managed landscapes*. Wallingford: CABI.

Kohler, M., Pyttel, P., Kuehne, C., Modrow, T. and Bauhus, J. (2020). On the knowns and unknowns of natural regeneration of silviculturally managed sessile oak (*Quercus petraea* (Matt.) Liebl.) forests: a literature review. *Annals of Forest Science*, 77(4), 101.

Kunz, J., Löffler, G. and Bauhus, J. (2018). Minor European broadleaved tree species are more drought-tolerant than *Fagus sylvatica* but not more tolerant than *Quercus petraea*. *Forest Ecology and Management*, 414, 15–27.

Lähde, E., Laiho, O. and Norokorpi, Y. (1999). Diversity-oriented silviculture in the boreal zone of Europe. *Forest Ecology and Management*, 118, 223–243.

Larsen, J.B., Angelstam, P., Bauhus, J., Carvalho, J.F., Diaci, J., Dobrowolska, D., Gazda, A., Gustafsson, L., Krumm, F., Knoke, T., Konczal, A., Kuuluvainen, T., Mason, B., Motta, R., Pötzelsberger, E., Rigling, A. and Schuck, A. (2022). *Closer-to-nature forest management*. From Science to Policy 12. European Forest Institute.

Lenth, R. (2025). *emmeans: Estimated marginal means, aka least-squares means*. R package version 1.10.7. Available at: https://CRAN.R-project.org/package=emmeans

Leonardsson, J., Löf, M. and Götmark, F. (2015). Exclosures can favour natural regeneration of oak after conservation-oriented thinning in mixed forests in Sweden: a 10-year study. *Forest Ecology and Management*, 354, 1–9.

Leppik, E., Jüriado, I. and Liira, J. (2011). Changes in stand structure due to the cessation of traditional land use in wooded meadows impoverish epiphytic lichen communities. *The Lichenologist*, 43, 257–274.

Lindblad, M. and Foster, D.R. (2010). Dynamics of long-lived foundation species: the history of *Quercus* in southern Scandinavia. *Journal of Ecology*, 98, 1330–1345.

Lindbladh, M., Axelsson, A.-L., Hultberg, T., Brunet, J. and Felton, A. (2014). From broadleaves to spruce: the borealization of southern Sweden. *Scandinavian Journal of Forest Research*, 29, 686–696.

Lopes-Fernandes, M., Martínez-Fernández, E., Alves, R., Boa-Nova, D., Branquinho, C., Bugalho, M.N., Campos-Mardones, F., Coca-Pérez, A., Frazão-Moreira, A., Marques, M. and Moreno-Ortiz, J. (2024). Cork oak woodlands and decline: a social-ecological review and future transdisciplinary approaches. *Agroforestry Systems*, 98(6), 1927–1944.

Long, J.W., Goode, R.W., Gutierrez, R.J., Lackey, J.J. and Anderson, M.K. (2016). Managing California black oak for tribal ecocultural restoration. *Journal of Forestry*.

Löf, M., Karlsson, M., Sonesson, K., Welander, T.N. and Collet, C. (2007). Growth and mortality in underplanted tree seedlings in response to variations in canopy closure of Norway spruce stands. *Forestry*, 80, 371–383.

Lüdecke, D. (2024). *sjPlot: Data visualization for statistics in social science*. R package version 2.8.17. Available at: https://CRAN.R-project.org/package=sjPlot

Lüdecke, D., Ben-Shachar, M.S., Patil, I., Waggoner, P. and Makowski, D. (2021). performance: An R package for assessment, comparison and testing of statistical models. *Journal of Open Source Software*, 6, 3139.

Lyubenova, A., Baranowska, M., Menkis, A., Davydenko, K., Nowakowska, J., Borowik, P. and Oszako, T. (2024). Prospects for oak cultivation in Europe under changing environmental conditions and increasing pressure from harmful organisms. *Forests*, 15(12), 2164.

Martín, J.A., Fuentes-Utrilla, P., Gil, L. and Witzell, J. (2010). Ecological factors in Dutch elm disease complex in Europe: a review. *Ecological Bulletins*, 53, 209–224.

Mason, W., Kerr, G. and Simpson, J. (1999). What is continuous cover forestry? Information Note. Edinburgh: Forestry Commission.

Mason, W.L., Diaci, J., Carvalho, J. and Valkonen, S. (2022). Continuous cover forestry in Europe: usage and the knowledge gaps and challenges to wider adoption. *Forestry: An International Journal of Forest Research*, 95(1), 1–12.

McGillycuddy, M., Warton, D.I., Popovic, G. and Bolker, B.M. (2025). Parsimoniously fitting large multivariate random effects in glmmTMB. *Journal of Statistical Software*, 112(1), 1–19.

Medina, M., Reyes-Martín, M.P., Levy, L., Lázaro-González, A., Andivia, E., Annighöfer, P., Assaad, F., Bauhus, J., Benavides, R., Böhlenius, H. and Cambria, V.E. (2024). Ex situ germination of European acorns: data from 93 batches of 12 *Quercus* species. *Annals of Forest Science*, 81(1), 50.

Meyer, J.B., Gallien, L. and Prospero, S. (2015). Interaction between two invasive organisms on the European chestnut: does the chestnut blight fungus benefit from the presence of the gall wasp? *FEMS Microbiology Ecology*, 91, fiv122.

Miller, G.W. (2000). Effect of crown growing space on the development of young hardwood crop trees. *Northern Journal of Applied Forestry*, 17(1), 28–35.

Mitchell, R.J., Bellamy, P.E., Ellis, C.J., Hewison, R.L., Hodgetts, N.G., Iason, G.R., Littlewood, N.A., Newey, S., Stockan, J.A. and Taylor, A.F.S. (2019). Collapsing foundations: the ecology of the British oak, implications of its decline and mitigation options. *Biological Conservation*, 233, 316–327.

Mitchell, R.J., Bellamy, P.E., Broome, A., Ellis, C.J., Hewison, R.L., Iason, G.R., Littlewood, N.A., Newey, S., Pozsgai, G., Ray, D. and Stockan, J.A. (2022). Cumulative impact assessments of multiple host species loss from plant diseases show disproportionate reductions in associated biodiversity. *Journal of Ecology*, 110(1), 221–231.

Mölder, A., Meyer, P. and Nagel, R.V. (2019). Integrative management to sustain biodiversity and ecological continuity in Central European temperate oak (*Quercus robur*, *Q. petraea*) forests: an overview. *Forest Ecology and Management*, 437, 324–339.

Moning, C., Werth, S., Dziock, F., Bässler, C., Bradtka, J., Hothorn, T. and Müller, J. (2009). Lichen diversity in temperate montane forests is influenced by forest structure more than climate. *Forest Ecology and Management*, 258, 745–751.

Mosandl, R. and Kleinert, A. (1998). Development of oaks (*Quercus petraea* (Matt.) Liebl.) emerged from bird-dispersed seeds under old-growth pine (*Pinus sylvestris* L.) stands. *Forest Ecology and Management*, 106, 35–44.

Näslund, M. (1936). *Skogsförsöksanstaltens gallringsförsök i tallskog* [Forest research institute's thinning experiments in Scots pine forests]. *Meddelanden från Statens skogsförsöksanstalt*.

National Forest Inventory, SLU. (2026). *Unpublished data*. Department of Forest Resource Management, Swedish University of Agricultural Sciences, Umeå. Available at: http://www.slu.se/en/nfi

Nascimbene, J., Marini, L. and Nimis, P.L. (2009b). Influence of tree species on epiphytic macrolichens in temperate mixed forests of northern Italy. *Canadian Journal of Forest Research*, 39, 785–791.

Nascimbene, J., Marini, L. and Ódor, P. (2012). Drivers of lichen species richness at multiple spatial scales in temperate forests. *Plant Ecology & Diversity*, 5(3), 355–363.

Nascimbene, J., Thor, G. and Nimis, P.L. (2013). Effects of forest management on epiphytic lichens in temperate deciduous forests of Europe: a review. *Forest Ecology and Management*, 298, 27–38.

Nicolescu, V.N., Vor, T., Brus, R., Đodan, M., Perić, S., Podrázský, V., Andrašev, S., Tsavkov, E., Ayan, S., Yücedağ, C. and Trajkov, P. (2025). Management of sessile oak (*Quercus petraea* (Matt.) Liebl.), a major forest species in Europe. *Journal of Forestry Research*, 36(1), 78.

Nixon, K.C. (2006). Global and neotropical distribution and diversity of oak (*Quercus*) and oak forests. In: Kappelle, M. (ed.) *Ecology and conservation of neotropical montane oak forests*. Ecological Studies, Vol. 185. Berlin: Springer, pp. 3–13.

Nordén, B., Rørstad, P.K., Magnér, J., Götmark, F. and Löf, M. (2019). The economy of selective cutting in recent mixed stands during restoration of temperate deciduous forest. *Scandinavian Journal of Forest Research*, 34, 709–717.

Norman, J., Ellingson, L., Boman, M. and Mattsson, L. (2010). The value of forests for outdoor recreation in southern Sweden: are broadleaved trees important? *Ecological Bulletins*, 53, 21–32.

Ogana, F.N., Holmström, E., Sharma, R.P., Langvall, O. and Nilsson, U. (2023). Optimizing height measurement for the long-term forest experiments in Sweden. *Forest Ecology and Management*, 532, 120843.

O'Hara, K.L. (1986). Developmental patterns of residual oaks and oak and yellow-poplar regeneration after release in upland hardwood stands. *Southern Journal of Applied Forestry*, 10, 244–248.

Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Cáceres, M., Durand, S., Evangelista, H., FritzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M., Lahti, L., McGlinn, D., Ouellette, M., Ribeiro Cunha, E., Smith, T., Stier, A., ter Braak, C., Weedon, J. and Borman, T.(2025). *vegan: Community ecology package*. R package version 2.6-10. Available at: https://CRAN.R-project.org/package=vegan

Palik, B.J., D'Amato, A.W., Franklin, J.F. and Johnson, K.N. (2020). *Ecological silviculture: foundations and applications*. Long Grove, IL: Waveland Press.

Paltto, H., Nordén, B. and Götmark, F. (2008). Partial cutting as a conservation alternative for oak (*Quercus* spp.) forest: response of bryophytes and lichens on dead wood. *Forest Ecology and Management*, 256(4), 536–547.

Paltto, H., Thomasson, I. and Nordén, B. (2010). Multispecies and multiscale conservation planning: setting quantitative targets for red-listed lichens on ancient oaks. *Conservation Biology*, 24(3), 758–768.

Petersson, L.K., Milberg, P., Bergstedt, J., Dahlgren, J., Felton, A.M., Götmark, F., Salk, C. and Löf, M. (2019). Changing land use and increasing abundance of deer cause natural regeneration failure of oaks: six decades of landscape-scale evidence. *Forest Ecology and Management*, 444, 299–307.

Petersson, L.K., Dey, D.C., Felton, A.M., Gardiner, E.S. and Löf, M. (2020). Influence of canopy openness, ungulate exclosure, and low-intensity fire for improved oak regeneration in temperate Europe. *Ecology and Evolution*, 10, 2626–2637.

Pisani, T., Paoli, L., Gaggi, C., Pirintsos, S.A. and Loppi, S. (2007). Effects of high temperature on epiphytic lichens: issues for consideration in a changing climate scenario. *Plant Biosystems*, 141, 164–169.

Pommerening, A. (2023). *Continuous cover forestry: theories, concepts, and implementation*. Hoboken, NJ: John Wiley & Sons.

R Core Team. (2025). *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. Available at: https://www.R-project.org/

Reboredo, F. and Pais, J. (2014). Evolution of forest cover in Portugal: a review of the 12th–20th centuries. *Journal of Forest Research*, 25, 249–256.

Riesco Muñoz, G., Remacha Gete, A. and Gasalla Regueiro, M. (2014). Sawing yield in oak (*Quercus robur*) wood affected by insect damage. *International Biodeterioration & Biodegradation*, 86, 102–107.

Rindi, F. and Guiry, M.D. (2002). Diversity, life history, and ecology of *Trentepohlia* and *Printzina* (Trentepohliales, Chlorophyta) in urban habitats in western Ireland. *Journal of Phycology*, 38(1), 39–54.

Rohner, B., Bigler, C., Wunder, J., Brang, P. and Bugmann, H. (2012). Fifty years of natural succession in Swiss forest reserves: changes in stand structure and mortality rates of oak and beech. *Journal of Vegetation Science*, 23, 892–905.

Rohner, B., Waldner, P., Lischke, H., Ferretti, M. and Thürig, E. (2017). Predicting individual-tree growth of central European tree species as a function of site, stand, management, nutrient, and climate effects. *European Journal of Forest Research*, 137, 29–44.

Ruiz-Alonso, M., Zapata, L., Pérez-Díaz, S., López-Sáez, J.A. and Fernández-Eraso, J. (2017). Selection of firewood in northern Iberia: archaeobotanical data from three archaeological sites. *Quaternary International*, 431, 61–72.

Sadeghi, S.M.M., Gordon, D.A. and Van Stan II, J.T. (2020). A global synthesis of throughfall and stemflow hydrometeorology. In: Van Stan, J., Gutmann, E. and Friesen, J. (eds.) *Precipitation partitioning by vegetation*. Cham: Springer, pp. 37–66.

Santesson, R., Moberg, R., Nordin, A., Tønsberg, T. and Vitikainen, O. (2004). *Lichen-forming and lichenicolous fungi in Fennoscandia*. Uppsala: Museum of Evolution, Uppsala University.

Schelhaas, M.-J., Hengeveld, G.M., Heidema, N., Thürig, E., Rohner, B., Vacchiano, G., Vayreda, J., Redmond, J., Socha, J., Fridman, J., Tomter, S., Polley, H., Barreiro, S. and Nabuurs, G.-J. (2018). Species-specific, pan-European diameter increment models based on data of 2.3 million trees. *Forest Ecosystems*, 5, 21.

Schmitt, A., Trouvé, R., Seynave, I. and Lebourgeois, F. (2020). Decreasing stand density favors resistance, resilience, and recovery of *Quercus petraea* trees to a severe drought, particularly on dry sites. *Annals of Forest Science*, 77, 52.

Schröder, J. and von Gadow, K. (1999). Testing a new competition index for maritime pine in northwestern Spain. *Canadian Journal of Forest Research*, 29(2), 280–283.

Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi, J. and Lexer, M.J. (2017). Forest disturbances under climate change. *Nature Climate Change*, 7(6), 395–402.

Sellers, K.F., Borle, S. and Shmueli, G. (2012). The COM-Poisson model for count data: a survey of methods and applications. *Applied Stochastic Models in Business and Industry*, 28, 104–116.

Singh, S.P. and Singh, J.S. (1986). Structure and function of the Central Himalayan oak forests. *Proceedings of the Indian Academy of Sciences (Plant Sciences)*, 96, 159–189.

Skogsdata. (2025). Current data on Swedish forests from the National Forest Inventory. Department of Forest Resource Management, *Swedish University of Agricultural Sciences*, Umeå.

Skogsstyrelsen. (2023). Förutsättningar för hyggesfritt skogsbruk och definition av naturnära skogsbruk i Sverige. Rapport 2023:16.

SLU Artdatabanken. (2020). *Rödlistade arter i Sverige 2020*. Uppsala: Swedish University of Agricultural Sciences.

SLU Artdatabanken. (2026). *Artfakta*. Available at: https://www.artfakta.se [Accessed 6 January 2026].

SLU (Swedish University of Agricultural Sciences). (2025). *Markfuktighet*. Available at: https://www.slu.se/om-slu/organisation/institutioner/markmiljo/miljoanalys/markinfo/standort/markfuktighet/ [Accessed 11 December 2025].

SMHI (Swedish Meteorological and Hydrological Institute). (2025). *Griddad nederbörd- och temperaturdata (PTHBV)*. Available at: https://www.smhi.se/data/nederbord-och-fuktighet/nederbord/griddad-nederbord--och-temperaturdata [Accessed 8 January 2026].

SMHI (Swedish Meteorological and Hydrological Institute). (2025). *Temperature*. Available at: https://www.smhi.se/en/climate/tools-and-inspiration/climate-indicators/temperature [Accessed 26 September 2025].

Spector, T. and Putz, F.E. (2006). Crown retreat of open-grown southern live oaks (*Quercus virginiana*) due to canopy encroachment in Florida, USA. *Forest Ecology and Management*, 228, 168–176.

Spinoni, J., Vogt, J.V., Naumann, G., Barbosa, P. and Dosio, A. (2018). Will drought events become more frequent and severe in Europe? *International Journal of Climatology*, 38, 1718–1736.

Stahl-Streit, J. (2004). Die Verjüngung der Eiche im Dauerwald: ein Diskussionsbeitrag für die Praxis [Oak regeneration under continuous cover forestry]. *Dauerwald*, 41–45.

Stavi, I., Thevs, N., Welp, M. and Zdruli, P. (2022). Provisioning ecosystem services related to oak (*Quercus*) systems: a review of challenges and opportunities. *Agroforestry Systems*, 96, 293–313.

Stimm, K., Heym, M., Uhl, E., Tretter, S. and Pretzsch, H. (2021). Height growth-related competitiveness of oak (*Quercus petraea* (Matt.) Liebl. and *Quercus robur* L.) under climate change in Central Europe: is silvicultural assistance still required in mixed-species stands? *Forest Ecology and Management*, 482.

Sumida, A., Ito, H. and Isagi, Y. (1997). Trade-off between height growth and stem diameter growth for an evergreen oak, *Quercus glauca*, in a mixed hardwood forest. *Functional Ecology*, 11, 300–309.

ter Steege, H. (2018). *Hemiphot.R: Free R scripts to analyse hemispherical photographs for canopy openness, leaf area index and photosynthetically active radiation under forest canopies*. Unpublished report. Leiden: Naturalis Biodiversity Center.

Trouvé, R., Bontemps, J.-D., Collet, C., Seynave, I. and Lebourgeois, F. (2017). Radial growth resilience of sessile oak after drought is affected by site water status, stand density, and social status. *Trees*, 31, 517–529.

Truffaut, L., Chancerel, E., Ducousso, A., Dupouey, J.-L., Badeau, V., Ehrenmann, F. and Kremer, A. (2017). Fine-scale species distribution changes in a mixed oak stand over two successive generations. *New Phytologist*, 215(1), 126–139.

Vallet, P. and Perot, T. (2016). Tree diversity effect on dominant height in temperate forest. *Forest Ecology and Management*, 381, 106–114.

Vanderpoorten, A. and Goffinet, B. (2009). *Introduction to bryophytes*. Cambridge: Cambridge University Press.

von Lüpke, B. (1998). Silvicultural methods of oak regeneration with special respect to shade-tolerant mixed species. *Forest Ecology and Management*, 106, 19–26.

von Lüpke, B. and Hauskeller-Bullerjahn, K. (1999). Kahlschlagfreier Waldbau: wird die Eiche an den Rand gedrängt? [Production forestry without clear felling: will oak become marginalized?]. *Forst und Holz*, 54, 563–568. (In German)

Wallgren, M. (2023). *BETT-försöket de första tio åren: Betets effekter på tallens tillväxt 2012–2022*. Skogforsk Arbetsrapport 1173–2023.

Ward, J.S. (2009). Intensity of precommercial crop tree release increases diameter growth and survival of upland oaks. *Canadian Journal of Forest Research*, 39, 118–130.

Watt, A.S. (1919). On the causes of failure of natural regeneration in British oakwoods. *Journal of Ecology*, 7, 173–203.

Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. New York: Springer. Available at: https://ggplot2.tidyverse.org

Wierzcholska, S., Łubek, A., Dyderski, M.K., Horodecki, P., Rawlik, M. and Jagodziński, A.M. (2024). Light availability and phorophyte identity drive epiphyte species richness and composition in mountain temperate forests. *Ecological Informatics*, 80, 102475.

Wing, J.T. (2012). Keeping Spain afloat: state forestry and imperial defense in the sixteenth century. *Environmental History*, 17, 116–145.

Wirth, V. (1995). *Die Flechten Baden-Württembergs. Teil 2*. Stuttgart: Eugen Ulmer GmbH & Co.

Wykoff, W.R. (1990). A basal area increment model for individual conifers in the Northern Rocky Mountains. *Forest Science*, 36, 1077–1104.

Yang, Y., Sun, H. and Körner, C. (2020). Explaining the exceptional 4270 m high elevation limit of an evergreen oak in the south-eastern Himalayas. *Tree Physiology*, 40(10), 1327–1342.

Zenner, E.K., Heggenstaller, D.J., Brose, P.H., Peck, J.L.E. and Steiner, K.C. (2012). Reconstructing the competitive dynamics of mixed-oak neighborhoods. *Canadian Journal of Forest Research*, 42, 1714–1723.

Popular science summary

Forests around the world are under growing pressure from climate change and human land use. Intensive forestry, large-scale plantations, and changes in traditional disturbance patterns have reduced forest biodiversity and altered how forests function. As a result, the remaining structurally diverse forests are increasingly important for maintaining biodiversity and ecosystem services. Oak forests are among the most valuable forest ecosystems in temperate regions. They provide timber, recreation, water regulation, and habitat for a wide range of species. Oaks live for centuries and create complex forest structures that support many insects, fungi, lichens, mosses, and birds. This complexity also makes oak forests more resilient to environmental change. Despite these strengths, many oak forests are struggling to replace old trees with younger ones. While seedlings may still appear, too few oaks manage to grow into larger trees that can form the future forest canopy.

In Sweden, oak forests are mainly found in the southern part of the country and today make up only a small fraction of the forest landscape. Most forests are dominated by Norway spruce and Scots pine, while oaks are largely confined to older age classes. Young and medium-sized oaks are rare, which raises concerns about the long-term survival of oak forests and the many species that depend on them. Historically, oak forests were shaped by grazing and different forms of selective cutting, that kept them relatively open. As these practices disappeared, forests became denser and shadier, favouring faster-growing, shade-tolerant trees over oaks. This shift has made it harder for oaks to regenerate and grow. One alternative forest management approach is continuous cover forestry (in Swedish: *hyggesfritt skogsbruk* or *kontinuitetsskogsbruk*), which avoids clear-cutting and aims to maintain forest cover at all times. This approach promotes structural diversity and biodiversity, often through selective cutting of individual trees. However, it remains unclear whether oaks can successfully regenerate and grow under these conditions without targeted management, since too little disturbance may favour competing tree species.

This thesis investigates oak recruitment, the critical stage when young oaks grow into established trees, and how it is affected by forest structure, selective cutting management, and climate. An oak recruit is defined here as a young oak tree, either pedunculate oak or sessile oak, with a trunk diameter between five and twenty centimetres. This stage represents a critical transition between small saplings and mature canopy trees, and it is increasingly recognized as a bottleneck for the long-term survival of oak forests. The thesis brings together four studies that span different time scales, reflecting the slower growth of oak trees. Two studies used field experiments to examine how young oaks respond to forest management over several years. Another study focused on mature oaks, investigating how forest management affects lichens and bryophytes living on oak trunks. A fourth study analysed long-term data from the Swedish National Forest Inventory to track growth of oak recruits over four decades. By combining long-term national forest data with field experiments across southern Sweden, the aim was to improve our understanding of how oak forests can be managed to promote oak recruitment and increase the chances of them growing into dominant, mature canopy trees.

Across all studies, the success of young oak trees was strongly limited by competition from surrounding trees. Dense forests with many shade-tolerant tree species, high overall tree number, and large amounts of standing timber consistently reduced the number and growth of young oaks. In the first experiment, short-term results showed that selective cutting can create more favourable conditions for oak recruits in oak-dominated forests. Lower tree density was linked to a higher number of oak recruits. More open canopies with tree species that allow more light to pass through their crowns appeared to support oak recruitment. These results highlight that both tree density and species composition are important considerations when managing forests to promote oak recruits. In a second, longer-term experiment, selective cutting was applied in a forest dominated by Norway spruce and Scots pine but that contained many oak recruits. Removing competing trees, particularly Norway spruce, clearly improved the diameter growth of oak recruits, although their height growth did not increase. Importantly, this treatment improved the position of young oaks relative to larger, dominant trees, increasing their chances of responding positively to future forest management and environmental change. Forests with a wider mix of tree sizes also provided better light conditions for oak growth. Stronger or repeated interventions may be necessary to help oaks progress to eventually reach the canopy.

The longest-running experiment showed that selective cutting also benefits epiphytic biodiversity linked to oak trees. Lichen diversity on mature oaks remained stable in managed forests but declined in unmanaged, dense stands. This was especially true for crustose lichens, the group that included all red-listed species recorded in the study. Mosses and liverworts were less common, making their responses harder to assess. Some declines in lichen groups could not be fully explained, indicating that factors such as local microclimate or broader environmental change may also play a role. The long-term analysis of the National Forest Inventory data strengthened the findings for oak recruits. Growth of oak recruits has steadily declined over the past forty years in Sweden, even after accounting for forest structure, site conditions, and climate. The strongest declines occurred in dense forests and where oak grew alongside many shade-tolerant tree species. Climate effects were also important but depended on soil moisture. Oaks grew better on dry sites when rainfall was higher, whereas warmer conditions reduced growth on moderately moist sites. This is especially relevant in Sweden, where oak grows near its northern range limit and may be less well adapted to recent warming trends.

Overall, the results show that forest management can successfully support oak-associated biodiversity while maintaining continuous forest cover. However, oak recruitment does not happen automatically under low-intervention management. To secure the future of oak forests, selective cutting must be applied deliberately and potentially repeatedly to reduce competition and maintain sufficient light. Encouragingly, oak regeneration and recruitment respond to similar forest conditions, meaning that well-designed management might be able to support the entire life cycle of oak trees. Without such targeted efforts, oak forests risk becoming dominated by older trees with few younger individuals to replace them in the future.

Populärvetenskaplig sammanfattning

Skogar världen över påverkas allt mer av klimatförändringar och mänsklig markanvändning. Intensivt skogsbruk, stora plantageliknande system och förändringar i hur skogar traditionellt har brukats har lett till minskad biologisk mångfald och förändrade ekosystemfunktioner. Därför har de skogar som fortfarande är strukturellt varierade fått en allt viktigare roll för att bevara biologisk mångfald och viktiga ekosystemtjänster. Ekskogar är bland de mest värdefulla skogstyperna i tempererade områden. De bidrar med virke, rekreation, vattenreglering och livsmiljöer för ett stort antal arter. Eftersom ekar kan leva i flera hundra år skapar de komplexa skogsstrukturer som gynnar många insekter, svampar, lavar, mossor och fåglar. Denna strukturella mångfald gör också ekskogar mer motståndskraftiga mot miljöförändringar. Trots detta har många ekskogar svårt att föryngra sig och unga träd blir sällan stora dominerande ekar. Även om små ekplantor ofta etableras i stort antal är det få som lyckas växa vidare till större träd som kan bilda framtidens krontak.

I Sverige finns ekskogar främst i den södra delen av landet och utgör i dag endast en liten del av skogslandskapet. De flesta skogar domineras av gran och tall, medan ekar huvudsakligen förekommer i äldre åldersklasser. Unga och medelstora ekar är ganska ovanliga, vilket väcker oro för både ekskogarnas långsiktiga överlevnad och för de många arter som är knutna till ek. Historiskt har ekskogar formats av bete, olika former av plockhuggning och andra störningar, vilket höll dem relativt öppna. När dessa brukningsformer försvann blev skogarna tätare och skuggigare, vilket gynnade snabbväxande och skuggtåliga trädslag på bekostnad av ek. Detta har gjort det svårare för ekar att både föryngras och växa vidare. Ett alternativt sätt att bruka skog är kontinuitetsskogsbruk, även kallat hyggesfritt skogsbruk, där kalavverkning undviks och skogstäcket behålls över tid. Metoden syftar till att främja variation i skogens struktur och biologisk mångfald, ofta genom plockhuggning av enskilda träd. Samtidigt är det oklart om ekar klarar att föryngras och växa framgångsrikt i sådana system utan särskilda skogsskötselåtgärder, eftersom en för låg störningsnivå kan gynna konkurrerande trädslag.

Denna avhandling fokuserar på rerytering av unga ekar, det vill säga det kritiska stadiet då unga ekar växer från små träd till etablerade individer med potential att nå krontaket, och hur denna process påverkas av skogsstruktur, selektiv avverkning och klimat. Här definieras rekryter av ek som en ung ek, antingen skogsek eller bergek, med en stamdiameter vid brösthöjd på mellan fem och tjugo centimeter. Detta steg utgör en viktig övergång mellan plantstadiet och vuxna träd och betraktas allt oftare som en flaskhals för ekskogars framtid. Avhandlingen omfattar fyra studier med olika tidsperspektiv, anpassade till ekens långsamma tillväxt. Två studier bygger på fältexperiment där unga ekars respons på skogsskötsel följdes under flera år. En tredje studie undersökte hur selektiv avverkning påverkar lavar och mossor som lever på äldre ekars stammar. Den fjärde studien analyserade långsiktiga data från Riksskogstaxeringen för att följa tillväxten hos rekryter av ek under fyra decennier. Genom att kombinera dessa angreppssätt var målet att bättre förstå hur ekskogar kan skötas för att öka chanserna för unga ekar att utvecklas till framtida dominerande träd.

Samtliga studier visar att konkurrens från omgivande träd kraftigt begränsar unga ekars framgång. Täta skogar med många skuggtåliga trädslag, högt stamantal och stora mängder stående virke minskade både antalet och tillväxten hos rekryter av ek. I det första experimentet visade kortsiktiga resultat att plockhuggning kan skapa bättre förutsättningar för unga ekar i skogar dominerade av ek. Lägre trädtäthet var kopplad till fler rekryter av ek, och mer öppna kronor samt trädslag som släpper igenom mer ljus verkade gynna rekryteringen. Detta visar att både stamtäthet och trädslagsammansättning är viktiga att beakta vid skötsel av ekskogar. I ett andra, mer långsiktigt experiment genomfördes plockhuggning i en skog dominerad av gran och tall men med många unga ekar. När konkurrerande träd, särskilt gran, togs bort ökade diametertillväxten hos rekryterna av ek tydligt, även om höjdtillväxten inte ökade. Behandlingen förbättrade också ekarnas konkurrensläge gentemot större träd, vilket ökade deras möjligheter att svara positivt på framtida åtgärder och miljöförändringar. Skogar med större variation i trädstorlekar gav dessutom bättre ljusförhållanden för ekens tillväxt. För att ekar ska kunna nå skogstaket kan därför kraftigare eller upprepade åtgärder behövas.

Den längst pågående studien visade att selektiv avverkning även har positiva effekter på biologisk mångfald knuten till ekar. Mångfalden av lavar på gamla ekar förblev stabil i skötta bestånd men minskade i täta, oskötta skogar. Detta gällde särskilt skorplavar, den grupp som omfattade alla rödlistade arter som påträffades. Mossor och levermossor var mindre vanliga, vilket gjorde deras respons svårare att tolka. Vissa minskningar i grupper av lavar kunde inte förklaras fullt ut, vilket tyder på att även faktorer som mikroklimat eller bredare miljöförändringar kan spela in. Den långsiktiga analysen av Riksskogstaxeringens data bekräftade mönstren för rekryter av ek. Tillväxten hos unga ekar har minskat stadigt under de senaste fyrtio åren, även när hänsyn tagits till skogsstruktur, ståndort och klimat. De största minskningarna skedde i täta skogar och där ekar växte tillsammans med många skuggtåliga trädslag. Klimatet hade också betydelse, men effekterna berodde också på markfuktighet. Ekar växte bättre på torra marker när nederbörden stundtals var hög, medan stundtals varmare förhållanden minskade tillväxten på måttligt fuktiga marker. Detta är särskilt viktigt i Sverige, där ek växer nära sin nordliga utbredningsgräns och kan vara sämre anpassad till den senaste tidens uppvärmning.

Sammanfattningsvis visar resultaten att skogsskötsel kan stödja biologisk mångfald knuten till ek. De visar samtidigt att rekrytering av ekar inte sker av sig själv vid lågintensiv skötsel. För att säkra framtiden för ekskogar krävs att plockhuggning används medvetet och vid behov upprepas för att minska konkurrens och säkerställa tillräckligt ljus. Ett positivt resultat är att både föryngring och rekrytering av ek gynnas av liknande skogliga förhållanden, vilket innebär att genomtänkt skötsel kan stödja hela ekens livscykel. Utan sådana riktade insatser riskerar ekskogar att domineras av gamla träd utan tillräckligt många yngre för framtiden.

Acknowledgements

When Magnus offered me this PhD position four and a half years ago, I never thought everything would turn out as well as it has. A PhD involves so much more than just a degree. Moving to a new country, learning about a new culture, and meeting so many fantastic people along the way, including many new friends, are the true rewards of this journey.

First, I would like to thank my supervisor group. Some might say that too many cooks spoil the broth (or in Swedish, the soup), but I think in this case it was just the right amount. Though I sometimes feel that the university might have put a cap on the number of supervisors just for you, Magnus.
Magnus, both of us started new jobs around the same time, and it has been quite a learning curve, but I think it all worked out in the end. Thank you for giving me room to grow, but also for being there whenever I needed support.
Annika and PO, your support meant the world to me. I was able to learn so much from you, and most importantly, when you challenged me, you always remained kind. I don't take that for granted, and I will never be able to bake enough cake to show my gratitude.
Jorge, you left the department for sunny Spain, and I could not fault you. The knowledge and happiness you brought to our meetings were ever-present, even over Zoom. At the beginning, I dreaded the moments when PO and Jorge told me, "Maybe you can try one more thing." By now, I was actually excited to hear which other ideas you might have =)
Emile and Björn, your support over Zoom was invaluable, especially considering all the early meetings for Emile.

Would I recommend six supervisors to anyone? Well, that depends. If it is a group of people like the ones above, who always try their best to help you in any situation and who bring joy to the table even when things are tough, then yes, 100 %.

The PhD journey is filled with ups and downs but having a PhD group that makes the boat ride seem less daunting is worth so much. Thank you for building such a supportive environment, something that is not a given in academia.

To all the colleagues at the department, thanks for all the nice fika and lunch breaks. Special thanks to Leonie, Adam, and Luis Andres for always keeping things entertaining.

Jorge and Carmen, you made me feel so welcome during my stay in Madrid. Thank you for showing me around.
Derek, the best office mate one could have wished for.
Jaime, Trini, Joan, Julia, and Donnie. Thanks for all the fun days we have shared so far. Let's keep our midsummer tradition going!
Leonie, Skåne Frozen Trail 2027? I think I needed more mental recovery from the previous two editions than from my PhD, but third time is the charm?
Julia, the joy it brings me that you understand all the German inside jokes, which really are not as funny when translated.

Mama, Papa, Opa, Lena, Alex, and Hugo. You don't really know what it is I am exactly doing, but your constant support nonetheless means the world. Hugo, video calling you made any work stress unimportant and always reminded me that there are far more important things in life. I highly recommend talking to a two-year-old to put things into perspective.
To all my additional family that came into my life over the years, thank you for everything. Grazie di tutto. Il panettone è stato fondamentale per scrivere la mia tesi =)
To Lina and Resi, I guess this might count as a good excuse for procrastinating your letter for six months by now =)

Laura and Henrik, it doesn't happen too often that you move to a different country and meet your people. I am so glad we all made these excellent choices that led us here. Looking forward to many more road trips, spontaneous or planned, and days spent together.

Fabian, Sharath, Ted, Peki, and Bonnie. Visits to Germany wouldn't be the same without my second home away from home. All the good food (courtesy of Chef Fabian), the long talks, and grovelling for the gatitos' attention made me realize that we don't see each other often enough. Still, I wouldn't trade this for anything, and I will be forever grateful for all your support and shared stories. Paxi, I cannot wait to meet you.

To all the dogs I loved before. Cau, Lingon, Valky, and Eskil, thank you for all the cuddles and walks.

Sierra, my big puppy. You have only been part of this craziness for seven months, but you couldn't have come into our lives at a better time.

Luca, my home. Maria gave us the chance, but you made everything possible. I cannot wait for what is to come.

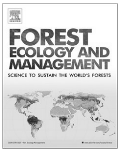
Maria Laura, so many decisions and an incredible amount of luck have led to me meeting you. Mariacina, who would have thought that you forwarding me a PhD position would lead me to happiness that I could have never dreamed of. If Luca is my home, then you are my person.

Forest Ecology and Management 586 (2025) 122721

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco



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

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ARTICLE INFO

Keywords:
Continuous cover forestry
Pedunculate oak
Quercus
Sessile oak
Shade-casting index

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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https://doi.org/10.1016/j.foreco.2025.122721
Received 16 January 2025; Received in revised form 3 April 2025; Accepted 10 April 2025

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

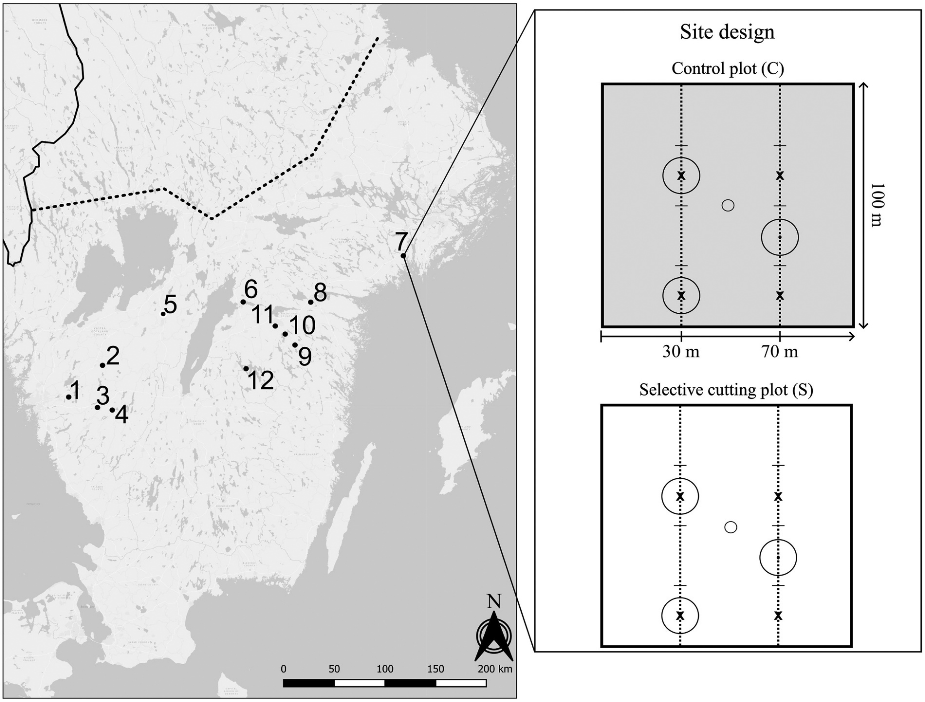

Fig. 1. Study region in Sweden and the location of the 12 experimental sites established in 2016 (left) south of “Limes Norrlandicus” (denoted by dashed line, Sjörs, 1999), with an example of the experimental design (right). Numbers 1–12 in the map correspond to the site numbers in Table 1. The experimental 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 °C 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 [°C]	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 ± 277 stems per ha^{-1} with 427 ± 122 overstory stems and 235 ± 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 ± 439 stems per ha^{-1} with 508 ± 194 overstory stems and 374 ± 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 ($\Delta AIC = -5.2$ 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 ($\Delta AIC = -1.1$), 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

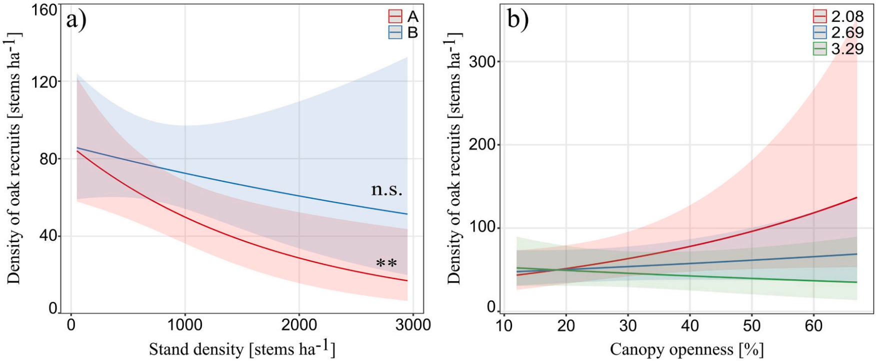

Fig. 2. Density of oak recruits in diameter class A and B as a function of stand density (a). Combined effect of the shade-casting index and canopy openness on density of oak recruits (b). Lines represent model predictions within the continuous variable range (a) and the other continuous variable set 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. “* *” $P \leq 0.01$ and “n.s.” $P > 0.05$. Note that the interaction terms illustrated in (b) were non-significant ($P = 0.071$), see Table S3.

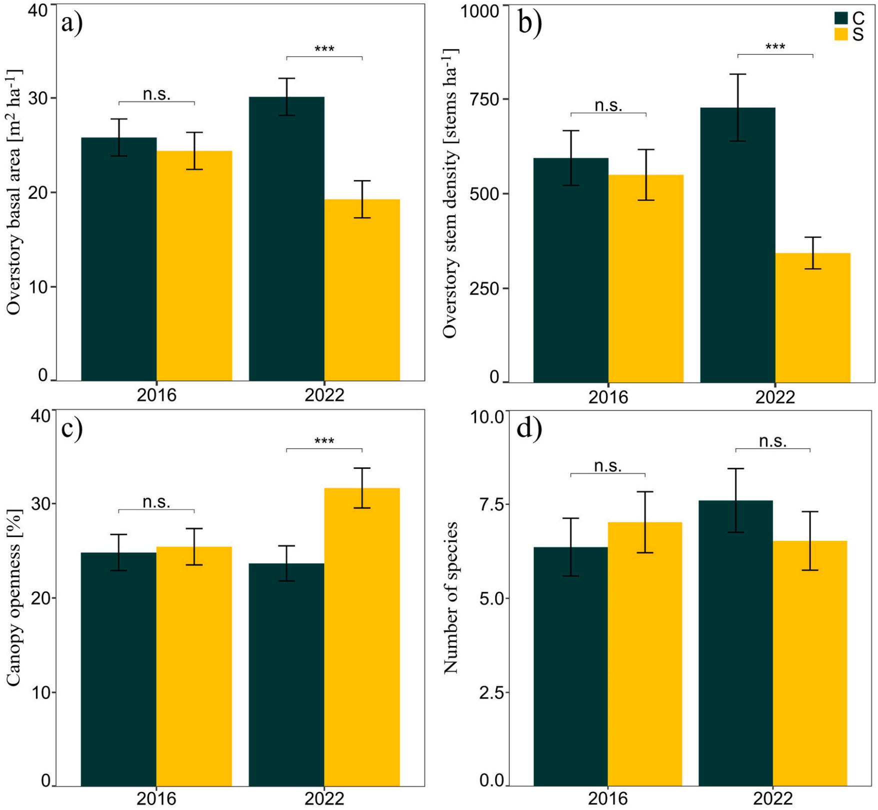

Fig. 3. Comparison of four stand structural attributes in control (C, green) and selective cutting (S, yellow) treatments. (a) mean basal area of overstory trees; (b) mean stem density of overstory trees; (c) mean canopy openness; and (d) mean number of tree species before (2016) and six years after 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 treeś 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

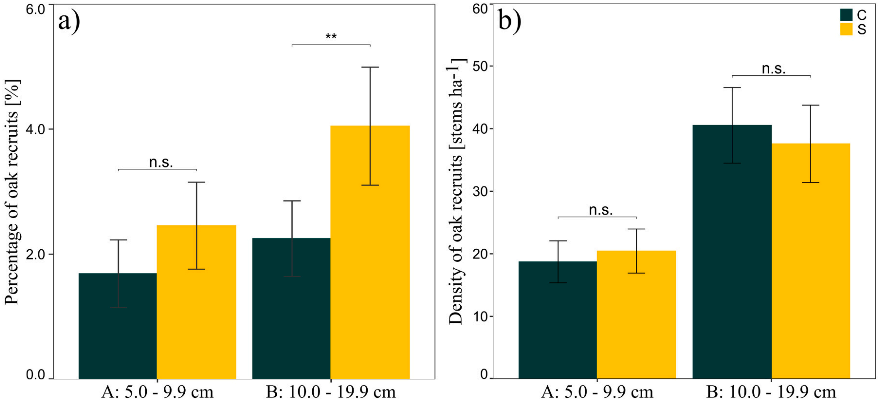

Fig. 4. Mean proportion of oak recruits relative to the total number of stems ha^{-1} (a), and mean stem density of oak recruits (b). The x-axis shows the two diameter classes ‘A’ (5.0–9.9 cm dbh) and ‘B’ (10.0–19.9 cm dbh) and the two treatments control (C) in green and selective cutting (S) in yellow in 2022. Error bars represent ± SE. “* *” P ≤ 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.

Acknowledgments

This work was supported by the Foundation Oscar and Lili Lamms Memory (grant 20201123); Eric and Ebba Larsson's and Thure Rignells foundation (protocol no 123, 19 February 2022); Swedish Research Council Formas (grant 2022–02070); the Research Council of Norway (SynForest project 336381); MCIN/AEI/10.13039/501100011033 and by the European Union "NextGenerationEU/PRTR." (grant RYC2021–033031-I); and the USDA Forest Service (Southern Research Station). The authors declare no conflict of interest.

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.

References

Annighöfer, P., Beckschafer, P., Vor, T., Ammer, C., 2015. Regeneration patterns of European oak species (Quercus petraea (Matt.) Liebl., Quercus robur L.) in dependence of environment and neighbourhood. PLoS One 10, e0134935. https://doi.org/10.1371/journal.pone.0134935.

Aussenac, G., 2000. Interactions between forest stands and microclimate: ecophysiological aspects and consequences for silviculture. Ann. Sci. 57, 287–301. https://doi.org/10.1051/forest:2000119.

Berg, Å., Ehnström, B., Gustafsson, L., Hallingbäck, T., Jonsell, M., Weslien, J., 1994. Threatened plant, animal, and fungus species in Swedish forests: distribution and habitat associations. Conserv Biol. 8, 718–731. https://doi.org/10.1046/j.1523-1739.1994.08030718.x.

Bobiec, A., Reif, A., Öllerer, K., 2018. Seeing the oakscape beyond the forest: a landscape approach to the oak regeneration in Europe. Land. Ecol. 33, 513–528. https://doi.org/10.1007/s10980-018-0619-y.

Bolte, A., Ammer, C., Löf, M., Madsen, P., Nabuurs, G.-J., Schall, P., Spathelf, P., Rock, J., 2009. Adaptive forest management in central Europe: climate change impacts, strategies and integrative concept. Scand. J. Res 24, 473–482. https://doi.org/10.1080/02827580903418224.

Brooks, M.E., Kristensen, K., van, Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Maechler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R. J. 9, 378–400. https://doi.org/10.32614/RJ-2017-066.

Brunet, J., Bukina, Y., Hedwall, P.-O., Holmström, E., von Oheimb, G., 2014. Pathogen induced disturbance in temperate forests: Evidence from a 100-year data set in southern Sweden. Basic Appl. Ecol. 15, 114–121. https://doi.org/10.32614/RJ-2017-066.

Buckley, Y.M., 2015. Generalized linear models. In: Fox, G.A., Negrete-Yankelevich, S., Sosa, V.J. (Eds.), Ecological Statistics: Contemporary theory and application, online edn. Oxford. https://doi.org/10.1093/acprof:oso/9780199672547.003.0007. Accessed 14 January 2025.

Canham, C.D., Finzi, A.C., Pacala, S.W., Burbank, D.H., 1994. Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. Can. J. Res 24, 337–349. https://doi.org/10.1139/x94-046.

Chakraborty, D., Ciceu, A., Ballian, D., Garzón, M.B., Bolte, A., Bozic, G., Buchacher, R., Čepl, J., Cremer, E., Ducousso, A., Gaviria, J., George, J.P., Hardtke, A., Ivankovic, M., Klisz, M., Kowalczyk, J., Kremer, A., Lstibůrek, M., Longauer, R., Mihai, G., Nagy, L., Petkova, K., Popov, E., Schirmer, R., Skrøppa, T., Solvin, T.M., Steffenrem, A., Stejskal, J., Stojnic, S., Volmer, K., Schueler, S., 2024. Assisted tree migration can preserve the European forest carbon sink under climate change. Nat. Clim. Chang. https://doi.org/10.1038/s41558-024-02080-5.

De Lombaerde, E., Verheyen, K., Van Calster, H., Baeten, L., 2019. Tree regeneration responds more to shade casting by the overstorey and competition in the understorey than to abundance per se. Ecol. Manag 450, 117492. https://doi.org/10.1016/j.foreco.2019.117492.

Depauw, L., Perring, M.P., Landuyt, D., Maes, S.L., Blondeel, H., De Lombaerde, E., Brūmelis, G., Brunet, J., Closset-Kopp, D., Decocq, G., Den Ouden, J., Härdtle, W., Hédl, R., Heinken, T., Heinrichs, S., Jaroszewicz, B., Kopecký, M., Liepina, I., Macek, M., Máliš, F., Schmidt, W., Smart, S.M., Ujházy, K., Wulf, M., Verheyen, K., 2020. Evaluating structural and compositional canopy characteristics to predict the light-demand signature of the forest understorey in mixed, semi-natural temperate forests. Appl. Veg. Sci. 24, e12532. https://doi.org/10.1111/avsc.12532.

Drössler, L., Attocchi, G., Jensen, A.M., 2012. Occurence and management of oak in southern Swedish forests. Forstarchiv 83, 163–169. https://doi.org/10.4432/0300-4112-83-163.

Ellenberg H., Weber H.E., Düll R., Wirth V., Werner W., Paulissen D. (1992) Zeigerwerte von Pflanzen in Mitteleuropa. 2nd edn. Scripta Geobotanica. Göttingen.

Fahlvik, N., Johansson, U., 2021. Growth of northern red oak in southern Sweden. Scand. J. Res 36, 442–447. https://doi.org/10.1080/02827581.2021.1973086.

Forrester, D.I., Ammer, C., Annighöfer, P.J., Barbeito, I., Bielak, K., Bravo-Oviedo, A., Coll, L., del Río, M., Drössler, L., Heym, M., Hurt, V., Löf, M., den Ouden, M., Pach, M., Gonzalez Pereira, M., Plaga, B.N.E., Ponette, Q., Skrzyszewski, J., Sterba, H., Svoboda, M., Zlatanov, T.M., Pretzsch, H., 2017. Effects of crown architecture and stand structure on light absorption in mixed and monospecific *Fagus sylvatica* and *Pinus sylvestris* forests along a productivity and climate gradient through Europe. J. Ecol. 106, 746–760. https://doi.org/10.1111/1365-2745.12803.

Gil-Pelegrín E., Peguero-Pina J.J., Sancho-Knapik D. (2017) Oaks Physiological Ecology. Exploring the Functional Diversity of Genus Quercus L. Tree Physiology. Springer, Cham.

Götmark, F., 2013. Habitat management alternatives for conservation forests in the temperate zone: review, synthesis, and implications. Ecol. Manag 306, 292–307. https://doi.org/10.1016/j.foreco.2013.06.014.

Götmark, F., Kiffer, C., 2014. Regeneration of oaks (Quercus robur/Q. petraea) and three other tree species during long-term succession after catastrophic disturbance (windthrow). Plant Ecol. 215, 1067–1080. https://doi.org/10.1007/s11258-014-0365-4.

Hale, S.E., Edwards, C., 2002. Comparison of film and digital hemispherical photography across a wide range of canopy densities. Agric. Meteor. 112, 51–56. https://doi.org/10.1016/S0168-1923(02)00042-4.

Hartig F. (2022) DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models. R package version 0.4.6. ⟨https://CRAN.R-project.org/package=DHARMa⟩.

Harvey, J.E., Smiljanić, M., Scharnweber, T., Buras, A., Cedro, A., Cruz-García, R., Drobyshev, I., Janecka, K., Jansons Ā, Kaczka, R., Klisz, M., Läänelaid, A., Matisons, R., Muffler, L., Sohar, K., Spyt, B., Stolz, J., van der Maaten, E., van der Maaten-Theunissen, M., Vitas, A., Weigel, R., Kreyling, J., Wilmking, M., 2020. Tree growth influenced by warming winter climate and summer moisture availability in northern temperate forests. Glob. Chang Biol. 26, 2505–2518. https://doi.org/10.1111/gcb.14966.

Hersbach H., Bell B., Berrisford P., Biavati G., Horányi A., Muñoz Sabater J., Nicolas J., Peubey C., Radu R., Rozum I., Schepers D., Simmons A., Soci C., Dee D., Thépaut J.-N. (2023) ERA5 monthly averaged data on single levels from 1940 to present. Copernicus Climate Change Service (C3S) Climate Data Store (CDS). https://doi.org/10.24381/cds.f17050d7.

Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous Inference in General Parametric Models. Biom. J. 50, 346–363. https://doi.org/10.1002/bimj.200810425.

Johnson P.S., Shifley S.R., Rogers R., Dey D.C., Kabrick J.M. (2019) The ecology and silviculture of oaks. 3d edition. CABI Publishing, UK.

Kanjevac, B., Krstić, M., Babić, V., Govedar, Z., 2021. Regeneration dynamics and development of seedlings in sessile oak forests in relation to the light availability and competing vegetation. Forests 12, 384. https://doi.org/10.3390/f12040384.

Király, I., Ódor, P., 2010. The effect of stand structure and tree species composition on epiphytic bryophytes in mixed deciduous–coniferous forests of Western Hungary. Biol. Conserv 143, 2063–2069. https://doi.org/10.1016/j.biocon.2010.05.014.

Kohler, M., Pyttel, P., Kuehne, C., Modrow, T., Bauhus, J., 2020. On the knowns and unknowns of natural regeneration of silvicultural managed sessile oak (*Quercus petraea* (Matt.) Liebl.) forests - a literature review. Annals of Forest Science 77, 101. https://doi.org/10.1007/s13595-020-00998-2.

Lenth R.V. (2023) emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.8.9. ⟨https://CRAN.R-project.org/package=emmeans⟩.

Leonardsson, J., Löf, M., Götmark, F., 2015. Exclosures can favour natural regeneration of oak after conservation-oriented thinning in mixed forests in Sweden: a 10-year study. Ecol. Manag 354, 1–9. https://doi.org/10.1016/j.foreco.2015.07.004.

Ligot, G., Balandier, P., Fayolle, A., Lejeune, P., Claessens, H., 2013. Height competition between *Quercus petraea* and *Fagus sylvatica* natural regeneration in mixed and uneven-aged stands. Ecol. Manag 304, 391–398. https://doi.org/10.1016/j.foreco.2013.05.050.

Lindbladh, M., Axelsson, A.-L., Hultberg, T., Brunet, J., Felton, A., 2014. From broadleaves to spruce – the borealization of southern Sweden. Scand. J. Res 29, 686–696. https://doi.org/10.1080/02827581.2014.960893.

Lindbladh, M., Foster, D.R., 2010. Dynamics of long-lived foundation species: the history of *Quercus* in southern Scandinavia. J. Ecol. 98, 1330–1345. https://doi.org/10.1111/j.1365-2745.2010.01733.x.

Löf, M., Karlsson, M., Sonesson, K., Welander, T.N., Collet, C., 2007. Growth and mortality in underplanted tree seedlings in response to variations in canopy closure of Norway spruce stands. Forestry 80, 371–383 https://doi.org/10.1093/fores try/cpm022.

Lüdecke D. (2023) sjPlot: Data Visualization for Statistics in Social Science. R package version 2.8.15. ⟨https://CRAN.R-project.org/package=sjPlot⟩.

Mason, W.L., Diaci, J., Carvalho, J., Valkonen, S., 2022. Continuous cover forestry in Europe: usage and the knowledge gaps and challenges to wider adoption. Forestry 95, 1–12. https://doi.org/10.1093/forestry/cpab038.

Modrow, T., Kuehne, C., Saha, S., Bauhus, J., Pyttel, P.L., 2019. Photosynthetic performance, height growth, and dominance of naturally regenerated sessile oak (Quercus petraea [Mattuschka] Liebl.) seedlings in small-scale canopy openings of varying sizes. Eur. J. Res 139, 41–52. https://doi.org/10.1007/s10342-019-01238-7.

Mölder, A., Meyer, P., Nagel, R.-V., 2019. Integrative management to sustain biodiversity and ecological continuity in Central European temperate oak (Quercus robur, Q. petraea) forests: an overview. Ecol. Manag 437, 324–339. https://doi.org/10.1016/j.foreco.2019.01.006.

Mosandl, R., Kleinert, A., 1998. Development of oaks (*Quercus petraea* (Matt.) Liebl.) emerged from bird-dispersed seeds under old-growth pine (*Pinus silvestris* L.) stands. Ecol. Manag 106, 35–44. https://doi.org/10.1016/S0378-1127(97)00237-5.

Navarro-González, I., Pérez-Luque, A.J., Bonet, F.J., Zamora, R., 2013. The weight of the past: land-use legacies and recolonization of pine plantations by oak trees. Ecol. Appl. 23, 1267–1276. https://doi.org/10.1890/12-0459.1.

Nordén, B., Rørstad, P.K., Magnér, J., Götmark, F., Löf, M., 2019. The economy of selective cutting in recent mixed stands during restoration of temperate deciduous forest. Scand. J. Res 34, 709–717. https://doi.org/10.1080/02827581.2019.1679876.

Norman, J., Ellingson, L., Boman, M., Mattsson, L., 2010. The value of forests for outdoor recreation in southern Sweden: are broadleaved trees important. Ecol. Bull. 53, 21–32. ⟨http://www.jstor.org/stable/41442016⟩.

Petersson, L.K., Dey, D.C., Felton, A.M., Gardiner, E.S., Löf, M., 2020. Influence of canopy openness, ungulate exclosure, and low-intensity fire for improved oak regeneration in temperate Europe. Ecol. Evol. 10, 2626–2637. https://doi.org/10.1002/ece3.6092.

Petersson, L.K., Milberg, P., Bergstedt, J., Dahlgren, J., Felton, A.M., Götmark, F., Salk, C., Löf, M., 2019. Changing land use and increasing abundance of deer cause natural regeneration failure of oaks: six decades of landscape-scale evidence. Ecol. Manag 444, 299–307. https://doi.org/10.1016/j.foreco.2019.04.037.

Pommerening, A., Murphy, S.T., 2004. A review of the history, definitions and methods of continuous cover forestry with special attention to afforestation and restocking. Forestry 77, 37–44. https://doi.org/10.1093/forestry/77.1.27.

R Core Team (2023) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Schmitt, A., Trouvé, R., Seynave, I., Lebourgeois, F., 2020. Decreasing stand density favors resistance, resilience, and recovery of *Quercus petraea* trees to a severe drought, particularly on dry sites. Ann. Sci. 77, 52. https://doi.org/10.1007/s13595-020-00959-9.

Shifley S.R. (2004) Oak Growth and Response to Thinning. Gen. Tech. Rep. SRS-73. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station, 198-205.

Sjörs, H., 1999. The background: Geology, climate and zonation. In: Rydin, H., Snoeijs, P., Diekmann, M. (Eds.), Swedish Plant Geography. Acta Phytogeography Suecica, 84. Uppsala, pp. 5–14.

SLU (Swedish University of Agricultural Sciences) (2020) Skogsdata 2020: aktuella uppgifter om de svenska skogarna från Riksskogstaxeringen. Dept For Res Manag, Swedish University of Agricultural Sciences (SLU), Umeå (In Swedish.).

SMHI (Swedish Meteorological and Hydrological Institute) (2024) "Sommaren 2018 - Extremt varm och solig". Available at: ⟨https://www.smhi.se/klimat/klimatet-da-och-nu/arets-vader/sommaren-2018-extremt-varm-och-solig-1.138134⟩ [January 14, 2025].

Stahl-Streit, J., 2004. Die Verjüngung der Eiche im Dauerwald – Ein Diskussionsbeitrag für die Praxis [Oak regeneration under continuous cover forestry. Dauerwald 30, 41–45.

Stavi, I., Thevs, N., Welp, M., Zdruli, P., 2022. Provisioning ecosystem services related with oak (*Quercus*) systems: a review of challenges and opportunities. Agroforest Sys 96, 293–313. https://doi.org/10.1007/s10457-021-00718-3.

Stimm, K., Uhl, E., Pretzsch, H., 2022. Chances and limitations of mixed oak regeneration under continuous canopy cover—evidence from long-term observations. Forests 3 2052. https://doi.org/10.3390/f13122052.

Sundberg S., Carlberg T., Sandström J., Thor G. (2019) Värdväxters betydelse för andra organismer – med fokus på vedartade värdväxter [The importance of vascular plants (notably woody species) to other organisms]. ArtDatabanken Rapporterar 22, Artdatabanken SLU, Uppsala (In Swedish.).

ter Steege, H. (2018) Hemiphot.R: Free R scripts to analyse hemispherical photographs for canopy openness, leaf area index and photosynthetic active radiation under forest canopies. Unpublished report. Naturalis Biodiversity Center, Leiden.

Trouvé, R., Bontemps, J.-D., Collet, C., Seynave, I., Lebourgeois, F., 2017. Radial growth resilience of sessile oak after drought is affected by site water status, stand density, and social status. Trees 31, 517–529. https://doi.org/10.1007/s00468-016-1479-1.

Verheyen, K., Baeten, L., De Frenne, P., Bernhardt-Römermann, M., Brunet, J., Cornelis, J., Decocq, G., Dierschke, H., Eriksson, O., Hédl, R., Heinken, T., Hermy, M., Hommel, P., Kirby, K., Naaf, T., Peterken, G., Petřík, P., Pfadenhauer, J., Van Calster, H., Walther, G.-R., Wulf, M., Verstraeten, G., 2012. Driving factors behind the eutrophication signal in understorey plant communities of deciduous temperate forests. J. Ecol. 100, 352–365. https://doi.org/10.1111/j.1365-2745.2011.01928.x.

von Lüpke, B., 1998. Silvicultural methods of oak regeneration with special respect to shade tolerant mixed species. Ecol. Manag 106, 19–26. https://doi.org/10.1016/S0378-1127(97)00235-1.

von Lüpke, B., Hauskeller-Bullerjahn, K., 1999. Kahlschlagfreier waldbau: wird die eiche an den rand gedrängt? [production forestry without clear felling: will oak become marginalized? Forst und Holz 54, 563–568 (In German).

Wilcke, R.A.I., Kjellström, E., Lin, C., Matei, D., Moberg, A., Tyrlis, E., 2020. The extremely warm summer of 2018 in Sweden – set in a historical context. Earth Syst. Dynam 11, 1107–1121. https://doi.org/10.5194/esd-11-1107-2020.

Zenner, E.K., Heggenstaller, D.J., Brose, P.H., Peck, J.L.E., Steiner, K.C., 2012. Reconstructing the competitive dynamics of mixed-oak neighborhoods. Can. J. Res 42, 1714–1723. https://doi.org/10.1139/x2012-119.

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Forest Ecology and Management 604 (2026) 123519

Contents lists available at ScienceDirect

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Effects of target diameter cutting on oak recruitment in a multilayered mixed conifer-broadleaved stand in southern Sweden

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ARTICLE INFO

Keywords:
Crown social position
Pedunculate oak
Recruitment
Sessile oak
Target diameter cutting

ABSTRACT

Managing multi-layered forest stands is increasingly promoted as a strategic adaptation measure to climate change. Pedunculate oak (*Quercus robur* L.) and sessile oak (*Q. petraea* (Matt.) Liebl.) are ecologically and economically important species and considered important components of future forest management. However, forest management is challenged by the unsuccessful recruitment of oak, particularly under selective cutting systems, due to the species' relatively high light requirements. In this study, we investigated the long-term effects of different selective cutting treatments on oak recruitment in multi-layered mixed stands over 16 years in southern Sweden. We studied the individual tree diameter growth, height growth, and transition of oak recruits into higher canopy positions. All target diameter cutting treatments significantly promoted the individual tree diameter growth of oak recruits, compared to the control. Observed height growth was lower in target diameter cutting treatments. However, target diameter cutting treatments increased the transitions of oak recruits into higher canopy positions. The higher diameter growth and canopy class transitions into higher classes are achieved by the treatment that removed more Norway spruce trees. Therefore, to promote the advancement of oak recruits into higher canopy positions, target diameter cutting could be an appropriate management alternative if it is sufficiently strong and is focused on removing the most competitive tree species.

1. Introduction

The two predominant oak species, pedunculate oak (*Quercus robur* L.) and sessile oak (*Q. petraea* (Matt.) Liebl.), are among the most important hardwood tree species in Central and Northern Europe from both ecological and forest management perspectives (Johnson et al., 2019; Mölder et al., 2019a; Kohler et al., 2020). The two species together constitute about 10 % of the stands in Europe, making them the second most common deciduous tree species in the region after European beech (*Fagus sylvatica* L.) (FOREST EUROPE, 2020). Oak-dominated forests provide a wide variety of forest ecosystem services, including high-value timber and habitats for key biodiversity, such as lichens, fungi, insects, birds, and small mammals (Löf et al., 2016). Given their tolerance to extreme climatic events such as drought (Mette et al., 2013; Kunz et al., 2018; Perkins et al., 2018) and storng wind (Nicolescu et al., 2025), these two oak species are widely considered important components of future climate-resilient mixed-species forests in the region. The establishment of mixed broadleaved forests has been considered as a strategic adaptation measure to climate change (Bolte et al., 2009). Therefore, their proportions in forest cover are expected to increase (Bolte et al., 2009; Löf et al., 2016; Schroeder et al., 2021). Despite this potential for adaptation of forest management to climate change, there remains uncertainty about the suitable silvicultural approaches promoting natural regeneration and recruitment of oak in multi-layered, mixed-species forests for sustainable oak management.

The two oak species in Sweden are limited to the south (Fig. 1), temperate region of the country (Lindbladh et al., 2000; Lindbladh and Foster, 2010). During the past century, oak forests were not only heavily affected by conifer plantations, especially of Norway spruce (*Picea abies* L.) and Scots pine (*Pinus sylvestris* L.), but also by intensive land use changes for agriculture (Lindbladh et al., 2000); as a result, oak now constitutes only less than 2 % of the standing volume in Sweden (Skogsdata, 2024). Most of these remaining oak forests are currently, or have been, managed for timber production by non-industrial private forest owners under diverse management regimes. The three common management regimes in oak forest management include: (1) intensive oak timber production targeting the production of high-value timber and following the contemporary silvicultural practices, (2) combined

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https://doi.org/10.1016/j.foreco.2026.123519
Received 25 July 2025; Received in revised form 23 December 2025; Accepted 6 January 2026

management for timber production and biodiversity, and (3) biodiversity conservation without management intervention (Löf et al., 2016). With appropriate management, these forests can yield high-value timber generating substantial economic returns.

Regeneration and recruitment are the two interconnected processes from the seedling stage to the development of mature trees. Successful natural regeneration of oaks is fundamental to sustaining oak forests. However, oak forests are experiencing widespread regeneration failures (Petersson et al., 2019). The natural regeneration success depends on several biotic and abiotic factors, where heavy browsing pressure, low light availability, and competing vegetation, among others, are significant factors that negatively affect natural regeneration (Löf, 2000; Mölder et al., 2019b; Kohler et al., 2020; Löf et al., 2021). Oak recruitment, or the transition of saplings into overstory canopy layers, is another important stand development process (Camp and Oliver, 2004) in which established saplings grow to pole and sawtimber-size trees. Successful oak recruitment is achieved when the desired species can compete and grow into dominant and codominant overstory trees (Dey, 2014). Disturbances are considered necessary for successful natural regeneration and recruitment of oaks (Götmark, 2007; Götmark and Kiffer, 2014). In these regards, silvicultural approaches in oak-dominated forests are necessary for enhancing light availability and controlling competing vegetation during different development stages to foster natural regeneration and recruitment of oak into upper canopy layers.

Given the ecological and economic importance of oaks, it is challenging to balance conservation of oak-dominated forests rich in biodiversity while maintaining their economic viability (Puettmann et al., 2015; Löf et al., 2016; Stimm et al., 2022). An alternative silvicultural approach, such as continuous cover forestry (CCF), could be an option for multipurpose forest management (Peura et al., 2018; Mason et al., 2022). The CCF approach is based on ecological and biological principles, with its most prominent tenet being the abandonment of large-scale clear-cutting in favour of more environmentally friendly harvesting practices, such as selective cutting, group selection, variable density thinning, and natural regeneration methods (Pommerening and Murphy, 2004; Brunner et al., 2025). Studies suggest that canopy gaps created by selective cutting are beneficial for successful oak natural regeneration because gaps enhance light availability and selective cutting removes competing trees (Březina and Dobrovolný, 2011; Modrow et al., 2019; Kanjevac et al., 2021; Plaugher and Schuler, 2025; Pohl et al., 2025). However, there remains a limited understanding of how different forms of selective cutting favour the development of oak recruits beyond establishment, especially those that are tall enough and freed from browsing pressure.

Target diameter cutting, among different selective cutting techniques, is a forest management approach in which selected trees that reach a specified diameter at breast height (DBH) are cut, aiming to balance economic and ecological sustainability. Target diameter cutting is often used to transform even-aged forests into uneven-aged or uneven-sized structures (Sterba and Zingg, 2001; Price and Price, 2006). Target diameter cutting approaches are more flexible and practical to apply in comparison with other forms of selective cutting systems because the DBH for cutting can be adjusted to different sites with varying growth conditions and tree species (Zell et al., 2004; Roessiger et al., 2016). As such, cutting of different species and tree individuals with large diameters creates canopy gaps that are beneficial for trees in lower canopy layers, especially for more light-demanding tree species. Understanding the response of oak recruits following such cuttings, in terms of tree crown social position within the stand, and height and diameter growth, could lead to reliable canopy manipulation strategies that promote oak recruits in multi-layered mixed temperate forests.

This study aims to determine the growth and advancement of oak recruits into higher levels of tree crown social position in response to

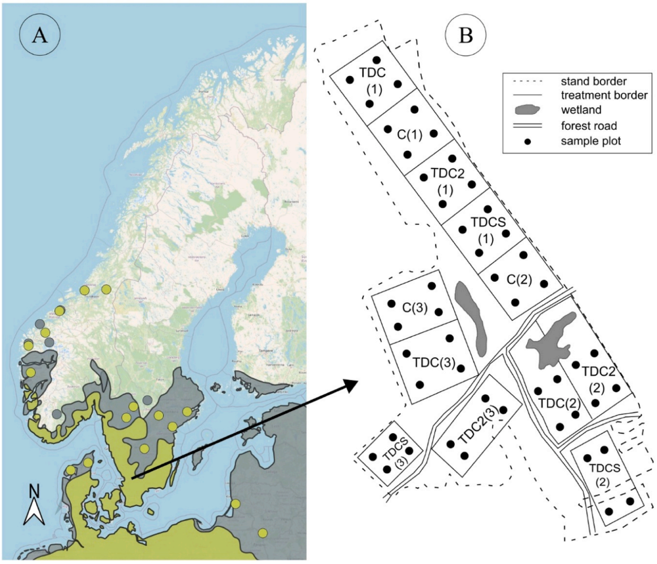

Fig. 1. Location of the experiment in southwestern Sweden (A), and the experimental design (B). Green colour in A represents distribution area of *Quercus petraea* (Matt. Liebl.), and grey colour represents distribution area of *Quercus robur* (L.) which overlap, and extends beyond, the distribution area of *Q. petraea*. TDC, TDC2, and TDCS represent different forms of target diameter cutting treatments, and C represents control without treatment. TDC stands for target diameter cutting, TDC2 is target diameter cutting with slightly modified target diameter, TDCS represent TDC and soil scarification treatment. In each treatment there were four permanent measurement plots (black filled circles). See Section 2.2 for detailed descriptions.

three different forms of selective cutting (here, different target diameter cuttings) over a period of 16 years. More specifically, we ask three research questions: (1) which stand structural and individual tree characteristics influence the diameter growth and height growth of oak recruits, (2) how does target diameter cutting influence diameter growth and height growth of oak recruits, and (3) how does target diameter cutting affect transition of oak recruits into higher tree crown/social classes?

2. Materials and methods

2.1. Study site and history

The study stand with a total area of 19 ha is located in southwest Sweden at Tönnersjöheden Experimental Forest, 20 km east of Halmstad (56°42′02″ N, 13°7′56″ E, Fig. 1). The stand is located on a productive site with site indices (dominant height at age 100) for Norway spruce and Scots pine of 32 m and 28 m, respectively (Drössler et al., 2012). The mean annual temperature is 6.7°C, and the mean annual precipitation is 1050 mm, with a vegetation period (growing season) lasting 215 days (Drössler et al., 2012). The soil type is a podzol on a sandy moraine. The forest floor is covered mainly by *Vaccinium myrtillus* L. and *Deschampsia flexuosa* L. Trin.

The study stand was established in 1912 by seeding of Scots pine with abundant natural regeneration of silver birch (*Betula pendula* Roth). Previously, the site was *Calluna* spp. heathland with some sparsely scattered trees across the landscape. Since then, many other species have established naturally over time. Currently, the stand is mainly composed of mature Scots pine and Norway spruce in the overstory. Broadleaved species, such as oak, silver birch, European beech, and European aspen (*Populus tremula* L.), are found in the under- and mid-stories. The first cutting in the stand was carried out in 1947, releasing single Scots pine trees, and thinning was then carried out several times (1947, 1953, 1958, 1974, and 1991) before the establishment of the current experiment.

2.2. Experimental design and data collection

The experiment consists of three blocks. Within each block, four treatments were randomly established, and each treatment area was 1 ha. The four treatments applied were: control without target diameter cutting (C); target diameter cutting (TDC); target diameter cutting with soil scarification (TDCS); and target diameter cutting with modified target diameters compared to the other two treatments (TDC2). DBH thresholds by tree species applied for cutting in each treatment are listed in Table 1. Target diameter thresholds applied in TDC and TDCS were chosen according to economic criteria based on timber quality and timber prices per tree species published annually by the South Swedish forest owner association for 2006 (Drössler et al., 2017). In TDC2, target diameter thresholds were slightly modified to remove more Norway spruce trees by lowering the target diameter for spruce, thereby promoting the development of broadleaved tree species. In all treatments, trees were cut when their DBH was equal to or greater than the thresholds listed in Table 1. However, retention trees were retained to increase the natural ecological value of the stand. In the TDC2 treatment, twenty retention trees per hectare were selected, while in the other two treatments, ten trees per hectare were retained. None of these retention trees were left in the sample plots. Cutting operations were carried out in the spring of 2008/2009, and soil scarification for the TDCS treatment was implemented in the autumn of 2010 using disc-trenching, which created 0.5 m wide rows with 2 m spacing. Soil scarification treatment was conducted to improve conditions for natural regeneration (see Drössler et al., 2017). The number and basal area of trees cut and the intensity of cutting (%) during target diameter cutting in each treatment within each block is shown in Table S1. Stand characteristics for each treatment are presented in Table 2 for the first inventory (pre-harvest) in 2006 and the last inventory conducted in 2021.

Table 1
Target diameter (DBH in cm) thresholds for each species and treatments during target diameter cutting in spring of 2008/2009. Class 1 and Class 2 represent the stem quality (Class 1 indicates trees with branches smaller than 6 cm in diameter, and Class 2 includes trees with low timber quality with branches thicker than 6 cm, spike-knots or forks).

Tree species	TDC/TDCS		TDC2
	Class 1	Class 2	
Scots pine	40	30	40
Norway spruce	36	26	26
Birch	30	20	30
Oaks	60	30	60
European beech	50	30	50

In each treatment within each block, four systematically distributed 10 m radius circular plots were established, resulting in a total of 48 sample plots (Fig. 1). Individual trees were numbered and repeatedly measured in 2006, 2016, and 2021. In each such circular plot, species and DBH (in millimetres) of all trees (DBH ≥ 5 cm) were recorded. DBH was measured using a caliper in two perpendicular directions, and the average value was used as tree's DBH. At each measurement, tree height was measured only for sample trees - i.e., the five largest DBH trees in each sample plot and a number of randomly selected trees of each species - using a Vertex hypsometer and transponder (Haglöf, Sweden AB). The randomly selected trees were chosen to represent all DBH classes within each sample plot. The observations of height-diameter pairs were used to estimate the height of all trees without height measurements using the height-diameter function (Eq. 1) presented by Näslund (1936). The Näslund function was used because it is the most frequently used function to describe the height-diameter relationships in northern Europe and under Scandinavian conditions (Holmström et al., 2018, Ogana et al., 2023).

$$H = 1.3 + \frac{\mathrm{DBH}^{\gamma}}{(\alpha + \beta \times \mathrm{DBH})^{\gamma}} \tag{1}$$

where, H is the tree height (metre), DBH is the diameter at breast height (cm), α and β are parameters to be estimated, and γ was 3 for Norway spruce and 2 for Scots pine, birch, European beech and oak (Holmström et al. 2018, Ogana et al. 2023). The model coefficients were estimated separately for each species, treatment, and measurement occasion. However, due to limited number of sample trees for birch and European beech, the height-diameter equation for oak was applied to estimate their heights. All calipered trees without height observations were assigned predicted heights. Survival status of trees was also recorded. The oak mortality rates were 2 %, 2.1 %, 1.9 %, and 1.7 % in control, TDC, TDC2, and TDCS treatment, respectively, with average DBH of dead oak recruits being 8.6 cm.

The tallest and largest tree within each sample plot, regardless of species, was used to classify the social position of individual trees. The largest and tallest trees were mostly Norway spruce or Scots pine and did not include oak recruits or other oak trees. At each measurement the individual trees were classified into four crown classes based on their social positions: (i) dominant - trees forming the dominant canopy layer or reaching at least fifth-sixths of the dominant tree height within the plot, (ii) codominant - trees slightly lower than the dominant trees, typically reaching fourth-sixth to fifth-sixths of the dominant tree height, (iii) intermediate - trees with their heights reaching between three-sixths and four-sixths of the dominant tree height, and (iv) suppressed - trees that reach less than three-sixths of the dominant tree height, with their canopies suppressed under those of surrounding trees.

In this study, we focused primarily on oak recruitment. We did not distinguish the two oak species because both species are ecologically overlapping. A total 348 oak trees were observed in all three

Table 2
Pre-harvest (2006) and post-harvest (2021) stand characteristics of each treatment. The values (mean ± standard deviation) were calculated from four subplots in each treatment within each block ($n = 12$) in the experiment in Eriksköp. CV is the coefficient of deviation.

	2006				**2021**			
Characteristics	**C**	**TDC**	**TDCS**	**TDC2**	**C**	**TDC**	**TDCS**	**TDC2**
Total tree density (tree/ha)	1148 ± 273	1042 ± 192	1079 ± 333	846 ± 230	1157 ± 218	851 ± 248	851 ± 324	703 ± 340
Broadleaved density	334 ± 129	411 ± 257	313 ± 192	342 ± 199	324 ± 134	361 ± 255	257 ± 189	297 ± 196
Conifer density	814 ± 129	631 ± 257	767 ± 192	504 ± 199	833 ± 134	491 ± 256	594 ± 189	405 ± 196
Total basal area (m^2/ha)	35.9 ± 8.6	36.0 ± 7.9	38.9 ± 7	33.6 ± 6.1	48.6 ± 8.7	34.0 ± 8.8	34.7 ± 6.3	31.2 ± 11.2
Broadleaved BA	5.2 ± 4.5	5.7 ± 3.3	5.4 ± 2.4	7.9 ± 5.8	7.2 ± 5.6	8.1 ± 5.7	6.0 ± 3.6	8.7 ± 4.5
Conifer BA	30.7 ± 9.9	30.3 ± 9.5	33.5 ± 7.8	25.9 ± 7.9	41.4 ± 11.6	25.9 ± 11.0	28.8 ± 6.2	22.6 ± 9.4
Quadratic mean diameter (cm)	20.0 ± 1.6	21.1 ± 2.1	21.4 ± 0.9	22.6 ± 0.6	23.8 ± 1.8	23.1 ± 2.0	23.2 ± 1.1	24.1 ± 1.0
Tree height (m)	14.4 ± 0.5	13.9 ± 1.3	13.9 ± 0.6	13.6 ± 0.8	17.5 ± 0.9	16.0 ± 1.5	17.0 ± 0.6	15.5 ± 0.4
CV of DBH (%)	55.7 ± 3.2	58.9 ± 7.6	58.4 ± 1.4	57.5 ± 4.7	52.6 ± 3.8	49.2 ± 4.8	48.6 ± 1.9	54.0 ± 4.4
CV of height (%)	37.6 ± 4.2	36.9 ± 3.4	40.1 ± 1.4	44.1 ± 2.5	34.8 ± 4.4	36.9 ± 4.4	35.1 ± 1.1	41.6 ± 2.3

measurements, excluding the dead oak trees (Table S2**, and** Figure S1). Oak recruits were defined as oak trees with an initial DBH of 5–20 cm that belong to the suppressed, intermediate, or codominant initial canopy classes. These recruits have the potential to develop into the upper canopy layers, benefiting from crown release resulting from target diameter cutting. A total of 302 oak recruits were included in the analysis.

2.3. Quantification of diameter growth, height growth and strand structural attributes

Individual tree diameter growth (cm year^{-1}) and height growth (m year^{-1}) were calculated from repeated measurements. Annual growth rates for each individual recruit were calculated over the measurement intervals 2006–2016 and 2016–2021. The diameter and height growth data were annualized by dividing the observed periodic growth by the number of years between measurements. We did not remove zero diameter growth values (2.8 % of the total growth observations) because they may represent poor growth conditions. Negative height growth values were excluded, but zero growth values were included as they may also represent poor growth conditions and high neighbourhood competition. Stand structural variables such as stand density (trees ha^{-1}), basal area (m^2 ha^{-1}), coefficient of deviation of DBH (CVd), and coefficient of deviation of height (CVh) were calculated for each plot within each treatment at each measurement occasion (Table 3). Stand density and basal area were derived separately for conifers (Norway spruce and Scots pine) and broadleaved species (birch, European beech, and oak). We also calculated the total basal area of larger trees (BAL) than the individual oak recruits (Wykoff, 1990; Schröder, 1999) to account for competition affecting oak recruits. BAL, or overtopping basal area, simultaneously considers a tree's relative dominance and stand density. BAL was calculated for each sample plot within each treatment at each measurement occasion. The BAL of the smallest diameter tree approximately equals the total stand basal area. We also calculated the total number of trees (trees ha^{-1}) and total basal area (m^2 ha^{-1}) removed during target diameter cutting (Table S1).

Table 3
Summary of Generalized Linear Mixed Model for assessing the stand and individual tree characteristics influencing diameter growth and height growth of oak recruits. BAL: basal area of trees larger than individual oak recruits; CVd: coefficient of variation of DBH; CVh coefficient of variation of height; SE: standard error; AIC: Akaike's information criterion. All explanatory variables were natural log-transformed. Diameter growth rates were square-root transformed (See Table S3 for description of the models).

	Diameter growth			**Height growth**		
Predictors	**Estimate**	**SE**	**p-value**	**Coefficient**	**SE**	**p-value**
Intercept	-0.10	0.35	0.77	0.69	1.14	0.54
Initial DBH	0.27	0.03	< 0.001	1.73	0.22	< 0.001
Initial height	-	-	-	-2.14	0.31	< 0.001
Conifer density	-0.05	0.03	0.07	-	-	-
Broadleaved density	-	-	-	-0.20	0.08	0.01
Broadleaved BA	-0.09	0.03	< 0.001	-	-	-
BAL	-0.16	0.03	< 0.001	-	-	-
CVd	0.11	0.07	0.10	0.88	0.31	0.004
CVh	0.11	0.05	0.03	-0.97	0.28	< 0.001
Number of trees cut	-	-	-	-0.05	0.02	0.004
Variance						
Tree	0.014			0.059		
Plot	0.005			0.006		
AIC	-722.9			-445.1		

2.4. Data analysis

All data analyses were conducted in R (R Core Team, 2024). We used Generalized Linear Mixed-effects Model (GLMM) for all statistical analysis. GLMMs were performed using the "glmmTMB" package (Brooks et al., 2017). The "emmeans" package (Lenth, 2025) was used for post-hoc tests, and model evaluation, including residual diagnostics and assumption checks, was conducted with "DHARMa" package (Hartig, 2025).

To address the first research question, we examined how individual oak tree characteristics and stand structural attributes affect the individual tree diameter and height growth rates using two separate GLMM. We considered initial tree characteristics of oak recruits (DBH, height and crown class) and stand structural characteristics including conifer density (trees ha^{-1}), broadleaved density (trees ha^{-1}), conifer basal area (m^2 ha^{-1}), broadleaved basal area (m^2 ha^{-1}), BAL (m^2 ha^{-1}), CVd, and CVh as explanatory variables. In addition, the number (trees ha^{-1}) and basal area (m^2 ha^{-1}) of trees removed during target diameter cutting in 2008/2009 were also considered as explanatory variables. All these variables were included in the full GLMMs (Table S3). Variables showing high collinearity were identified using the variance inflation factor (VIF), and any variables with VIF > 5 was sequentially remove. After each removal, the models were refitted until all remaining fixed-effects variables had VIF below 5. Conifer basal area and the total basal cut during target diameter cutting were removed during this process and the remaining variables were retained in the models. The "MuMIn" package (Bartoń 2025) was then used to select the optimal models. To represent the stand conditions affecting the diameter and height growth rates, the variables derived from the first of two consecutive measurements were included in the models. A Gaussian distribution with identity link function was used in the diameter model. Diameter growth values were square-root transformed to ensure that model residuals met the assumptions of a Gaussian distribution. The height growth model included a Tweedie distribution to handle continuous height growth values, including zero. We considered individual trees nested within plots as random effects in both diameter and height growth models.

To address the second research question, which investigates how target diameter cutting influence diameter and height growth of oak recruits, we compared growth rates across treatments using GLMM. The descriptions of the models are provided in Table S3. Annual growth rates were compared among treatments by including the interaction between treatment and measurement year as fixed effects. Individual trees nested within plots were included as random effects (Table S3). A gaussian distribution with identity link function was used in the diameter model. The height growth model included a Tweedie distribution to handle continuous height growth values, including zero.

Further, we examined how target diameter cutting affects the transition of oak recruits to the higher crown classes. We defined trees that moved to higher canopy classes as 1 and, and those that remained in the same class as in the previous measurement as 0, regardless of the specific transition class (e.g., from suppressed to intermediate and intermediate to codominant). The interactions between treatments and measurement years were considered as fixed effects in GLMM. In addition, we also assessed the factors influencing the transition of oak recruits into higher canopy classes. We included individual tree variables, stand structural variables, and the number and basal area of trees cut as fixed effects, and the plots was included as random effects (Table S3). A binomial distribution with a logit link function was used in all models analysing tree crown transitions. The variable and optimal model selections were performed following the procedure as described above.

3. Results

3.1. Stand structural and individual tree characteristics affecting the diameter and height growth of oak recruits

Initial tree diameter showed a strong positive effect ($p < 0.001$) on the individual tree diameter growth of oak recruits (Table 3). A negative effect of broadleaved basal area ($p < 0.001$) and the total basal area of trees larger than individual oak recruits ($p < 0.001$) was observed. The coefficient of variation of height was found to have a positive effect ($p = 0.03$) on diameter growth.

Initial oak diameter showed a significant positive effect ($p < 0.001$), while initial tree height exhibited a negative effect ($p = 0.001$) on individual tree height growth (Table 3). Further, negative effects on height growth of oak recruits were observed for broadleaved density ($p = 0.002$), the coefficient of variation of tree height ($p < 0.001$), and the number of trees removed during target diameter cutting ($p = 0.004$). In contrast, the coefficient of variation of DBH ($p = 0.004$) had positive effects on height growth.

3.2. The effect of target diameter cutting on the diameter and height growth of oak recruits

The results indicate a significant positive influence of target diameter cutting on the diameter growth of oak recruits. Regardless of treatment types, the diameter growth rates in treatment plots were significantly higher than those in the control plots (Fig. 2**a**). The mean DBH growth rates (cm year^{-1}) in each treatment were 0.11, 0.24, 0.26, and 0.21 for control, TDC, TDC2, and TDCS, respectively. There were no significant differences ($p > 0.05$) among the three different selective cutting treatments (Fig. 2a). Eight years following selective cutting, in 2016, the diameter growth rate in TDC ($p < 0.001$) and TDC2 ($p < 0.001$) treatments was statistically higher than in C (Fig. 2b). TDCS showed no significant difference from the other two treatments or control. Sixteen years following selective cutting, in 2021, the growth rate of oak recruits was significantly higher in all selective cutting treatments compared to the control (Fig. 2b). Again, no significant differences among the selective cutting treatments were observed. In 2021, the growth rate was slightly decreased across all treatments, and the control plot showed the significantly lowest growth rate.

We found that height growth rates in TDC and TDCS treatments were significantly lower than the control without cutting (Fig. 3a). The average height growth rates (m year^{-1}) of oak recruits were 0.23, 0.17, 0.19, and 0.16 for control, TDC, TDC2, and TDCS respectively. There were no significant differences in height growth rates among the three different selective cutting treatments. Eight years after target diameter cutting, height growth rates in TDC treatment were significantly lower than in control and TDC2 treatment (Fig. 3b). However, sixteen years after cutting, height growth rates in TDCS treatment were lowest among all treatments including control, and were significantly lower than those in TDC and control.

3.3. Effects of target diameter cutting on the transition of oak recruits into higher canopy classes

Only 18 recruits in codominant positions were observed, and none of these recruits were transitioned into dominant canopy positions. We combined these 18 trees with intermediate canopy class, which did not significantly affect the results. The TDC2 treatment showed the highest transition rate of oak recruits into higher canopy classes Fig. 4a). Significant higher transition rate in TDC2 treatment (31 %) was observed than in the TDC (13 %) and TDCS (13 %) treatments, although the difference was not statistically significant compared to the control (17 %). Eight years after target diameter cutting (in 2016), no significant differences in the probability of canopy transition were observed across all

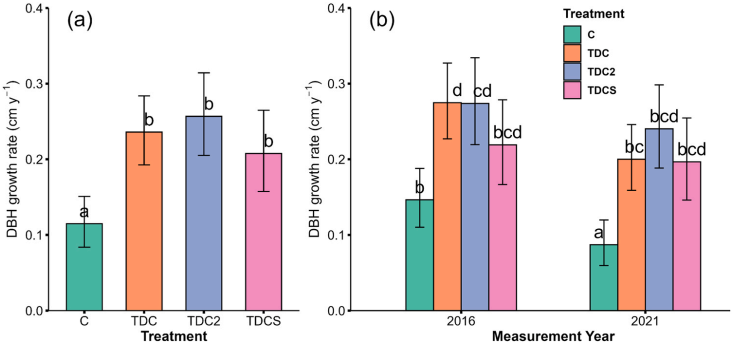

Fig. 2. Diameter growth rates of individual oak recruits in different treatments from 2006 to 2021 (a), in different measurement years (b). Measurement year 2016 in (b) represents the diameter growth between 2006 and 2016, and 2021 represents diameter growth between 2016 and 2021. Error bars indicate the ± standard error for the mean diameter growth rate. Letters in common show no significant differences ($p > 0.05$).

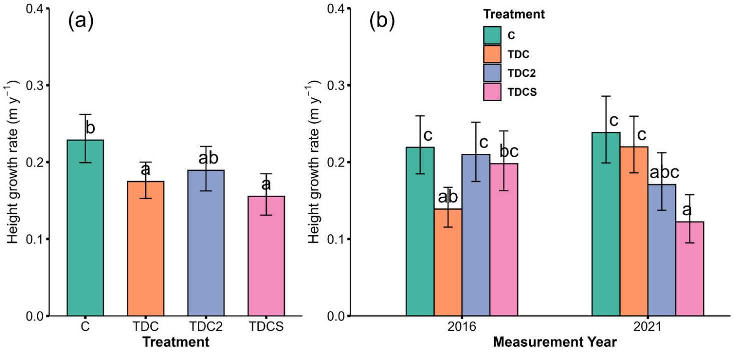

Fig. 3. Height growth of individual oak recruits in different treatments from 2006 to 2021 (a), in different measurement years (b). Measurement year 2016 in (b) represents the height growth between 2006 and 2016, and 2021 represents height growth between 2016 and 2021. Error bars indicate the ± standard error for the mean height growth rate. Letters in common show no significant differences ($p > 0.05$).

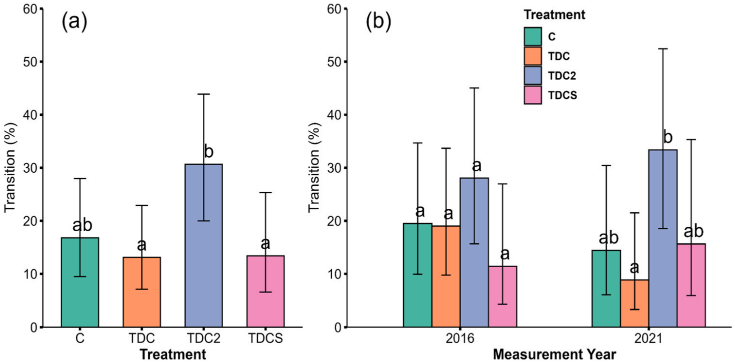

Fig. 4. The observed probability of oak recruits moving to higher canopy classes in different treatments from 2006 to 2021 (a), and in different measurement years (b). Measurement year 2016 includes all transitions between 2006 and 2016, and 2021 includes transitions between 2016 and 2021. This included all transitions, i.e., from suppressed into intermediate, intermediate into codominant. Error bars indicate the ± standard error for the mean probability of canopy class transition. Letters in common indicate no significant differences ($p > 0.05$).

treatments (Fig. 4b). Following the third measurement, conducted in 2021, the overall probability of transition to higher canopy classes was significantly higher in the TDC2 (33 %) compared to the TDC (8 %) treatment. No significant differences were observed compared to the TDCS (16 %) treatment and the control (14 %).

The probability of transition of oak recruits into higher canopy classes is dependent on initial tree characteristics and stand structure. The results indicate that oak recruits with larger DBH ($p < 0.001$) have a higher chance of advancing into higher canopy classes (Table 4). Trees already in intermediate canopy class have lower probability of transitioning into higher canopy classes compared to suppressed trees ($p < 0.001$). A higher coefficient of variation of height ($p = 0.008$) within a stand promote the probability of transition of oak recruits into higher canopy classes.

Table 4
Summary of GLMM showing the factors affecting the probability of transition of oak recruits into higher canopy classes. CVh: coefficient of variation of height. All explanatory variables were natural log-transformed. Crown class variables are categorial variables with two categories: suppressed and intermediate.

Predictors	Estimate	Standard error	p-value
Intercept	-17.53	4.35	< 0.001
Initial DBH	0.47	0.08	< 0.001
Initial height	0.18	0.11	0.09
Initial crown class (Intermediate)	-3.26	0.49	< 0.001
Broadleaved BA	-0.57	0.35	0.10
CVh	2.85	1.07	0.008
Variance			
Treatment:plot	0.63		
AIC	383.7		

4. Discussion

4.1. *Stand structural and individual tree characteristics affecting the diameter and height growth of oak recruits*

The diameter and height growth of oak recruits was influenced by initial tree DBH, with larger recruits exhibiting a higher diameter and height growth. A higher basal area of larger trees (BAL) than the individual oak recruits reduced diameter growth. This suggests that an increased number of trees larger than the individual oak recruits in the area reduces the diameter growth of those recruits. BAL accounts simultaneously for a target tree's social ranking and the density of the stand (Wykoff, 1990; Schröder, 1999), and similar negative effects on the diameter growth of oak were observed in previous studies (Rohner et al., 2017; Schelhaas et al., 2018). In our study, Norway spruce and Scots pine constitute over 70 % of the stem density, and their combined stem density and basal area of broadleaved species (birch, European beech and oak) further negatively affected the diameter growth of oak recruits. This finding aligns with earlier studies that have reported negative effects of density on oak growth (Adame et al., 2008; Noguchi and Yoshida, 2009; Rohner et al., 2017; Pohl et al., 2025).

Although height growth is generally expected to decline with increasing DBH (Johnson et al., 2019), a positive effect of DBH on height growth was observed. This is likely because our study focused on relatively small recruits. In line with previous studies (Sumida et al., 1997; Trouve et al., 2015), the results indicate that height growth decreases as tree height increases. The stand structural variables of broadleaved density showed negative effects on the height growth. In dense stands with more broadleaved trees, light becomes a major limiting factor negatively affecting the growth of oak recruits. Managing stand density is thus very important to favour the oak recruit's growth. Compared to several other tree species, oaks need more light for sustainable height growth (Modrow et al., 2019; Petersson et al., 2020). For example, while beech needs about 10 % of above-canopy light, oak requires twice as much to reach an optimum growth (Ligot et al., 2013).

Managing stand density through target diameter cutting also alters tree size variation. The negative effect of CVh on height growth of oak recruits suggests that structurally heterogeneous stands, where taller individuals strongly dominate and height variation is large, intensify asymmetric competition and suppress height growth smaller recruits. Our results contrast with those of a previous study (e.g., Stimm et al., 2021), who reported positive effects of stand density and vertical stand structure on height growth of oak. However, their study focused on relatively large oaks with a mean DBH ranging from 35.6 to 47.8 cm and mean height ranging from 22.5 to 27.9 m in different forest types with different species mixture. The positive effects of CVd on height growth indicate that stand structure complexity may facilitate height growth of oak recruits. Higher variation in tree DBH creates a more irregular forest structure with spatially heterogeneous light conditions that could promote height growth of light-demanding oak recruits. In addition, we observed a negative relationship between height growth and the number of trees removed during target diameter cutting. High-intensity selective cutting may not benefit the height growth of oak recruits, even after competition is reduced and light availability is improved. A previous study by Vallet and Perot (2016) also reported a lower growth rate of oak as light availability increased.

4.2. *The effects of target diameter cutting on diameter and height growth of oak recruits*

Our results indicate that target diameter cutting promoted the diameter growth of oak recruits. Target diameter cutting reduced competition for resources such as soil water, nutrients, growing space, and light availability by decreasing the stand density and basal area (Yoshida and Kamitani, 1998; Götmark, 2009; Gorrod et al., 2024), which in turn positively affected the diameter growth of oaks. Although a slight decrease in the annual growth rate was observed across all treatments over time, the positive effects of selective cutting on oak diameter growth persisted for at least 16 years post-selective cutting. This long-term response is consistent with a 25-year post-thinning study carried out in planted oak (*Q. robur*) forests in Southern Sweden (Barbeito et al., 2024). They reported that the initial benefits of thinning on oak growth tend to diminish over time. Similar long-term positive effects of thinning but diminishing effects on the growth of different oak species have also been reported in previous studies in coppice stands (Cabon et al., 2018; Đodan et al., 2024).

Target diameter cuttings did not promote the height growth of oak recruits. In contrast to diameter growth, our results indicate a significant negative effect of target dimeter cutting on the height growth of oak recruits. Therefore, it seems that the different forms of target diameter cutting promoted the diameter growth of oak recruits rather than height growth. Under partial shade, oaks are less responsive in height growth (Johnson et al., 2019). These results are further supported by several other studies (Miller, 2000; Đodan et al., 2024). For example, Miller (2000) found that crop tree release treatment promoted the diameter growth, but the total height growth was reduced by heavy release. However, released crop trees tend to maintain their initial crown class better than unreleased trees (Miller, 2000). Furthermore, a study in a thinning experiment in oak (*Q. petraea*)-hornbeam coppice stands (Fedorová et al., 2016) revealed that thinning promotes primarily diameter growth rather than height increment. Further, Cañellas et al., (2004) reported that in a *Q. pyrenaica* (Willd.) coppice stand subjected to thinning treatments of varying intensities, there were no significant differences in height increment among the treatments. In addition, regardless of light conditions, the growth of other broadleaved species, such as European beech, may grow faster than oaks (Ligot et al., 2013).

4.3. *The effect of target diameter cutting on the transition into higher canopy classes*

Without release from competition, small oaks, especially sapling and pole-size trees, in the lower canopy layers are more likely to die (Miller, 2000; Ward, 2009). Therefore, the effect of target diameter cutting on canopy class transition may be more important to examine than its effect on height growth. Oaks that are suppressed beneath the canopy at a younger age are likely to remain suppressed as they grow older; therefore, silvicultural interventions are necessary to prevent oak recruits from eventually becoming permanently overtopped and unable to recover (Zenner et al., 2012). After silvicultural interventions, such as target diameter cutting, remaining trees experience not only reduced competition from the surrounding trees but also a potential shift in social position since trees are removed from the stand. We found that the transitions of a recruit's social positions into higher canopy classes were higher in the TDC2 treatment 16 years following selective cutting treatments. The TDC2 treatment was designed to favour the growth of broadleaved species by removing dominant species, such as Norway spruce, by lowering the target diameter thresholds for cutting compared to the other two treatments, TDC and TDCS. By cutting more Norway spruce trees, the resulting lower stem density and stand basal area are likely to promote the development of suppressed recruits into upper canopy positions. A study on the effect of release cutting on the development of red oak (*Q. rubra* L.) in North America also reported that only a few intermediate (<10 %) and suppressed (<1 %) oaks were able to recruit into the higher canopy layers without thinning (Ward, 2009). Since the recruits in our study is relatively small, active management is essential to promote the growth and to ensure that successfully established oak recruits develops to larger individuals that can advance into the upper canopy layers, as competitive pressure can undermine the recruitment process into the overstory (Zenner et al., 2012; Dey, 2014).

While target diameter cutting reduces stand density and alters tree size distribution by removing trees of specified sizes, it may not fundamentally alter the underlying mechanisms of how trees compete and transition into higher social positions. We observed that larger recruits, in terms of DBH and height, have a higher chance of transitioning into higher canopy classes when canopy openings are created by silvicultural interventions. Trees that are already in the intermediate positions are less likely to advance into higher canopy classes compared to suppressed trees. Suppressed trees, which are half or less of the total height as defined in this study, are more likely to advance to intermediate canopy position when canopy openings occur due to selective cutting. It is likely that the higher probability of the advancement of suppressed trees into the intermediate canopy class was due to shift in social position following selective cutting of larger competing trees. Intermediate trees, on the other hand, are less limited by light availability than suppressed trees, although they still experience lateral competition for light. Selective cutting could benefit crown development (Attocchi, 2015) of recruits in intermediate and codominant canopy classes. Our results are consistent with those of (Willis et al., 2018), who reported that the recruitment of large trees did not accelerate 14 years after thinning. In our study, following 16 years post-target diameter harvesting, the pattern of transitions into higher canopy classes is likely increasing gradually. Studies (O'Hara, 1986; Zenner et al., 2012) have reported the latent dominance capacity of oaks, in which they can persist in suppressed positions for decades and gradually transition into higher canopy positions. However, thinning or selective cutting are necessary to ensure oak survival and growth as competitive dynamics in the overstory positions during the recruitment process may increase oak mortality (Ward and Stephens, 1994; Dey, 2014). Greater tree height variation may enhance upward transitions in canopy positions. This is also primarily because selective removal of larger and taller individuals alters canopy stratification, allowing previously suppressed individuals to gain space even if their height growth remains limited.

The success of oak forest management depends on sustaining oak recruitment. This study provides an important piece of information for the management of oak forests. Selective cutting can help ensure the sustainable management of oak forests. In our experiments, target diameter cutting intensity reached an average of up to nearly 40 % across all treatments. Our results highlighted that selective cutting of larger individuals promote diameter growth but reduce height growth of oak recruits. Repeated but lower intensity selective cutting could maintain enhanced height growth while still releasing oak recruits for higher diameter growth. To maintain a dynamic light environment, selective cutting may need to retain scattered large trees, as CVd positively affected height growth. Therefore, selective cutting should focus on competitors directly above young oaks to promote height growth. In addition, retaining mixed size classes (higher CVd) while keeping overall stand density moderate produces beneficial light environments (Pohl et al., 2025) that could promote oak recruitments. However, it should also be noted that target diameter cutting, which remove the most vigorous trees, can compromise future forest health and long-term sustainability (Curtze et al., 2022). Therefore, selective cutting should be implemented to retain mixed size classes, preserving trees with high-quality phenotypes, creating canopy openings to promote light availability and reduced competition. This approach could promote oak recruitment while maintaining stand productivity and genetic diversity.

5. Conclusion

This study examined the effects of different forms of target diameter cutting on the growth and advancement of oak recruits into higher social positions over a period of 16 years. Our results indicate that all three different forms of target diameter cutting primarily promoted the diameter growth of recruits, and that this growth persisted 16 years following cutting. Height growth was not likely to be promoted by selective cutting, as oak recruits invested more in diameter growth. Target diameter cutting was likely to promote the transition of oak into the higher canopy positions, and this could be due to a combination of removal of other trees, even if height growth of the oak recruits remains limited. Basal area of larger trees negatively affected diameter growth of oak recruits. The recruitment process into higher canopy positions is a long-term process and a period of 16 years, as in this study, may not be sufficient to monitor this process. Therefore, longer-term studies are needed with repeated selective cutting. The findings highlight the critical role of silvicultural practices in supporting oak growth and recruitment process. This study suggests that target diameter cutting could be an alternative forest management approach to facilitate the growth and recruitment of oak and to ensure the sustainability of oak-dominated forests.

CRediT authorship contribution statement

Nora Sophie Pohl: Writing – review & editing, Writing – original draft, Methodology, Conceptualization. **Kyaw Thu Moe:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Conceptualization. **Magnus Löf:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Jorge Aldea:** Writing – review & editing, Funding acquisition.

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.

Acknowledgements

This work was supported by Carl Trygger Foundation (Project Number CTS 23: 2464), the Foundation Oscar and Lili Lamms Memory (grant 20201123); Swedish Research Council Formas (grant 2022–02070); Erik and Ebba Larssons and Thure Rignells Foundation (19 February 2022 and 12 April 2025); the grant RYC2021–033031-I funded by MCIN/AEI/10.13039/501100011033 and by the European Union “NextGenerationEU/PRTR”. We thank Ulf Johansson, Martin Goude and the staff at the experimental forest in Tönnersjöheden for their work in this experiment.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2026.123519.

References

Adame, P., Hynynen, J., Cañellas, I., del Río, M., 2008. Individual-tree diameter growth model for rebollo oak (*Quercus pyrenaica* Willd.) coppices. For. Ecol. Manag. 255, 1011–1022.

Attocchi, G., 2015. Silviculture of Oak for High-Quality Wood Production. Effects of thinning on crown size, volume growth and stem quality in even-aged stands of pedunculate oak (*Quercus robur* L.) in Northern Europe. Doctoral Thesis. Faculty of Forest Sciences, Southern Swedish Forest Research Centre. Swedish University of Agricultural Sciences, Alnarp.

Barbeito, I., Aldea, J., Johansson, U., Ekö, P.M., 2024. Thinning intensity and frequency enhance *Quercus robur* L. growth responses to drought in Southern Sweden. Scand. J. For. Res. 39, 411–420.

Bolte, A., Ammer, C., Löf, M., Madsen, P., Nabuurs, G.-J., Schall, P., Spathelf, P., Rock, J., 2009. Adaptive forest management in central Europe: climate change impacts, strategies and integrative concept. Scand. J. For. Res. 24, 473–482.

Březina, I., Dobrovolný, L., 2011. Natural regeneration of sessile oak under different light conditions. J. For. Sci. 57, 359–368.

Brooks, M.E., Kristensen, K., Benthem, K.Jv, Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Mächler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R. J. 9/12.

Brunner, A., Valkonen, S., Goude, M., Holt Hanssen, K., Erefur, C., 2025. Definitions and terminology: what is continuous cover forestry in fennoscandia? In: Rautio, P., Routa, J., Huuskonen, S., Holmström, E., Cedergren, J., Kuehne, C. (Eds.), Continuous Cover Forestry in Boreal Nordic Countries. Springer Nature Switzerland AG, pp. 11–43.

Cabon, A., Mouillot, F., Lempereur, M., Ourcival, J.-M., Simioni, G., Limousin, J.-M., 2018. Thinning increases tree growth by delaying drought-induced growth cessation in a Mediterranean evergreen oak coppice. For. Ecol. Manag. 409, 333–342.

Camp, A.E., Oliver, C.D., 2004. Silviculture, Forest Dynamics. In: Burley, J. (Ed.), Encyclopedia of Forest Sciences. Elsevier, Oxford, pp. 1053–1062.

Cañellas, I., Del Río, M., Roig, S., Montero, G., 2004. Growth response to thinning in *Quercus pyrenaica* Willd. coppice stands in Spanish central mountain. Ann. For. Sci. 61, 243–250.

Curtze, A.C., Muth, A.B., Larkin, J.L., Leites, L.P., 2022. Seeing past the green: structure, composition, and biomass differences in high graded and silviculture-managed forests of similar stand density. For. Ecol. Manag. 526, 120598.

Dey, D.C., 2014. Sustaining oak forests in eastern North America: regeneration and recruitment, the pillars of sustainability. For. Sci. 60, 926–942.

Đodan, M., Nicolescu, V.N., Perić, S., Jazbec, A., Bartlett, D., 2024. Long-term effects of thinning in sub-mountainous Thermophilic Sessile Oak (*Quercus petraea* Mill.) and

European Beech (*Fagus sylvatica* L.) coppices in the Croatian Dinarides. Sustainability 16, 9340.

Drössler, L., Fahlvik, N., Ekö, M., 2012. Stand structure and future development of a managed multi-layered forest in southern Sweden: Erikssköp-A case study. Report No. 46. Swedish University of Agricultural Sciences, Southern Swedish Forest Research Centre, Alnarp.

Drössler, L., Fahlvik, N., Wysocka, N.K., Hjelm, K., Kuehne, C., 2017. Natural regeneration in a multi-layered *Pinus sylvestris-Picea abies* forest after target diameter harvest and soil scarification. Forests 8, 35.

Fedorová, B., Kadavý, J., Adamec, Z., Kneifl, M., Knott, R., 2016. Response of diameter and height increment to thinning in oak-hornbeam coppice in the southeastern part of the Czech Republic. J. For. Sci. 62, 229–235.

Forest Europe, 2020. State of Europe's Forests 2020.

Gorrod, E., White, L., Bedward, M., Hope, B., Chu, N., McAllister, D., 2024. Restoration thinning accelerates small tree growth but may slow large tree growth in a multi-age flood-dependent forest. J. Appl. Ecol. 61, 1560–1572.

Götmark, F., 2007. Careful partial harvesting in conservation stands and retention of large oaks favour oak regeneration. Biol. Conserv. 140, 349–358.

Götmark, F., 2009. Experiments for alternative management of forest reserves: effects of partial cutting on stem growth and mortality of large oaks. Can. J. For. Res. 39, 1322–1330.

Götmark, F., Kiffer, C., 2014. Regeneration of oaks (*Quercus robur/Q. petraea*) and three other tree species during long-term succession after catastrophic disturbance (windthrow). Plant Ecol. 215, 1067–1080.

Hartig, F., 2025. Residual diagnostics for hierarchical (multi-level/mixed) regression models. R. Package Version 0 (4), 7.

Holmström, E., Goude, M., Nilsson, O., Nordin, A., Lundmark, T., Nilsson, U., 2018. Productivity of Scots pine and Norway spruce in central Sweden and competitive release in mixtures of the two species. For. Ecol. Manag. 429, 287–293.

Johnson, P.S., Shifley, S.R., Rogers, R., 2019. The ecology and silviculture of oaks, Third Edition. CABI International.

Kanjevac, B., Krstić, M., Babić, V., Govedar, Z., 2021. Regeneration dynamics and development of seedlings in Sessile oak forests in relation to the light availability and competing vegetation. Forests 12, 384.

Kohler, M., Pyttel, P., Kuehne, C., Modrow, T., Bauhus, J., 2020. On the knowns and unknowns of natural regeneration of silviculturally managed sessile oak (*Quercus petraea* (Matt.) Liebl.) forests-a literature review. Ann. For. Sci. 77 (101), 1–119.

Kunz, J., Löffler, G., Bauhus, J., 2018. Minor European broadleaved tree species are more drought-tolerant than *Fagus sylvatica* but not more tolerant than *Quercus petraea*. For. Ecol. Manag. 414, 15–27.

Lenth, R., 2025. emmeans: estimated marginal means, aka Least-Squares Means. R. Package Version 1 (11), 1.

Ligot, G., Balandier, P., Fayolle, A., Lejeune, P., Claessens, H., 2013. Height competition between *Quercus petraea* and *Fagus sylvatica* natural regeneration in mixed and uneven-aged stands. For. Ecol. Manag. 304, 391–398.

Lindbladh, M., Bradshaw, R., Holmqvist, B.H., 2000. Pattern and process in south Swedish forests during the last 3000 years, sensed at stand and regional scales. J. Ecol. 88, 113–128.

Lindbladh, M., Foster, D.R., 2010. Dynamics of long-lived foundation species: the history of *Quercus* in southern Scandinavia. J. Ecol. 98, 1330–1345.

Löf, M., 2000. Establishment and growth in seedlings of *Fagus sylvatica* and *Quercus robur*: influence of interference from herbaceous vegetation. Can. J. For. Res. 30, 855–864.

Löf, M., Barrere, J., Engman, M., Petersson, L.K., Villalobos, A., 2021. The influence of fencing on seedling establishment during reforestation of oak stands: a comparison of artificial and natural regeneration techniques including costs. Eur. J. For. Res. 140, 807–817.

Löf, M., Brunet, J., Filyushkina, A., Lindbladh, M., Skovsgaard, J.P., Felton, A., 2016. Management of oak forests: striking a balance between timber production, biodiversity and cultural services. Int. J. Biodivers. Sci. Ecosyst. Serv. Manag. 12, 59–73.

Mason, W.L., Diaci, J., Carvalho, J., Valkonen, S., 2022. Continuous cover forestry in Europe: usage and the knowledge gaps and challenges to wider adoption. Forestry 95, 1–12.

Mette, T., Dolos, K., Meinardus, C., Bräuning, A., Reineking, B., Blaschke, M., Pretzsch, H., Beierkuhnlein, C., Gohlke, A., Wellstein, C., 2013. Climatic turning point for beech and oak under climate change in Central Europe. Ecosphere 4 (12), 145.

Miller, G.W., 2000. Effect of crown growing space on the development of young hardwood crop trees. North. J. Appl. For. 17 (1), 28–35.

Modrow, T., Kuehne, C., Saha, S., Bauhus, J., Pyttel, P.L., 2019. Photosynthetic performance, height growth, and dominance of naturally regenerated sessile oak (*Quercus petraea* [Mattuschka] Liebl.) seedlings in small-scale canopy openings of varying sizes. Eur. J. For. Res. 139, 41–52.

Mölder, A., Meyer, P., Nagel, R.V., 2019a. Integrative management to sustain biodiversity and ecological continuity in Central European temperate oak (*Quercus robur*, *Q. petraea*) forests- An overview. For. Ecol. Manag. 437, 324–339.

Mölder, A., Sennhenn-Reulen, H., Fischer, C., Rumpf, H., Schönfelder, E., Stockmann, J., Nagel, R.V., 2019b. Success factors for high-quality oak forest (*Quercus robur*, *Q. petraea*) regeneration. For. Ecosyst. 6 (49), 1–17.

Näslund, M., 1936. Skogsförsöksanstaltens gallringsförsök i tallskog (Forest research institute's thinning experiments in Scots pine forests). Meddelanden från Statens (1936) skogsförsöksanstalt.

Nicolescu, V.-N., Vor, T., Brus, R., Đodan, M., Perić, S., Podrázský, V., Andrašev, S., Tsavkov, E., Ayan, S., Yücedağ, C., Trajkov, P., Kolevska, D.D., Buzatu-Goanţă, C., Pástor, M., Mačejovský, V., Modranský, J., Klisz, M., Gil, W., Lavnyy, V., Madsen, P., La Porta, N., Bartlett, D., 2025. Management of sessile oak (*Quercus petraea* (Matt.) Liebl.), a major forest species in Europe. J. For. Res. 36, 78.

Noguchi, M., Yoshida, T., 2009. Individual-scale responses of five dominant tree species to single-tree selection harvesting in a mixed forest in Hokkaido, northern Japan. J. For. Res. 14, 311–320.

Ogana, F.N., Holmström, E., Sharma, R.P., Langvall, O., Nilsson, U., 2023. Optimizing height measurement for the long-term forest experiments in Sweden. For. Ecol. Manag. 532, 120843.

O'Hara, K.L., 1986. Developmental patterns of residual Oaks and Oak and Yellow-Poplar regeneration after release in upland hardwood stands. South. J. Appl. For. 10, 244–248.

Perkins, D., Uhl, E., Biber, P., Du Toit, B., Carraro, V., Rötzer, T., Pretzsch, H., 2018. Impact of climate trends and drought events on the growth of oaks (*Quercus robur* L. and *Quercus petraea* (Matt.) Liebl.) within and beyond their natural range. Forests 9, 108.

Petersson, L.K., Dey, D.C., Felton, A.M., Gardiner, E.S., Lof, M., 2020. Influence of canopy openness, ungulate exclosure, and low-intensity fire for improved oak regeneration in temperate Europe. Ecol. Evol. 10, 2626–2637.

Petersson, L.K., Milberg, P., Bergstedt, J., Dahlgren, J., Felton, A.M., Götmark, F., Salk, C., Löf, M., 2019. Changing land use and increasing abundance of deer cause natural regeneration failure of oaks: six decades of landscape-scale evidence. For. Ecol. Manag. 444, 299–307.

Peura, M., Burgas, D., Eyvindson, K., Repo, A., Mönkkönen, M., 2018. Continuous cover forestry is a cost-efficient tool to increase multifunctionality of boreal production forests in Fennoscandia. Biol. Conserv. 217, 104–112.

Plaugher, P., Schuler, J., 2025. The 10-year response of natural northern red oak reproduction to strip clearcutting an Appalachian hardwood stand. For. Ecol. Manag. 586 (122701), 122701.

Pohl, N.S., Hedwall, P.-O., Aldea, J., Felton, A.M., Gardiner, E.S., Muraro, L., Nordén, B., Löf, M., 2025. Effects of stand structural attributes on oak recruitment in mixed temperate forests. For. Ecol. Manag. 586, 122721.

Pommerening, A., Murphy, S.T., 2004. A review of the history, definitions and methods of continuous cover forestry with special attention to afforestation and restocking. Forestry 77, 27–44.

Price, M., Price, C., 2006. Creaming the best, or creatively transforming? Might felling the biggest trees first be a win–win strategy? For. Ecol. Manag. 224, 297–303.

Puettmann, K.J., Wilson, S.M., Baker, S.C., Donoso, P.J., Drössler, L., Amente, G., Harvey, B.D., Knoke, T., Lu, Y., Nocentini, S., Putz, F.E., Yoshida, T., Bauhus, J., 2015. Silvicultural alternatives to conventional even-aged forest management - what limits global adoption? For. Ecosyst. 2, 8.

R Core Team (2024) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Roessiger, J., Ficko, A., Clasen, C., Griess, V.C., Knoke, T., 2016. Variability in growth of trees in uneven-aged stands displays the need for optimizing diversified harvest diameters. Eur. J. For. Res. 135, 283–295.

Rohner, B., Waldner, P., Lischke, H., Ferretti, M., Thürig, E., 2017. Predicting individual-tree growth of central European tree species as a function of site, stand, management, nutrient, and climate effects. Eur. J. For. Res. 137, 29–44.

Schelhaas, M.-J., Hengeveld, G.M., Heidema, N., Thürig, E., Rohner, B., Vacchiano, G., Vayreda, J., Redmond, J., Socha, J., Fridman, J., Tomter, S., Polley, H., Barreiro, S., Nabuurs, G.-J., 2018. Species-specific, pan-European diameter increment models based on data of 2.3 million trees. For. Ecosyst. 5, 21.

Schröder, J.G., Klaus, von, 1999. Testing a new competition index for Maritime pine in northwestern Spain. Can. J. For. Res. 29, 280–283.

Schroeder, H., Nosenko, T., Ghirardo, A., Fladung, M., Schnitzler, J.P., Kersten, B., 2021. Oaks as beacons of hope for threatened mixed forests in Central Europe. Front. For. Glob. Change 4, 670797.

Skogsdata, 2024. Forest statistics 2024. Official Statistics of Sweden. Institutionen för skoglig resurshushållning. Swedish University of Agricultural Sciences, Umeå.

Sterba, H., Zingg, A., 2001. Target diameter harvesting - a strategy to convert even-aged forests. For. Ecol. Manag. 151, 95–105.

Stimm, K., Heym, M., Uhl, E., Tretter, S., Pretzsch, H., 2021. Height growth-related competitiveness of oak (*Quercus petraea* (Matt.) Liebl. and *Quercus robur* L.) under climate change in Central Europe. Is silvicultural assistance still required in mixed-species stands? For. Ecol. Manag. 482.

Stimm, K., Uhl, E., Pretzsch, H., 2022. Chances and limitations of mixed oak regeneration under continuous canopy cover— evidence from long-term observations. Forests 13, 2052.

Sumida, A., Ito, H., Isagi, Y., 1997. Trade-off between height growth and stem diameter growth for an evergreen Oak, *Quercus glauca*, in a mixed hardwood forest. Funct. Ecol. 11, 300–309.

Trouve, R., Bontemps, J.D., Seynave, I., Collet, C., Lebourgeois, F., 2015. Stand density, tree social status and water stress influence allocation in height and diameter growth of *Quercus petraea* (Liebl.). Tree Physiol. 35, 1035–1046.

Vallet, P., Perot, T., 2016. Tree diversity effect on dominant height in temperate forest. For. Ecol. Manag. 381, 106–114.

Ward, J.S., 2009. Intensity of precommercial crop tree release increases diameter growth and survival of upland oaks. Can. J. For. Res. 39, 118–130.

Ward, J.S., Stephens, G.R., 1994. Crown class transition rates of maturing Northern Red Oak (*Quercus rubra* L.). For. Sci. 40, 221–237.

Willis, J.L., Roberts, S.D., Harrington, C.A., 2018. Variable density thinning promotes variable structural responses 14 years after treatment in the Pacific Northwest. For. Ecol. Manag. 410, 114–125.

Wykoff, W.R., 1990. A basal area increment model for individual conifers in the Northern Rocky Mountains. For. Sci. 36, 1077–1104.

Yoshida, T., Kamitani, T., 1998. Effects of crown release on basal area growth rates of some broad-leaved tree species with different shade-tolerance. J. For. Res. 3, 181–184.

Zell, J., Hanewinkel, M., Seeling, U., 2004. Financial optimisation of target diameter harvest of European beech (*Fagus sylvatica*) considering the risk of decrease of timber quality due to red heartwood. For. Policy Econ. 6, 579–593.

Zenner, E.K., Heggenstaller, D.J., Brose, P.H., Peck, J.E., Steiner, K.C., 2012. Reconstructing the competitive dynamics of mixed-oak neighborhoods. Can. J. For. Res. 42, 1714–1723.

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DOCTORAL THESIS NO. 2026:9

In this thesis, I provide new findings regarding the growth of oak recruits (dbh 5–20 cm) under continuous cover forestry by combining long-term observational data with field experiments. Oak recruitment was consistently constrained by high stand density, basal area, and shade-tolerant species. Selective cutting enhanced diameter growth over longer periods and buffered lichen diversity loss but did not increase short-term recruit density. Long-term data revealed a persistent growth decline, highlighting recruitment as a critical bottleneck requiring targeted management.

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ISSN 1652-6880
ISBN (print version) 978-91-8124-206-5
ISBN (electronic version) 978-91-8124-226-3